



Two new species of *Hemiphyllodactylus* (Reptilia: Gekkonidae) from Laos

SAMUEL J. ELIADES^{1,2,4}, SOMPHOUTHONE PHIMMACHAK³, NIANE SIVONGXAY³,
CAMERON D. SILER² & BRYAN L. STUART¹

¹North Carolina Museum of Natural Sciences, 11 W. Jones St., Raleigh NC 27601, USA.

E-mails: sjeliades@ou.edu, bryan.stuart@naturalsciences.org

²Current Address: Sam Noble Oklahoma Museum of Natural History and Department of Biology, University of Oklahoma, 2401 Chautauqua Ave., Norman OK 73072-7029, USA. E-mail: camsiler@ou.edu

³National University of Laos, Faculty of Natural Sciences, Department of Biology, P.O. Box 2273, Dong Dok Campus, Vientiane, Laos. E-mails: somphouthone26@hotmail.com, sivongxain@gmail.com

⁴Corresponding author

Abstract

Two new species of the gekkonid lizard genus *Hemiphyllodactylus* are described based on specimens collected from Champasak Province in southern Laos and Houaphanh Province in northern Laos. Phylogenetic analyses recover *H. indosobrinus* **sp. nov.** from Champasak Province as the sister lineage to the Thai endemic *H. flaviventris*. *Hemiphyllodactylus indosobrinus* **sp. nov.** can be diagnosed by having 15 supralabial scales, eight chin scales, 4-5-5-4 subdigital lamellae on Fingers II–V, 4-5-5-5 subdigital lamellae on Toes II–V, and 18 continuous precloacofemoral pores. Phylogenetic analyses recover *H. serpispecus* **sp. nov.** from Houaphanh Province to be most closely related to the Vietnamese endemic *H. banaensis*. *Hemiphyllodactylus serpispecus* **sp. nov.** differs from congeners by having seven chin scales; 3-4-4-4 subdigital lamellae on Fingers II–V; 3-4-4-5 subdigital lamellae on Toes II–V; and 11 continuous precloacofemoral pores. The recognition of these two new species doubles the number of *Hemiphyllodactylus* known from Laos.

Key words: Champasak Province, endemism, Houaphanh Province, Indochina, Slender Gecko

Introduction

The genus *Hemiphyllodactylus* Bleeker, 1860 consists of 27 gekkonid species found across South and Southeast Asia and the Indo-Pacific (Zug 2010; Grismer *et al.* 2013, Cobos *et al.* 2016; Yan *et al.* 2016; Sukprasert *et al.* 2018). All species in the genus are small, arboreal, and nocturnal, with inconspicuous body coloration, and are usually restricted to high elevation or insular habitats (Grismer *et al.* 2013). Secretive behaviors and cryptic body coloration of *Hemiphyllodactylus* have contributed to infrequent observations in the field and, consequently, many of the species remain poorly represented in natural history collections. Interestingly, recent taxonomic studies have begun to reveal significant new diversity in the genus. Prior to 2010, only seven species of *Hemiphyllodactylus* were recognized (Zug 2010); however, during the past eight years, 20 additional species have been described from Southeast Asia (Grismer *et al.* 2013, 2014a,b, 2015, 2017; Nguyen *et al.* 2013, 2014; Guo *et al.* 2015; Cobos *et al.* 2016; Yan *et al.* 2016; Sukprasert *et al.* 2018).

Recent systematic studies have focused primarily on species from mainland Southeast Asia, particularly lineages occurring in Malaysia, Myanmar, Thailand, and Vietnam (e.g. Grismer *et al.* 2013, 2014b, 2015, 2017; Nguyen *et al.* 2013; Cobos *et al.* 2016; Sukprasert *et al.* 2018). However, within this region, little is known about the diversity of *Hemiphyllodactylus* in Laos. Only two described species have been reported from the country: *H. kiziriani* Nguyen, Botov, Le, Nophaseud, Zug, Bonkowski, & Ziegler, 2014 and *H. yunnanensis* (Boulenger, 1903). *Hemiphyllodactylus kiziriani* is known from the karst forests of Luang Prabang Province in northern Laos (Nguyen *et al.* 2014), whereas *H. yunnanensis* is recognized currently as a widespread species found in China, Myanmar, northern Thailand, and northern Vietnam, with its occurrence in Laos based on two historical museum specimens from Phongsaly Province in the northern part of the country (Zug 2010).

During field surveys of amphibians and reptiles in Laos during September 1999 and September 2015, we collected two *Hemiphyllodactylus* specimens. In September 1999, an adult male was found at the top of the Bolaven Plateau in Champasak Province, southern Laos (FMNH 258695; Fig. 1A). Sixteen years later, during an expedition in 2015, another adult male was collected from Tham Ngou Leium cave in Houaphanh Province, northern Laos (NUOL 00476; Fig. 1A). Neither specimen could be identified to any named species based on morphology and were assigned tentatively to the species *H. yunnanensis* since the dates of collection. Over the past five years, phylogenetic analyses of mitochondrial DNA of the Champasak specimen revealed that the individual is divergent genetically from all congeners (Grismer *et al.* 2013, 2014a,b, 2015, 2017; Ngo *et al.* 2013, 2014; Nguyen *et al.* 2014; Yan *et al.* 2016); however, no phylogenetic analyses have included the Houaphanh specimen. Herein, we show that the Champasak and Houaphanh specimens are unique evolutionary lineages, each possessing a suite of diagnostic, morphological features that differentiate them from each other and all other members of the genus. Additionally, phylogenetic analyses recover both lineages as divergent from each other and all congeners, adding support to the hypothesis that these lineages represent new and distinct species. Considering both morphological and genetic data, we describe each lineage in Laos as a new species of *Hemiphyllodactylus*.

Materials and methods

Field surveys and specimen preparation. Amphibian and reptile diversity surveys were conducted in Champasak Province, southern Laos and Houaphanh Province, northern Laos in September 1999 and September 2015, respectively. Specimens of *Hemiphyllodactylus* were collected by hand in the field and fixed in 10% buffered formalin after preserving liver in 95% ethanol or RNAlater (Invitrogen). Specimens were later transferred to 70% ethanol and deposited at the Field Museum of Natural History (FMNH) and the National University of Laos, Faculty of Natural Sciences, Department of Biology (NUOL). Both specimens were borrowed and examined at the North Carolina Museum of Natural Sciences (NCSM) for this study.

Morphological data. Mensural and meristic characteristics were taken from preserved specimens following Zug *et al.* (2003), Zug (2010), and Grismer *et al.* (2013). Morphological data were collected by SJE with Mitutoyo digital calipers under a Meiji dissecting microscope to the nearest 0.1 mm. All measurements and scale counts were taken on the left side of the body unless otherwise noted. Mensural characteristics evaluated were: snout–vent length (SVL), taken from the tip of the snout to the vent; trunk length (TrunkL), taken from the posterior margin of the fore-limb at its insertion point to the anterior margin of the hind limb at its insertion point; forearm length (ForeaL), taken from the apex of the elbow to the base of the palmar surface; crus length (CrusL), taken from the apex of the knee to the base of the heel on the foot; tail length (TailL), taken from the anterior end of the vent to the tip of the tail; tail width (TailW), taken at the widest part of the tail; head length (HeadL), taken from the occiput to the snout tip; head width (HeadW), taken at the widest part of the head; head depth (HeadD), taken from the top of the ventral surface to the bottom of the dorsal surface on the head, posterior to the eyes; ear diameter (EarL), taken at the widest diameter of the ear opening; orbit diameter (OrbD), taken at the maximal diameter of the eye opening; nares–eye distance (NarEye), measured from the posterior end of the nasal opening to the anterior margin of the eye opening; snout–eye distance (SnEye), measured from the tip of the snout to the anterior margin of the eye opening; eye–ear distance (EyeEar), measured from the anterior margin of the ear opening to the posterior margin of the eye opening; and snout width (SnW), internarial distance measured between the medial boundaries of the nasal openings.

Meristic characteristics evaluated included: supralabial scale count (Suplab), number of enlarged scales bordering the mouth on the upper jaw from the rostral to a point in line with the posterior margin of the orbit; infralabial scale count (Inflab), number of enlarged scales bordering the mouth on the lower jaw from the mental to a point in line with the posterior margin of the orbit; chin scale count (Chin), number of scales contacting infralabials and mental on the ventral surface from the juncture of the second and third infralabials on the left side of the head to the juncture of the second and third infralabials on the right side of the head; circumnasal scale count (CircNa), number of scales abutting external naris, exclusive of the rostral and first supralabial; internasal scale count (Internas), number of scales in a linear row between supranasals; tubercle row count (Tub), number of dorsal tubercle rows across the midbody; dorsal scale count (Dorsal), number of longitudinal rows of dorsal scales at the midbody contained within one orbital diameter; ventral scale count (Ventral), number of longitudinal rows of

ventral scales at the midbody contained within one orbital diameter; preloacal and femoral pore series count (Pore), number of preloacal and femoral pores (referred to as preloacofemoral pores if found in a continuous series); cloacal spur count (CloacS), number of scales (larger than preloacal scales with pores) in contact on the side of the tail base; subdigital lamellae count on Finger I (IFingLm), number of undivided, rectangular lamellae on the first digit of the hand; subdigital lamellae count on Toe I (IToeLm), number of undivided, rectangular lamellae on the first digit of the foot; subdigital lamellae formula for Fingers II–V (II–VFingLm), numbers of enlarged, paired, U-shaped lamellae on Fingers II–V (distal most lamella not enlarged nor paired and is excluded from counts); total lamellae on hand (TotFingLm), total number of enlarged, paired, U-shaped lamellae on Fingers II–V; subdigital lamellae formula for Toes II–V (II–VToeLm), numbers of enlarged, paired, U-shaped lamellae on Toes II–V, (distal most lamella again excluded); total lamellae on foot (TotToeLm), total number of enlarged, paired, U-shaped lamellae on Toes II–V. Values in parentheses for subdigital lamellae formulae indicate intraspecific variation reported in the literature. To increase utility and comparability of color descriptions, color terminology and referenced codes follow Köhler (2012).

