

Four new Burmese species of *Hemiphyllodactylus* Bleeker (Squamata: Gekkonidae) from distantly related parapatric clades from the Shan Plateau and Salween Basin

L. LEE GRISMER^{1*}, PERRY L. WOOD, JR.², EVAN S. H. QUAH^{1,3}, MYINT KYAW THURA⁴, JAMIE R. OAKS², & AUNG LIN⁵

¹Herpetology Laboratory, Department of Biology, La Sierra University, 4500 Riverwalk Parkway, Riverside, California 92515, USA. lgrismer@lasierra.edu

²Department of Biological Sciences & Museum of Natural History, Auburn University, Auburn, Alabama 36849, USA Email: joaks@auburn.edu; perryleewoodjr@gmail.com

^{1,3}Institute of Tropical Biodiversity and Sustainable Development, Universiti Malaysia Terengganu, 21030 Kuala Nerus, Terengganu, Malaysia. Email: evanquah@umt.edu.my ⁴Myanmar Environment Sustainable Conservation, Yangon, Myanmar. Email: mgmyint.banca@gmail.com

^{4,5}Fauna and Flora International, No(35), 3rd Floor, Shan Gone Condo, Myay Ni Gone Market Street, Sanchaung Township, Yangon, Myanmar. Email: aung.lin@fauna-flora.org

Abstract

An integrative taxonomic analysis based on morphology, color pattern, and the mitochondrial gene ND2 recovered four new species of *Hemiphyllodactylus* Bleeker that are endemic to the Shan Plateau or Salween Basin in eastern Myanmar. *Hemiphyllodactylus ngwelwini* **sp. nov.** from the Shan Plateau is part of the earlier described “eastern Myanmar clade” renamed herein as the north lineage and *H. kyaiktiyoensis* **sp. nov.** and *H. pinlaungensis* **sp. nov.** of the Shan Plateau and *H. zwegabinensis* **sp. nov.** of the Salween Basin compose an entirely new Burmese clade herein referred to as the south lineage. Although the north and south lineages come within 46 km of one another on the Shan Plateau, they are not sister lineages but sequentially separated by two lineages from Yunnan, China and another from northwestern Thailand. *Hemiphyllodactylus zwegabinensis* **sp. nov.** is the first species of this genus to be recorded from the Salween Basin and is known only from a wind-blown cloud forest on the top of the insular, karstic mountain Zwegabin in Kayin State. All other Burmese species except for *H. typus*, are endemic to the various localities throughout the Shan Plateau. These four new species bring the total number of *Hemiphyllodactylus* in Myanmar to at least 10 which is certainly an extreme underestimate of the diversity of this genus given that we discover new species at every upland locality we survey.

Key words: Myanmar, Burma, gecko, integrative taxonomy, phylogeny, upland endemism

Introduction

The gekkonid genus *Hemiphyllodactylus* Bleeker contains 35 species that collectively range from southern India to the South Pacific (Zug 2010; Grismer *et al.* 2013, 2018; Agarwal *et al.* 2019). Despite this broad distribution, however, their relatively small size (SVL < 45 mm), low densities, localized distributions, and cryptic coloration, render them inconspicuous components of the microenvironments they inhabit. Additionally, with the exception of the wide-ranging parthenogenetic species *H. typus* Bleeker their distributions are generally circumscribed and restricted to tropical and sub-tropical montane regions or islands (Zhou *et al.* 1981; Zug 2010; Grismer *et al.* 2013, 2014a, b, 2017, 2018; Ngo *et al.* 2014; Nguyen *et al.* 2013, 2014; Sukprasert *et al.* 2018; Guo *et al.* 2015; Cobos *et al.* 2016; Yan *et al.* 2016; Sung *et al.* 2018; Agarwal *et al.* 2019; Elides *et al.* 2019). As noted by Grismer *et al.* (2017), these factors, coupled with data gathering inconsistencies among researchers, misidentifications, and the construction of classifications based on morphological similarity rather than common ancestry, resulted in a convoluted nomenclatural history (see Zug 2010 for review). The disentanglement of that history began with the construction of a phylogenetic taxonomy wherein lineage boundaries were inferred on the basis of a molecular genealogy and the

descriptions and diagnoses of those boundaries (*i.e.* species) were constructed using morphological data (Grismer *et al.* 2013). This baseline molecular phylogeny delimited two major monophyletic lineages: the *harterti* group of Peninsular Malaysia and the *typus* group composed of seven different clades that encompassed the