DNA extraction, purification, and amplification. We extracted genomic DNA from a liver sample of the recently-collected adult specimen from Houaphanh Province, northern Laos (NUOL 00476) using the DNeasy Blood & Tissue Kit (Qiagen). A fragment of mitochondrial (mt) DNA was amplified and sequenced following Grismer *et al.* (2017). The amplified region encompassed part of the tRNA^{Met}, the NADH dehydrogenase subunit 2 (ND2) gene, tRNA^{Trp}, tRNA^{Ala}, tRNA^{Asn}, tRNA^{Cys}, and tRNA^{Tyr}, and part of the cytochrome c oxidase subunit I (COI) gene. The resulting sequence (1,387 bp) was deposited in GenBank under accession MK307996.

Alignment and phylogenetic analysis. We downloaded all available homologous sequences of *Hemiphyllodactylus* from GenBank, including the sequence of the Champasak Province specimen (FMNH 258695; GenBank accession JN393935) that was made available by Heinicke *et al.* (2011). Additionally, we downloaded homologous sequences of *Hemidactylus frenatus* Duméril & Bibron, 1836 (accession GQ245970) and *Gehyra variegata* (Duméril & Bibron, 1836) [accession AY369026] for inclusion as outgroup species, following higher-level phylogenetic studies of gekkonid diversity (Heinicke *et al.* 2011; Gamble *et al.* 2012). GenBank and newly generated sequences were aligned using the default parameters in MAFFT v. 7 (Kato & Standley 2013). A maximum of five sequences per species was retained in the alignment for analysis [all pruned sequences differed by <1.0% uncorrected pairwise distance (*p*-distance) from retained sequences], except *H. yunnanensis* for which all sequences were retained owing to its widespread geographic distribution and genetic variation (Grismer *et al.* 2013).

The best partitioning scheme and best-fitting model of sequence evolution for each partition were selected using the Bayesian Information Criterion (BIC) in PartitionFinder v. 1.1.0 (Lanfear *et al.* 2012). The four selected partitions and models were K81uf+ Γ for the first codon position of COI + the combined tRNAs; TVM+I+ Γ for the ND2 first codon position; GTR+ Γ for the combined second codon positions of COI and ND2; and GTR+ Γ for the combined third codon positions of COI and ND2.

Partitioned Bayesian phylogenetic analyses were performed using MrBayes v. 3.2.6 (Ronquist *et al.* 2012) on the Cyberinfrastructure for Phylogenetic Research (CIPRES) Science Gateway v. 3.3 (Miller *et al.* 2010). Four independent analyses were performed, each with four chains (one cold, three heated) that were run for 20 million generations using the default priors, the chain temperature set to 0.1, with trees sampled every 4,000 generations, and the first 25% of trees discarded as ‘burn-in’. The resulting trace plots were viewed using Tracer v. 1.6 (Rambaut *et al.* 2014), and the Effective Sample Size (ESS) values of all parameters were $\geq 2,836$. A 50% majority-rule consensus of the post burn-in trees was constructed to calculate the posterior probabilities of nodes, and those nodes with posterior probabilities (PP) ≥ 0.95 were considered to have strong statistical support (Erixon *et al.* 2003). Uncorrected pairwise distances (*p*-distance) were calculated using PAUP* v. 4.0b10 (Swofford 2002).

Results

The specimen from the Bolaven Plateau in Champasak Province, southern Laos (FMNH 258695; GenBank accession JN393935), was recovered as the sister lineage to the recently described *H. flaviventris* Sukprasert, Sutthiwises, Lauhachinda, & Taksintum, 2018 (GenBank accessions MG322161–66) from Chanthaburi Province, eastern Thailand (PP = 1.00; Fig. 2). The clade containing the Champasak specimen and *H. flaviventris* was in turn

recovered to be sister to *H. aurantiacus* (Beddome, 1870) [GenBank accession JN393933] from Tamil Nadu, Yercaud, India (PP = 1.00; Fig. 2). The Champasak sequence had a *p*-distance of 15.7–16.7% from the *H. flaviventris* sequences and 20.0% from the *H. aurantiacus* sequence. The relationships inferred among these three lineages have also been observed in numerous other studies that utilized the same mitochondrial sequence data (Grismer *et al.* 2013, 2014a,b, 2015, 2017; Nguyen *et al.* 2013, 2014; Ngo *et al.* 2014; Yan *et al.* 2016; Sukprasert *et al.* 2018).

The specimen from Tham Ngou Leium Cave in Houaphanh Province, northern Laos (NUOL 00476; GenBank accession MK307996), was recovered as the sister lineage to a paratype of *H. banaensis* Ngo, Grismer, Thai, & Wood, 2014 from Da Nang, central Vietnam (GenBank accession KF219783; PP = 1.00; Fig. 2). The Houaphanh sequence differed from the *H. banaensis* sequence by 12.6% (*p*-distance).

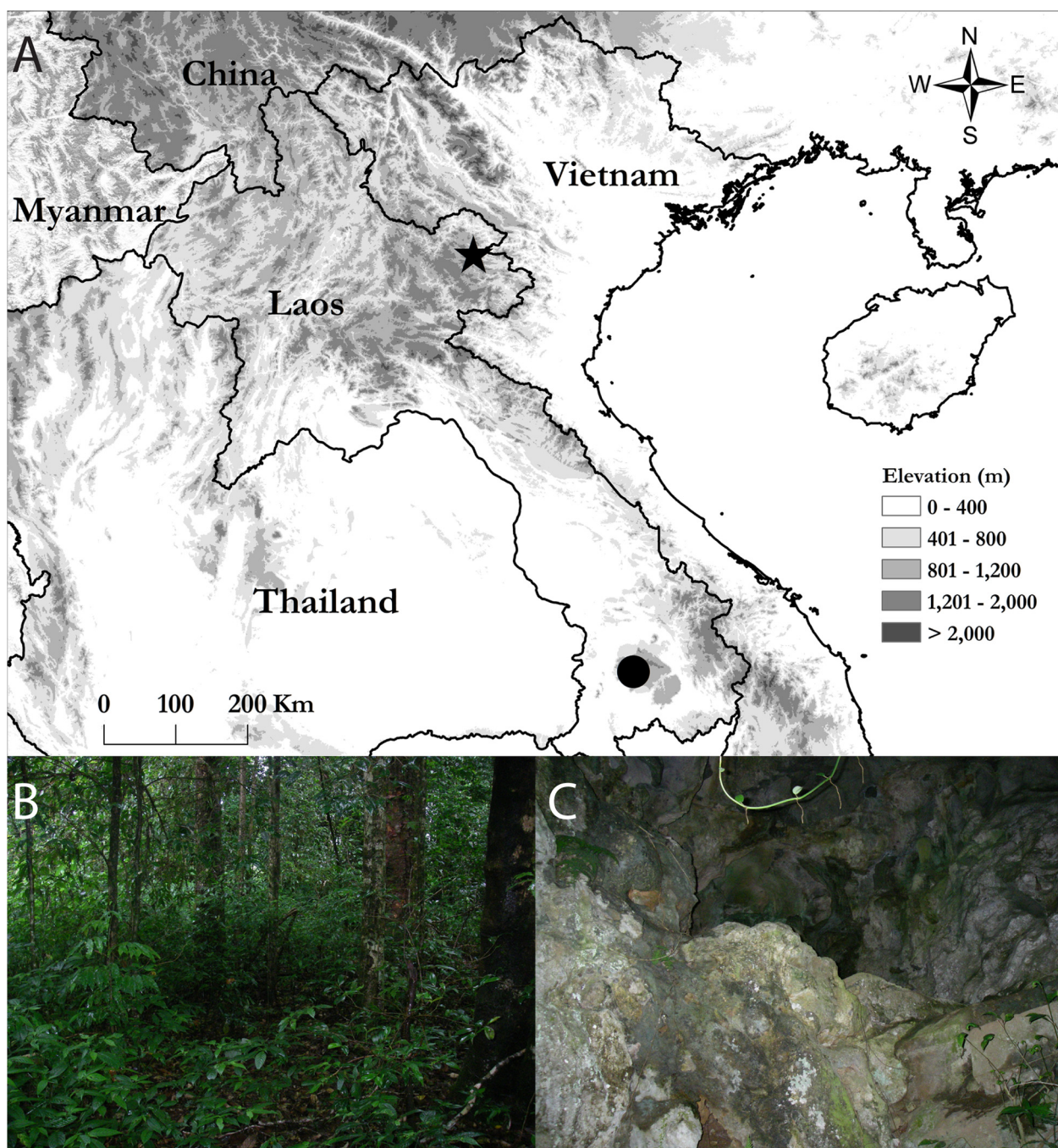


FIGURE 1. (A) Map showing the type localities of *Hemiphyllodactylus indosobrinus* sp. nov. in Pakxong District, Champasak Province, Laos (circle) and *Hemiphyllodactylus serpispecus* sp. nov. in Viengxay District, Houaphanh Province, Laos (star). (B) Habitat at the type locality of *H. indosobrinus* sp. nov. and (C) habitat at the type locality of *H. serpispecus* sp. nov.

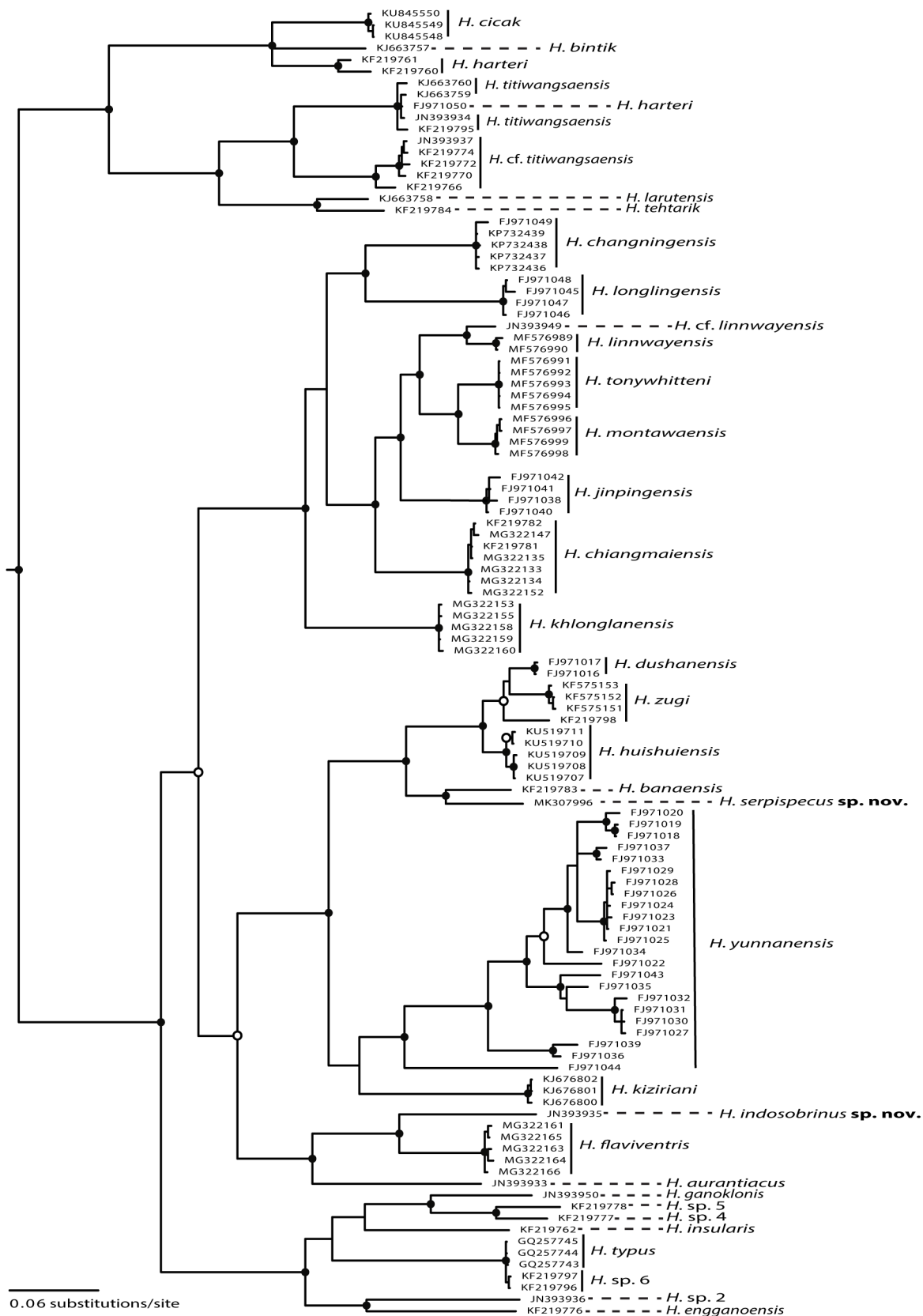


FIGURE 2. Maximum clade credibility topology resulting from Bayesian analysis of mitochondrial DNA (ND2 coding region, flanking tRNAs, and part of the COI coding region) from *Hemiphyllodactylus* geckos. *Hemidactylus frenatus* (GenBank accession GQ245970) and *Gehyra variegata* (GenBank accession AY369026) were used as outgroups (not shown). Black circles at nodes indicate Bayesian posterior probabilities ≥ 0.99 , and open circles at nodes indicate Bayesian posterior probabilities ≥ 0.95 . Nodes without circles represent support values < 0.95 . GenBank accession numbers are included at branch tips.

TABLE 1. Diagnostic characters of all named species of *Hemiphyllodactylus* from mainland Southeast Asia and southern China. A forward slash (/) indicates that data are not available.

	<i>indosobrinus</i> sp. nov.	<i>serripicus</i> sp. nov.	<i>aurantiacus</i>	<i>baenaensis</i>	<i>changningensis</i>	<i>chiangmaiensis</i>	<i>dushanensis</i>	<i>flaviventris</i>	<i>huishuensis</i>
Max SVL (mm)	39.8	41.9	37.9	51.0	43.8	41.2	51.0	39.2	51.2
Chin scales	8	7	10–14	6 or 7	7 or 8	8–12	/	7–10	8–10
Postmentals distinctly enlarged (1) or not (0)	1	1	0	1	1	1	1	/	1
Circumnasal scales	3	3	2–4	3	3 or 4	3 or 4	/	5	3
Internasal scales	3	2	3–6	4–11	2 or 3	1–3	/	1–5	2 or 3
Supralabial scales	15	11	10–13	9–12	8–11	9–11	9–12	9–12	9–11
Infralabial scales	12	9	8–12	9–11	8–10	9–12	8–12	8–11	9–11
Dorsal scales (within one OrbD)	30	26	11–17	17–20	11–15	11–21	/	16–18	13–15
Ventral scales (within one OrbD)	11	10	8–12	9–12	6–8	6–10	/	8–10	7–9
Lamellae on Fingers II–V	4554	3444	2222	3(4)(5)(5)4	33(4)3(4)3	333(4)3	3444	4444	3(4)(5)(5)4
Total lamellae on hand	18	15	8	15–18	12–14	12 or 13	15	16	15–18
Lamellae on Toes II–V	4555	3445	2232(3)	4555	33(4)3(4)3(4)	33(4)33	4555	4555	44(5)54(5)
Total lamellae on foot	19	16	9 or 10	19	12–15	12 or 13	19	19	17–19
Lamellae on Finger I	4	4	3 or 4	5	3 or 4	3 or 4	6	5	3
Lamellae on Toe I	5	4	4 or 5	4 or 5	3 or 4	3 or 4	7	5	3
Precloacal and femoral pores	18	11	16–25	15–21	19–22	17–25	22–29	9	0–20
Precloacal and femoral pore series separate (1) or continuous (0)	0	0	1	0	0	0	/	/	0
Cloacal spurs on each side	1	2	1–3	1	1 or 2	1	/	1 or 2	1

.....continued on the next page

TABLE 1. (Continued)

	<i>jinpingensis</i>	<i>khlonglanensis</i>	<i>kiziriani</i>	<i>linwayensis</i>	<i>longlingensis</i>	<i>montawagensis</i>	<i>tonywhitteni</i>	<i>yunnanensis</i>	<i>zugii</i>
Max SVL (mm)	53.5	43.1	40.8	41.5	46.0	40.1	38.8	49.3	46.6
Chin scales	/	7 or 8, 10	6–9	4–6	8	4–7	5–8	6–11	9–12
Postmentals distinctly enlarged (1) or not (0)	1	/	1	1	1	1	1	1	1
Circumnasal scales	/	5	4	5	/	4–6	3–5	2–4	2 or 3
Internasal scales	/	2–4	2 or 3	2	/	1–4	2–4	II–V	3–5
Supralabial scales	8–10	9–12	10 or 11	9 or 10	7–10	8–10	8 or 9	8–13	10–13
Infralabial scales	9–11	8–11	9–11	8	8–11	8 or 9	8	8–12	10–12
Dorsal scales (within one OrbD)	/	10–15	18–27	13 or 14	/	13 or 14	13–16	9–18	19–22
Ventral scales (within one OrbD)	/	7–10	11–15	8	/	7 or 8	7–9	6–12	14–16
Lamellae on Fingers II–V	3444	3(4)444	3444	4444	3333	33(4)3(4)3	44(5)4(5)4	3333	3444
Total lamellae on hand	15	15 or 16	15	16	12	12–14	16–18	12	15
Lamellae on Toes II–V	4555	4444	44(5)4(5)4	454(5)4	3444	3(4)4(5)4(5)4(5)	3(4)4(5)4(5)4(5)	3444	4555
Total lamellae on foot	19	16	16–18	17 or 18	15	15–19	15–19	15	19
Lamellae on Finger I	6	5 or 6	5	3 or 4	6	3 or 4	3	4–6	4 or 5
Lamellae on Toe I	5	5	5	4 or 5	5	3 or 4	3 or 4	4–7	4 or 5
Precloacal and femoral pores	24–31	19 or 20	8–13	/	13–28	19–21	20–26	11–25	18–21
Precloacal and femoral pore series separate (1) or continuous (0)	/	0	0	/	/	0	0	0	0
Cloacal spurs on each side	/	1	1 or 2	1	/	1	1	0–2	1

The specimen from the Bolaven Plateau in Champasak Province and the specimen from Tham Ngou Leium Cave in Houaphanh Province are both geographically isolated from congeners in the region. The Champasak Province specimen was collected approximately 500 air km from the type locality of *H. flaviventris* in eastern Thailand (Sukprasert *et al.* 2018), and approximately 3,040 air km from the locality of the *H. aurantiacus* sample from India (Heinicke *et al.* 2011). The Houaphanh Province specimen was found approximately 630 air km from the type locality of *H. banaensis* in Vietnam (Ngo *et al.* 2014). Given the high levels of endemism found within the genus (Zug 2010; Grismer *et al.* 2013), such allopatric distributions add support for the distinctiveness of these two lineages.

Finally, the Champasak and Houaphanh Province specimens can each be differentiated from all recognized congeners by having unique combinations of diagnostic morphological features (Table 1). Based on all molecular and morphological data available, we describe both lineages as new species below.

Taxonomic accounts

Hemiphyllodactylus indosobrinus sp. nov.

(Figures 3, 4A–C)

Hemiphyllodactylus sp. nov. 8 Grismer, Wood, Anuar, Quah, Muin, Chan, Sumarli, & Loredó 2015:863.

Hemiphyllodactylus sp. nov. 9 Grismer, Wood, Anuar, Muin, Quah, McGuire, Brown, Ngo, & Pham 2013:852; Grismer, Riyanto, Iskandar, & McGuire 2014:490; Grismer, Wood, & Cota 2014:69; Ngo, Grismer, Pham, & Wood 2014:541; Nguyen, Botov, Le, Nophaseud, Zug, Bonkowski, & Ziegler 2014:46; Yan, Lin, Guo, Li, & Zhou 2016:544; Grismer, Wood, Thura, Zin, Quah, Murdoch, Grismer, Li, Kyaw, & Lwin 2017:6; Sukprasert, Sutthiwises, Lauhachinda, & Taksintum 2018:365.

Hemiphyllodactylus cf. *yunnanensis* Nguyen, Lehmann, Le, Duong, Bonkowski, & Ziegler 2013:91.

Holotype. FMNH 258695 (field number HKV 63933), adult male, Bolaven Plateau, Dong Hua Sao National Protected Area, Pakxong District, Champasak Province, Laos, 15.07694°N, 106.13750°E, WGS84 (Fig. 1A), ca. 1,000 m elev., collected 13 September 1999 by BLS, Harold F. Heatwole, and Bee Thaovanseng.

Diagnosis. *Hemiphyllodactylus indosobrinus* sp. nov. can be distinguished from all congeners by having the following combination of characters: supralabials 15; infralabials 12; precloacofemoral pores 18 in males (females unknown); subdigital lamellae on Fingers II–V 4-5-5-4; total lamellae on hand 18; subdigital lamellae on Toes II–V 4-5-5-5; total lamellae on foot 19; dorsal scales across midbody within one orbital diameter 30; ventral scales across midbody within one orbital diameter 11; cloacal spurs two; chin scales eight; and internasal scales three.

Description of holotype. Adult male; head triangular in dorsal profile, distinct from neck (HeadL 9.7 mm; HeadW 7.4 mm; HeadD 3.9 mm); rostrum long (NarEye 3.0 mm; NarEye/HeadL 31%); prefrontal region slightly concave; canthus rostralis smooth, rounded; snout long (SnEye 3.8 mm; SnEye/HeadL 39%), narrow (SnW 1.6 mm), rounded in dorsal profile; eye large (OrbD 2.4 mm); ear small, ovoid (EarL 0.7 mm); EyeEar greater than orbital diameter (EyeEar 3.3 mm; EyeEar/OrbD 138%); rostral scale wider than high, bordered posteriorly by two large supranasals and three internasals (Internas); nares bordered anteriorly by rostral scale, ventrally by first supralabial, dorsally by supranasal, posteriorly by two postnasals (CircNa); supralabials square, 15/15 (left/right), tapering from rostral to a point in line with posterior margin of orbit (Suplab); infralabials square, 12/12, tapering from mental to a point in line with posterior margin of orbit (Inflab); scales on head small, rounded, largest on rostrum; superciliaries unequally sized, imbricate; mental triangular, bordered by first infralabials and posteriorly by two large postmentals; each postmental bordered anterolaterally by first infralabial; eight chin scales touching infralabials and mental (Chin); scales in gular region rounded, non-overlapping, becoming larger and more ovoid on venter.

Body small, elongate (SVL 39.8 mm; TrunkL 20.2 mm), widest at midbody; ventrolateral fold absent; dorsal body scales small, granular, scales within one orbital diameter 30 (Dorsal); tubercles absent (Tub); ventral body scales smooth, somewhat rounded, subimbricate, scales within one orbital diameter 11 (Ventral); enlarged precloacal and femoral scales 20; continuous precloacofemoral pore series 18 (Pore); precloacal groove absent; fore-limbs relatively short (ForeL 4.0 mm), covered dorsally with granular, subimbricate scales, smaller smooth scales ventrally; palmar scales flat, unevenly shaped, non-overlapping; Finger I vestigial, clawless, subdigital

lamellae rectangular, four (IFingLm); Fingers II–V well-developed; proximal subdigital lamellae undivided, rectangular; distal subdigital lamellae divided, angular, U-shaped, except terminal lamellae rounded, undivided; lamellar formula on Fingers II–V 4-5-5-4 on left hand, 3-5-5-4 on right hand (II–VFingLm), total lamellae on hand 18 (TotFingLm); claws on Fingers II–V well-developed, unsheathed, strongly curved; hind limbs short (CrusL 5.1 mm), covered dorsally with granular, subimbricate, unevenly sized scales, covered ventrally with smooth scales, larger than dorsal scales; plantar scales small, smooth; Toe I vestigial, clawless, subdigital lamellae rectangular, five (IToeLm); Toes II–V well-developed; proximal subdigital lamellae undivided, rectangular; distal lamellae divided, angular, and U-shaped except terminal lamellae rounded, undivided; lamellar formula on Toes II–V 4-5-5-5 on both feet (II–VToeLm), total lamellae on foot 19 (TotToeLm); cloacal spurs two (CloacS); tail short, round in cross-section, partially regenerated (TailL 27.1 mm), narrow (TailW 2.7 mm); dorsal scales on tail larger than on body and head, smaller than subcaudals, subcaudals large, flat, imbricate.

Coloration in preservative. Dorsal surfaces of head and body Raw Sienna (Color 32), mottled with light patches of Pale Buff (Color 1) and dark patches of Dusky Brown (Color 285). Faint postorbital stripe of Light Buff (Color 2). Dorsal surface of tail fades posteriorly from Pale Pinkish Buff (Color 3) to Drab Gray (Color 256). Triangular marking at base of dorsal surface of tail Vandyke Brown (Color 282), outlined posteriorly in Pale Pinkish Buff (Color 3). Ventral surfaces of head and body Pale Buff (Color 1) in gular region, fading posteriorly to Light Buff (Color 2) near vent, with Tawny Olive (Color 17) speckling. Ventral surface of original portion of tail Pale Buff (Color 1) with speckling of Raw Sienna (Color 32) and Vandyke Brown (Color 282). Ventral surface of regenerated portion of tail Raw Sienna (Color 32), fading to Drab Gray (Color 256) posteriorly (Figs. 3, 4A–C).

Distribution and natural history. *Hemiphyllodactylus indosobrinus* **sp. nov.** is known only from the holotype that was collected approximately 1 m above the ground inside of a vertical palm tree in wet evergreen forest during the morning (Fig. 1B). It is currently unknown as to whether this species occurs beyond the type locality in Dong Hua Sao National Protected Area. Additional surveys for the species in the vicinity of the type locality were conducted during 28 July–4 August 2010 by BLS and NS, and during 24–28 July 2018 by SP, but failed to yield additional specimens. The species probably persists at the type locality but is either uncommon or difficult to sample.

Etymology. The specific epithet is taken from the Latin *indus* for belonging to India, and *sobrinus* for maternal cousin, in reference to its close relationship, along with *H. flaviventris*, in maternally-inherited mitochondrial sequence data to the Indian endemic *H. aurantiacus* (Fig. 2; Grismer *et al.* 2013, 2014a,b, 2015, 2017; Nguyen *et al.* 2013, 2014; Ngo *et al.* 2014; Yan *et al.* 2016; Sukprasert *et al.* 2018).

Comparisons. *Hemiphyllodactylus indosobrinus* **sp. nov.** can be differentiated from all other congeners in mainland Southeast Asia and southern China by a combination of the following characters: chin scales eight (*versus* ≥ 10 in *H. aurantiacus* and ≤ 6 in *H. linnwayensis* Grismer, Wood, Thura, Zin, Quah, Murdoch, Grismer, Li, Kyaw, & Lwin, 2017); postmentals distinctly enlarged (*versus* not enlarged in *H. aurantiacus*); circumnasal scales three (*versus* ≥ 4 in *H. flaviventris*, *H. khlonglanensis* Sukprasert, Sutthiwises, Lauhachinda, & Taksintum, 2018, *H. kiziriani*, and *H. linnwayensis*); supralabial scales 15 [*versus* ≤ 13 in *H. aurantiacus*, *H. banaensis*, *H. changningensis* Guo, Zhou, Yan, & Li, 2015, *H. Chiangmaiensis* Grismer, Wood, & Cota, 2014, *H. dushanensis* (Zhou & Liu, 1981), *H. flaviventris*, *H. huishuiensis* Yan, Lin, Guo, Li, & Zhou, 2016, *H. jinpingensis* (Zhou & Liu, 1981), *H. khlonglanensis*, *H. kiziriani*, *H. linnwayensis*, *H. longlingensis* (Zhou & Liu, 1981), *H. montawaensis* Grismer, Wood, Thura, Zin, Quah, Murdoch, Grismer, Li, Kyaw, & Lwin, 2017, *H. tonywhitteni* Grismer, Wood, Thura, Zin, Quah, Murdoch, Grismer, Li, Kyaw, & Lwin, 2017, *H. yunnanensis*, and *H. zugi* Nguyen, Lehmann, Le, Duong, Bonkowski, Ziegler, 2013]; infralabial scales 12 (*versus* ≤ 10 in *H. changningensis*, *H. linnwayensis*, *H. montawaensis*, and *H. tonywhitteni*); dorsal scales within one orbital diameter 30 (*versus* ≤ 27 in *H. aurantiacus*, *H. banaensis*, *H. changningensis*, *H. Chiangmaiensis*, *H. flaviventris*, *H. huishuiensis*, *H. khlonglanensis*, *H. kiziriani*, *H. linnwayensis*, *H. montawaensis*, *H. tonywhitteni*, *H. yunnanensis*, and *H. zugi*); ventral scales within one orbital diameter 11 (*versus* ≤ 9 in *H. changningensis*, *H. huishuiensis*, *H. linnwayensis*, *H. montawaensis*, *H. tonywhitteni*, and 14–16 in *H. zugi*); total lamellae on hand 18 (*versus* ≤ 16 in *H. aurantiacus*, *H. changningensis*, *H. Chiangmaiensis*, *H. dushanensis*, *H. flaviventris*, *H. jinpingensis*, *H. khlonglanensis*, *H. kiziriani*, *H. linnwayensis*, *H. longlingensis*, *H. montawaensis*, *H. yunnanensis*, and *H. zugi*); total lamellae on foot 19 (*versus* ≤ 16 in *H. aurantiacus*, *H. changningensis*, *H. Chiangmaiensis*, *H. khlonglanensis*, *H. longlingensis*, and *H. yunnanensis*); subdigital lamellae on Finger I four (*versus* three in *H. huishuiensis*, *H. tonywhitteni* and ≥ 5 in *H. banaensis*, *H. dushanensis*, *H. flaviventris*, *H. jinpingensis*, *H. khlonglanensis*, *H. kiziriani*, and *H. longlingensis*);

subdigital lamellae on Toe I five (versus ≤ 4 in *H. changningensis*, *H. Chiangmaiensis*, *H. huishuiensis*, *H. montawaensis*, *H. tonywhitteni*, and seven in *H. dushanensis*); and continuous precloacofemoral pores 18 (versus ≥ 20 in *H. dushanensis*, *H. jinpingensis*, *H. tonywhitteni*, and ≤ 13 in *H. flaviventris*, *H. kiziriani*).

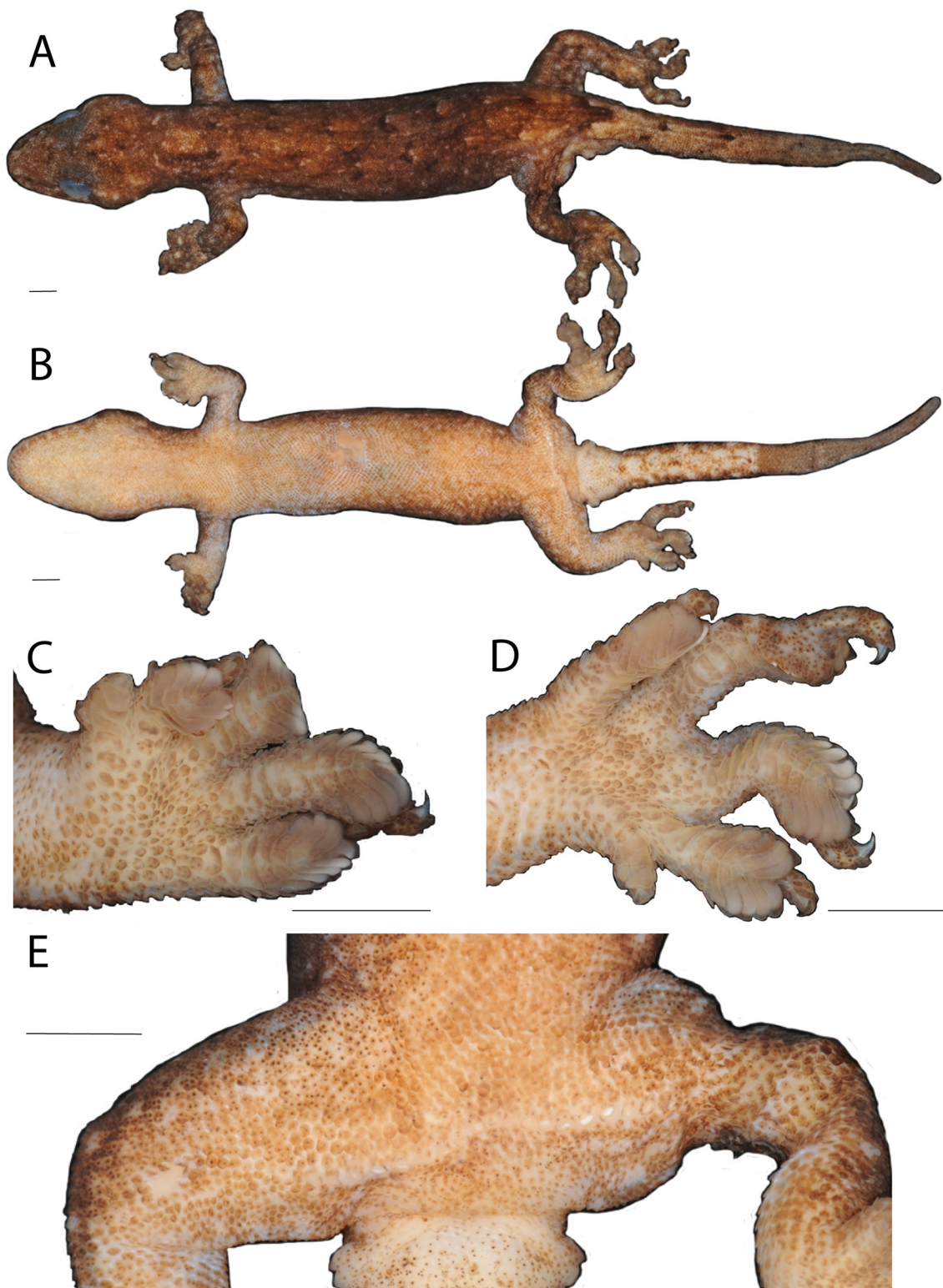


FIGURE 3. (A) Dorsal and (B) ventral views of the preserved holotype male (FMNH 258695) of *Hemiphyllodactylus indosobrinus* sp. nov.. Ventral surface of (C) left hand and (D) left foot. (E) Ventral view of pubis and hind limbs showing pore series. Scale bars equal 2 mm.

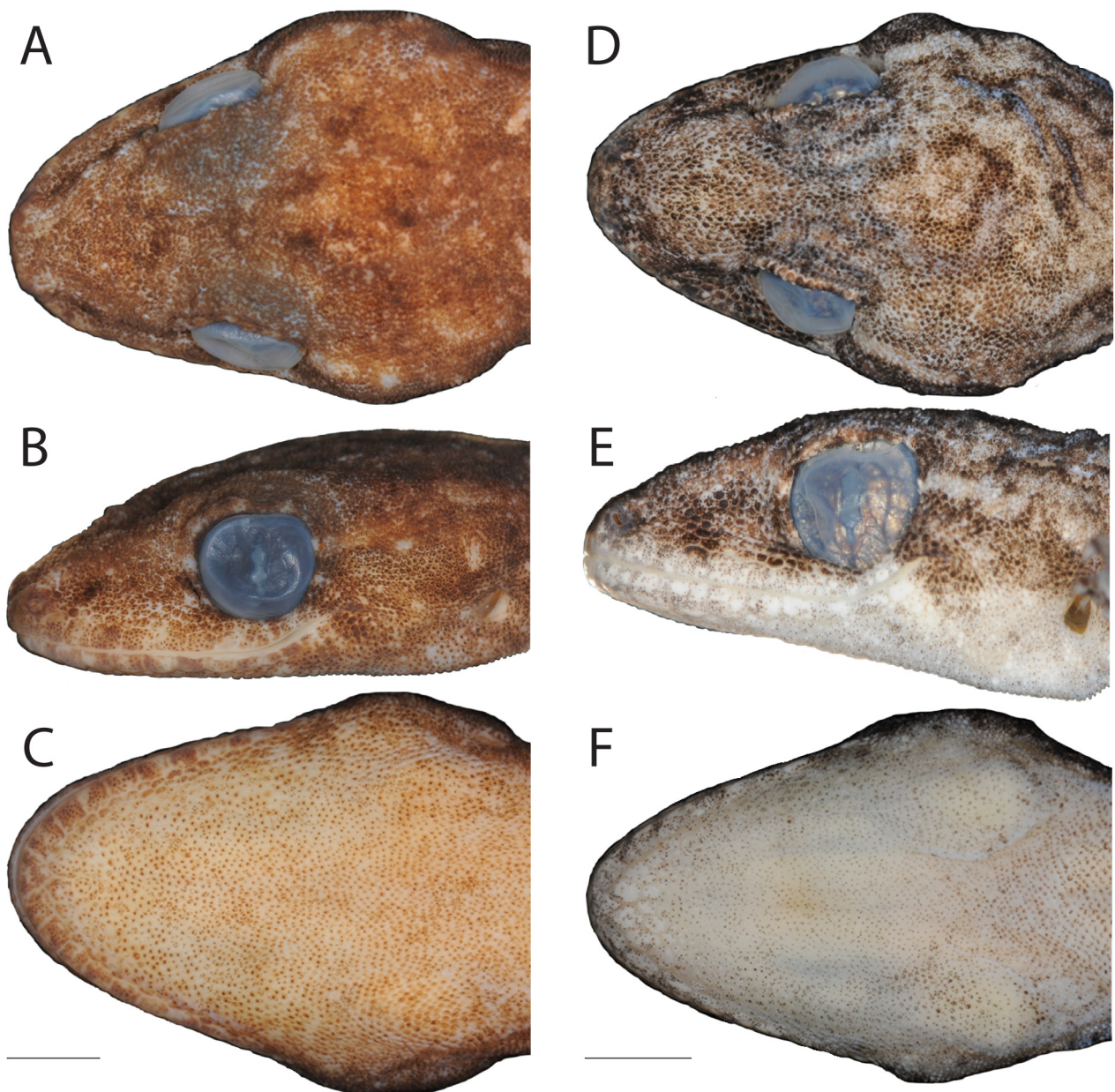


FIGURE 4. (A) Dorsal, (B) ventral, and (C) lateral view of head of the preserved holotype male (FMNH 258695) of *Hemiphyllodactylus indosobrinus* **sp. nov.**. (D) Dorsal, (E) ventral, and (F) lateral view of the head of the preserved holotype male (NUOL 00476) of *Hemiphyllodactylus serpispecus* **sp. nov.**. Scale bars equal 2 mm.

***Hemiphyllodactylus serpispecus* sp. nov.**

(Figs. 4D–F, 5, 6)

Holotype. NUOL 00476 (field number BLS 17278), adult male, Tham Ngou Leium Cave, Viengxay District, Houaphanh Province, Laos, 20.40725°N, 104.23068°E, WGS84 (Fig. 1A), 889 m elev., collected 19 September 2015 by BLS, SP, Fongfany Lybounyasao, and Phousavanh Inthapanya.

Diagnosis. *Hemiphyllodactylus serpispecus* **sp. nov.** can be distinguished from all congeners by having the following combination of characters: supralabials 11; infralabials nine; precloacofemoral pores 11 in males (females unknown); subdigital lamellae on Fingers II–V 3-4-4-4; total lamellae on hand 15; subdigital lamellae on Toes II–V 3-4-4-5; total lamellae on foot 16; dorsal scales across midbody within one orbital diameter 26; ventral scales across midbody within one orbital diameter 10; cloacal spurs two; chin scales seven; and internasals two.

Description of holotype. Adult male; head triangular in dorsal profile, distinct from neck (HeadL 10.4 mm; HeadW 7.7 mm; HeadD; 4.6 mm); loreal and interorbital regions smooth; rostrum long (NarEye 3.3 mm; NarEye/HeadL 32%); prefrontal region slightly concave; canthus rostralis smooth, rounded; snout long (SnEye 4.0 mm; SnEye/HeadL 38%), narrow (SnW 1.5 mm), rounded in dorsal profile; eye large (OrbD 2.4 mm); ear small, ovoid (EarL 0.5 mm); EyeEar greater than orbit diameter (EyeEar 4.0 mm; EyeEar/OrbD 167%); rostral scale wider than high, bordered posteriorly by two large supranasals and two internasals (Internas); nares bordered anteriorly by rostral scale, ventrally by first supralabial, dorsally by supranasal, posteriorly by two postnasals (CircNa); supralabials square, 11/11 (left/right), tapering from rostral to a point in line with posterior margin of orbit (Suplab); infralabials square, 9/9, tapering from mental to a point in line with posterior margin of orbit (Inflab); scales on head small, rounded, largest on rostrum; superciliaries unequally sized, imbricate; mental triangular, bordered laterally by first infralabials and posteriorly by two large postmentals; each postmental bordered anterolaterally by first infralabial; seven chin scales touching infralabials and mental (Chin); scales in gular region rounded, non-overlapping, becoming larger and more ovoid on venter.

Body small, elongate (SVL 41.9 mm; TrunkL 21.4 mm); widest at midbody; ventrolateral fold absent; dorsal body scales small, granular, scales within one orbital diameter 26 (Dorsal); tubercles absent (Tub); ventral body scales smooth, somewhat rounded, subimbricate, scales within one orbital diameter 10 (Ventral); enlarged precloacal and femoral scales 17; continuous precloacal and femoral scales with pores 11 (Pore); precloacal groove absent; fore-limbs relatively short (ForeL 4.6 mm), dorsally covered with granular, subimbricate scales, smaller smooth scales ventrally; palmar scales flat, unevenly shaped, non-overlapping; Finger I vestigial, clawless, subdigital lamellae rectangular, four (IFingLm); Fingers II–V well-developed; proximal subdigital lamellae undivided, rectangular; distal lamellae divided, angular, U-shaped, except terminal lamellae rounded, undivided; lamellar formula on Fingers II–V 3-4-4-4 on both hands (II–VFingLm), total lamellae on hand 15 (TotFingLm); claws on Fingers II–V well-developed, unsheathed, strongly curved; hind limbs short (CrusL 6.0 mm), dorsally covered with granular, subimbricate, unevenly sized scales, ventrally covered with smooth scales, larger than dorsal scales; plantar scales small, smooth; Toe I vestigial, clawless; subdigital lamellae rectangular, four (IToeLm); Toes II–V well-developed; proximal subdigital lamellae undivided rectangular; distal lamellae divided, angular, and U-shaped except terminal lamellae rounded, undivided; lamellar formula on Toes II–V 3-4-4-5 on left foot and 3-5-5-5 on right foot (II–VToeLm), total lamellae on foot 16 (TotToeLm); cloacal spurs two (CloacS); tail long (TailL 35.2 mm), round in cross-section, narrow (TailW 3.1 mm), intact, tapers towards tip; dorsal scales on tail larger than on body and head, smaller than subcaudals; subcaudals large, flat, imbricate.

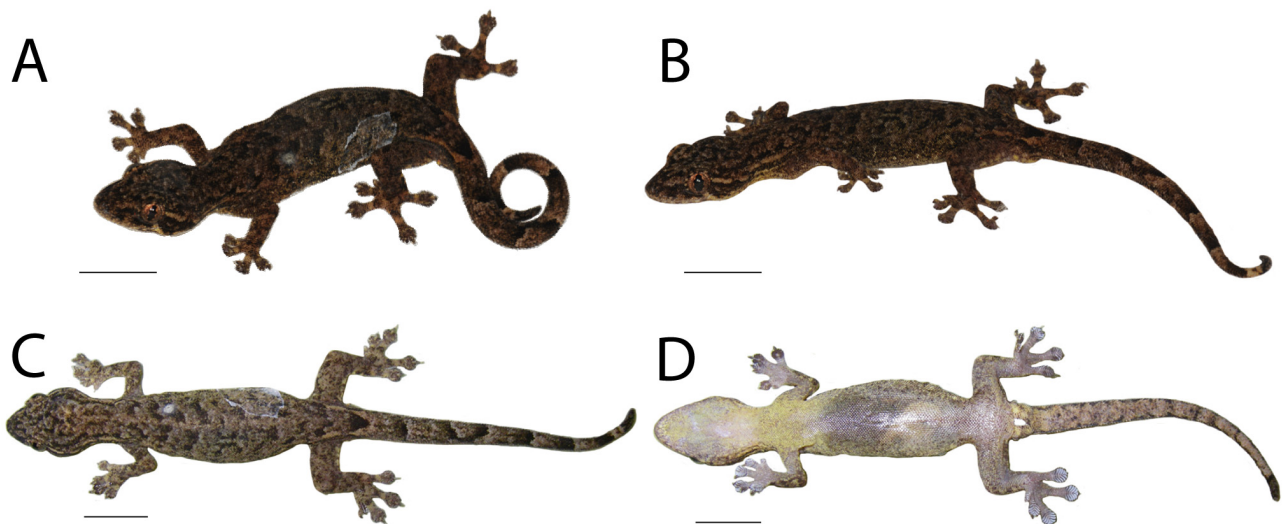


FIGURE 5. (A) Dorsal and (B) dorsolateral views in life, and (C) dorsal and (D) ventral views after euthanasia but prior to preservation of the holotype male (NUOL 00476) of *Hemiphyllodactylus serpispecus* **sp. nov.** Scale bars equal 10 mm.

Coloration in life. Dorsal surfaces of head and body Olive-Brown (Color 278), mottled with light and dark brown patches ranging from Smoke Gray (Color 267) to Dusky Brown (Color 285). Weak chevron pattern of Dusky Brown (Color 285) on paravertebral surfaces from neck to base of tail. Faint postorbital stripe of Drab Gray

(Color 256) from posterior edge of eye to level of fore-limb. Labial scales Smoke Gray (Color 266) with darker speckles ranging from Smoke Gray (Color 267) to Dusky Brown (Color 285). Medium Sulphur Yellow (Color 94) speckles on dorsolateral and ventrolateral surfaces posterior to the jaw. Sharp contrast of Dusky Brown (Color 285) to Smoke Gray (Color 267) in supraciliary region. Dorsal surface of tail Brownish Olive (Color 276), mottled with patches ranging from Smoke Gray (Color 267) to Dusky Brown (Color 285). Triangular marking at base of dorsal surface of tail Dusky Brown (Color 285), outlined posteriorly in Ground Cinnamon (Color 270). Weak lateral stripe along length of tail Dusky Brown (Color 285). Ventral surfaces mostly Smoky White (Color 261) with speckles of Raw Umber (Color 280) and Medium Sulphur Yellow (Color 94) (Fig. 5A–B).

Coloration in alcohol. As in life, except dorsal surfaces of the head, body, limbs, and tail faded to Grayish-Horn Color (Color 268); (2) lateral stripe on tail not visible; (3) chevron pattern on paravertebral surfaces not visible; (4) postorbital stripe faded to Smoky White (Color 261); (5) labial coloration faded to Smoky White (Color 261) with speckling of Raw Umber (Color 280); (6) all yellow coloration on dorsolateral, ventrolateral, and ventral surfaces faded to Smoky White (Color 261) (Figs. 4D–F, 6).

Distribution and natural history. *Hemiphyllodactylus serpispecus* **sp. nov.** is known only from the holotype that was collected at night (2045 h) approximately 1 m above the ground on a limestone karst formation near the entrance to Tham Ngou Leium Cave (Fig. 1C). The cave had been developed for tourism at the time of our visit and only scrub and secondary vegetation surrounded the limestone karst block containing the cave.

Etymology. The specific epithet is derived from the Latin *serpens* for snake and *specus* for cave, in reference to the type locality of Tham Ngou Leium, which means “Python Cave” in the Lao language.

Comparisons. *Hemiphyllodactylus serpispecus* **sp. nov.** can be differentiated from all other congeners in mainland Southeast Asia and southern China by a combination of the following characters: chin scales seven (*versus* ≥ 9 in *H. aurantiacus* and *H. zugi*); postmentals distinctly enlarged (*versus* not enlarged in *H. aurantiacus*); circumnasal scales three (*versus* ≥ 4 in *H. flaviventris*, *H. khlonglanensis*, *H. kiziriani*, and *H. linnwayensis*); internasal scales two (*versus* 4–11 in *H. banaensis*); supralabial scales 11 (*versus* eight or nine in *H. tonywhitteni*); dorsal scales within one orbital diameter 26 (*versus* ≤ 22 in *H. aurantiacus*, *H. banaensis*, *H. changningensis*, *H. changmaiensis*, *H. flaviventris*, *H. huishuiensis*, *H. khlonglanensis*, *H. linnwayensis*, *H. montawaensis*, *H. tonywhitteni*, *H. yunnanensis*, and *H. zugi*); ventral scales within one orbital diameter 10 (*versus* ≤ 8 in *H. changningensis*, *H. linnwayensis*, *H. montawaensis*, and 14–16 in *H. zugi*); total lamellae on hand 15 (*versus* ≤ 13 in *H. aurantiacus*, *H. changmaiensis*, *H. longlingensis*, and *H. yunnanensis*); total lamellae on foot 16 (*versus* ≤ 13 in *H. aurantiacus*, *H. changmaiensis* and 19 in *H. banaensis*, *H. dushanensis*, *H. flaviventris*, and *H. zugi*); subdigital lamellae on Finger I four (*versus* three in *H. huishuiensis*, *H. tonywhitteni* and ≥ 5 in *H. banaensis*, *H. dushanensis*, *H. flaviventris*, *H. jinpingensis*, *H. khlonglanensis*, *H. kiziriani*, and *H. longlingensis*); subdigital lamellae on Toe I four (*versus* three in *H. huishuiensis* and ≥ 5 in *H. dushanensis*, *H. flaviventris*, *H. jinpingensis*, *H. khlonglanensis*, *H. kiziriani*, and *H. longlingensis*); and continuous precloacofemoral pores 11 (*versus* ≥ 13 in *H. aurantiacus*, *H. banaensis*, *H. changningensis*, *H. changmaiensis*, *H. dushanensis*, *H. jinpingensis*, *H. khlonglanensis*, *H. longlingensis*, *H. montawaensis*, *H. tonywhitteni*, and *H. zugi*).

Discussion

The recognition of *Hemiphyllodactylus indosobrinus* **sp. nov.** and *H. serpispecus* **sp. nov.** brings the number of described species of *Hemiphyllodactylus* in Laos to four, along with *H. kiziriani* and *H. yunnanensis*. *Hemiphyllodactylus indosobrinus* **sp. nov.** represents the only record of the genus from southern Laos, with all other species known from the northern regions of the country.

The geographic ranges of each species of slender gecko in Laos remain uncertain. *Hemiphyllodactylus kiziriani*, *H. indosobrinus* **sp. nov.**, and *H. serpispecus* **sp. nov.** are each known only from their type localities (Nguyen *et al.* 2014; this study), and the presence of *H. yunnanensis* in northern Laos is documented by two historical specimens (FMNH 14451, 14452; Zug 2010). Given the limited sample sizes for each *Hemiphyllodactylus* species in museum collections, particularly from Laos (*H. kiziriani* n=10, *H. yunnanensis* n=2, *H. indosobrinus* **sp. nov.** n=1, and *H. serpispecus* **sp. nov.** n=1), additional survey work is needed to better understand the distributions of these secretive species.

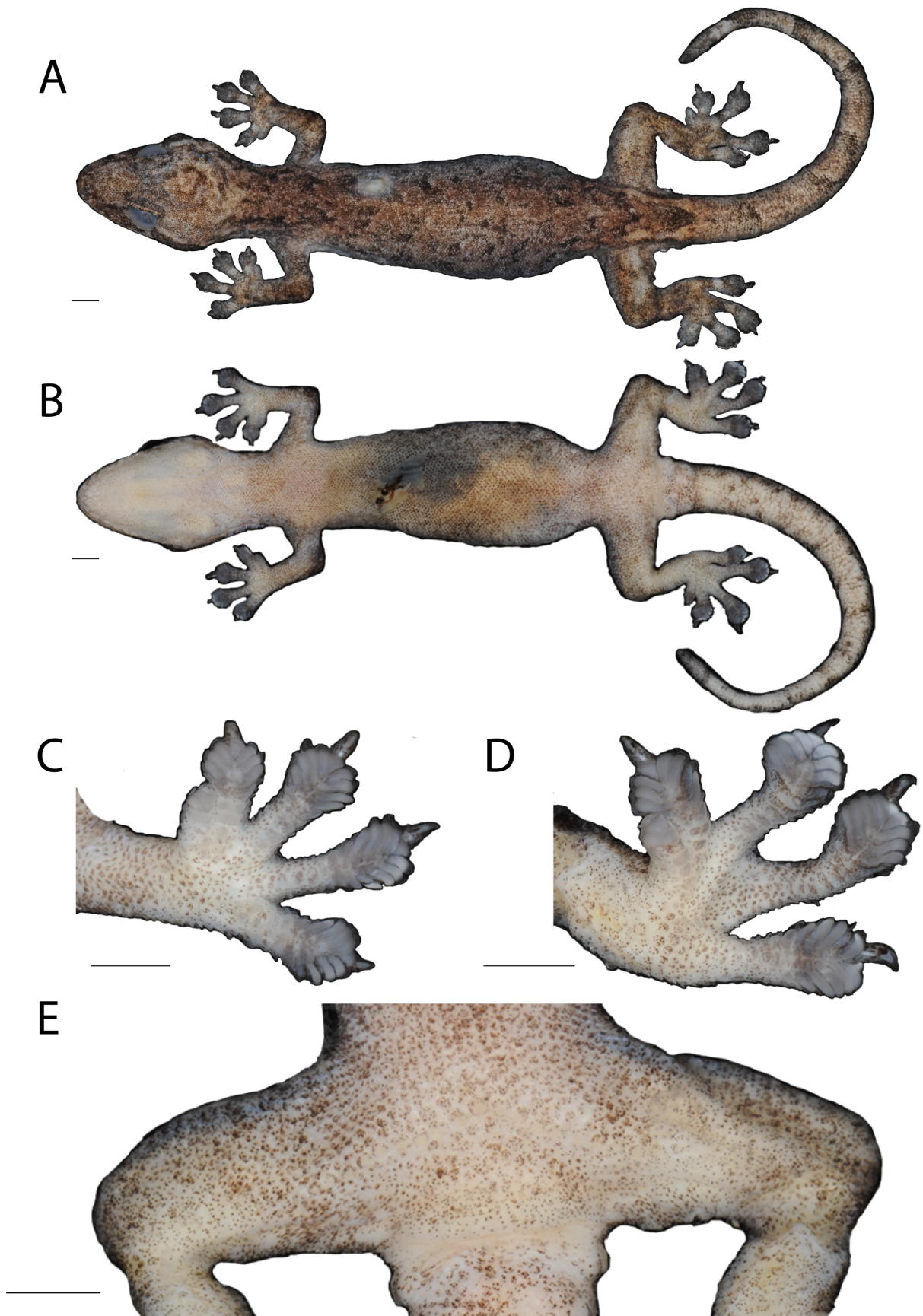


FIGURE 6. (A) Dorsal and (B) ventral views of the preserved holotype male (NUOL 00476) of *Hemiphyllodactylus serpispecus* sp. nov.. Ventral surface of (C) left hand and (D) left foot. (E) Ventral view of pubis and hind limbs showing pore series. Scale bars equal 2 mm.

At this time, we hypothesize that both new species are restricted to montane habitats. Upland endemism appears commonly in *Hemiphyllodactylus* in mainland Southeast Asia (Zug 2010; Grismer *et al.* 2013) and, given that both type localities described in this study occur above 850 m in elevation, we find it likely that these lineages represent mid- to high-elevation taxa. The type locality of *H. serpispecus* **sp. nov.** is located within the Northwest Uplands biogeographic region as defined by Bain & Hurley (2011), which contains large expanses of limestone karst forest in northern Laos and Vietnam. This region contains high reptile diversity (Bain & Hurley 2011), including all three *Hemiphyllodactylus* species that are known currently from northern Laos (Zug 2010; Nguyen *et al.* 2014; this study).

Although most *Hemiphyllodactylus* species from Laos occur in the northern portion of the country, *H. indosobrinus* **sp. nov.** is found within the Southern Lao Uplands biogeographic region (Bain & Hurley 2011). This region has been poorly surveyed for reptiles (Bain & Hurley 2011), and the discovery of *H. indosobrinus* **sp. nov.** in the Southern Lao Uplands suggests that future survey efforts there may reveal additional *Hemiphyllodactylus* species diversity.

Acknowledgements

The Ministry of Natural Resources and Environment (formerly Ministry of Agriculture and Forestry), Vientiane, Laos, granted permission for field work and provided specimen export permits. Phousavanh Inthapanya, Fongfany Lybounyasao, Sengvilay Seateun, Harold F. Heatwole, Bounthavy Phommachanh, and Bee Thaovanseng assisted with fieldwork. The Wildlife Conservation Society Laos Program provided invaluable logistical support. Live geckos were handled in accordance with protocol NCSM 2011-01 of the Institutional Animal Care and Use Committee of the North Carolina Museum of Natural Sciences. Alan Resetar (FMNH) kindly loaned specimens in his care. Lee Grismer and George Zug helped to interpret *Hemiphyllodactylus* characters in the literature and improved the manuscript. The National Geographic Society (grant 6247-98 to Harold F. Heatwole and BLS, **and grant WW-236R-17 to SP**) and the U.S. National Science Foundation (grant DEB-1145922 to BLS), a Professional Development Grant from the World Wildlife Fund's Russell E. Train Education for Nature Program (to SP), a U.S.-ASEAN Fulbright Scholarship (to SP), and the Partnerships for Enhanced Engagement in Research (PEER) Science program (grant PGA-2000003545 to Anchalee Aowphol, SP, and NS), which is a partnership between the U.S. Agency for International Development (USAID) and the U.S. National Science Foundation, funded this research.

References

- Bain, R.H. & Hurley, M.M. (2011) A biogeographic synthesis of the amphibians and reptiles of Indochina. *Bulletin of the American Museum of Natural History*, 360, 1–138.
<https://doi.org/10.1206/360.1>
- Beddome, R.H. (1870) Descriptions of some new Lizards from the Madras Presidency, with 2 Plates. *Madras Monthly Journal of Medical Science*, 1, 30–35.
- Bleeker, P. (1860) Reptilien van Agam. *Natuurkundig Tijdschrift voor Nederlandsch Indie*, 20, 325–329.
- Boulenger, G.A. (1903) XLI.—Descriptions of new lizards in the collection of the British Museum. *Annals and Magazine of Natural History*, Series 7, 12, 429–435.
<https://doi.org/10.1080/00222930308678877>
- Cobos, A., Grismer, L.L., Wood Jr., P.L., Quah, E.S.H., Anuar, S. & Muin, M.A. (2016) Phylogenetic relationships of geckos of the *Hemiphyllodactylus harterti* group, a new species from Penang Island, Peninsular Malaysia, and a likely case of true cryptic speciation. *Zootaxa*, 4107 (3), 367–380.
<http://doi.org/10.11646/zootaxa.4107.3.5>
- Duméril, A.M.C. & Bibron, G. (1836) *Erpetologie Générale ou Histoire Naturelle Complete des Reptiles*. Vol. 3. Roret, Paris, 528 pp.
<https://doi.org/10.5962/bhl.title.45973>
- Erixon, P., Svennblad, B., Britton, T. & Oxelman, B. (2003) Reliability of Bayesian posterior probabilities and bootstrap frequencies in phylogenetics. *Systematic Biology*, 52, 665–673.
- Gamble, T., Greenbaum, E., Jackman, T.R., Russell, A.P. & Bauer, A.M. (2012) Repeated origin and loss of adhesive toepads in geckos. *PLoS ONE*, 7, e39429.

<https://doi.org/10.1371/journal.pone.0039429>

- Grismer, L.L., Wood Jr., P.L., Anuar, S., Muin, M.A., Quah, E.S.H., McGuire, J.A., Brown, R.M., Tri, N.V. & Pham, T.H. (2013) Integrative taxonomy uncovers high levels of cryptic species diversity in *Hemiphyllodactylus* Bleeker, 1860 (Squamata: Gekkonidae) and the description of a new species from Peninsular Malaysia. *Zoological Journal of the Linnean Society*, 169, 849–880.
<https://doi.org/10.1111/zoj.12064>
- Grismer, L.L., Riyanto, A., Iskandar, D.T. & McGuire, J.A. (2014a) A new species of *Hemiphyllodactylus* Bleeker, 1860 (Squamata: Gekkonidae) from Pulau Enggano, southwestern Sumatra, Indonesia. *Zootaxa*, 3821 (4), 485–495.
<https://doi.org/10.11646/zootaxa.3821.4.7>
- Grismer, L.L., Wood Jr., P.L. & Cota, M. (2014b) A new species of *Hemiphyllodactylus* Bleeker, 1860 (Squamata: Gekkonidae) from northwestern Thailand. *Zootaxa*, 3760 (1), 67–78.
<https://doi.org/10.11646/zootaxa.3760.1.4>
- Grismer, L.L., Wood Jr., P.L., Anuar, S., Quah, E.S.H., Muin, M.A., Chan, K.O., Sumarli, A.X. & Loredó, A.I. (2015) Repeated evolution of sympatric, palaeoendemic species in closely related, co?distributed lineages of *Hemiphyllodactylus* Bleeker, 1860 (Squamata: Gekkonidae) across a sky?island archipelago in Peninsular Malaysia. *Zoological Journal of the Linnean Society*, 174, 859–876.
<https://doi.org/10.1111/zoj.12254>
- Grismer, L.L., Wood Jr., P.L., Thura, M.K., Zin, T., Quah, E.S., Murdoch, M.L., Grismer, M.S., Li, A., Kyaw, H. & Lwin, N. (2017) Phylogenetic taxonomy of *Hemiphyllodactylus* Bleeker, 1860 (Squamata: Gekkonidae) with descriptions of three new species from Myanmar. *Journal of Natural History*, 52, 881–915.
<https://doi.org/10.1080/00222933.2017.1367045>
- Guo, W., Zhou, K., Yan, J. & Li, P. (2015) A new species of *Hemiphyllodactylus* Bleeker, 1860 (Squamata: Gekkonidae) from western Yunnan, China. *Zootaxa*, 3974 (3), 377–390.
<https://doi.org/10.11646/zootaxa.3974.3.5>
- Heinicke, M.P., Greenbaum, E., Jackman, T.R. & Bauer, A.M. (2011) Phylogeny of a trans-Wallacean radiation (Squamata, Gekkonidae, *Gehyra*) supports a single early colonization of Australia. *Zoologica Scripta*, 40, 584–602.
<https://doi.org/10.1111/j.1463-6409.2011.00495.x>
- Katoh, K. & Standley, D.M. (2013) MAFFT Multiple Sequence Alignment software version 7: improvements in performance and useability. *Molecular Biology and Evolution*, 30, 772–780.
<https://doi.org/10.1093/molbev/mst010>
- Köhler, G. (2012) *Color Catalogue for Field Biologists*. Herpeton, Offenbach, 300 color swatches, 49 pp.
- Lanfear, R., Calcott, B., Ho, S.Y.W. & 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/mss020>
- Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *2010 Gateway Computing Environments Workshop (GCE)*, New Orleans, Louisiana, 14 November 2010, 1–8.
<https://doi.org/10.1109/GCE.2010.5676129>
- Ngo, T. V., Grismer, L.L., Thai, P.H. & Wood Jr., P.L. (2014) A new species of *Hemiphyllodactylus* Bleeker, 1860 (Squamata: Gekkonidae) from Ba Na–Nui Chua Nature Reserve, Central Vietnam. *Zootaxa*, 3760 (4), 539–552.
<https://doi.org/10.11646/zootaxa.3760.4.3>
- Nguyen, T.Q., Lehmann, T., Le, M.D., Duong, H.T., Bonkowski, M. & Ziegler, T. (2013) A new species of *Hemiphyllodactylus* (Reptilia: Gekkonidae) from northern Vietnam. *Zootaxa*, 3736 (1), 89–98.
<https://doi.org/10.11646/zootaxa.3736.1.5>
- Nguyen, T.Q., Botov, A., Le, M.D., Nophaseud, L., Zug, G., Bonkowski, M. & Ziegler, T. (2014) A new species of *Hemiphyllodactylus* (Reptilia: Gekkonidae) from northern Laos. *Zootaxa*, 3827 (1), 45–56.
<https://doi.org/10.11646/zootaxa.3827.1.4>
- Rambaut A., Suchard, M.A., Xie, D. & Drummond, A.J. (2014) *Tracer: Version 1.6*. Available from: <http://tree.bio.ed.ac.uk/software/tracer/> (accessed 9 July 2018)
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model spaces. *Systematic Biology*, 61, 1–4.
<https://doi.org/10.1093/sysbio/sys029>
- Sukprasert, A., Sutthiwiset, S., Lauhachinda, V. & Taksintum, W. (2018) Two new species of *Hemiphyllodactylus* Bleeker (Squamata: Gekkonidae) from Thailand. *Zootaxa*, 4369 (3), 363–376.
<https://doi.org/10.11646/zootaxa.4369.3.4>
- Swofford, D.L. (2002) PAUP*: (Phylogenetic Analysis Using Parsimony* and other methods). Version 4.0b10. Sinauer Associates, Sunderland, Massachusetts, USA. Available from: <http://paup.phylosolutions.com> (accessed 9 July 2018)
- Yan, J., Lin, Y., Guo, W., Li, P. & Zhou, K. (2016) A new species of *Hemiphyllodactylus* Bleeker, 1860 (Squamata: Gekkonidae) from Guizhou, China. *Zootaxa*, 4117 (4), 543–554.
<https://doi.org/10.11646/zootaxa.4117.4.6>
- Zhou, K.-Y. & Liu, Y.-Z. (1981) Three new subspecies of *Hemiphyllodactylus yunnanensis* (Boulenger) from China

- (Lacertiformes: Gekkonidae). Ota, H. (translator). 1996. *In*: Zhou, K.-Y., Liu, Y.-Z. & Yang, G.-P. (Eds.), *Smithsonian Herpetological Information Service*, 110, pp. 2–6.
<https://doi.org/10.5479/si.23317515.110.1>
- Zug, G.R. (2010) Speciation and dispersal in a low diversity taxon: the slender geckos *Hemiphyllodactylus* (Reptilia, Gekkonidae). *Smithsonian Contributions to Zoology*, 631, 1–70.
<https://doi.org/10.5479/si.00810282.631>
- Zug, G.R., Watling, D., Alefaio, T., Alefaio, S. & Ludescher, C. (2003) A new gecko (Reptilia: Squamata: genus *Lepidodactylus*) from Tuvalu, south-central Pacific. *Proceedings of the Biological Society of Washington*, 116, 38–46.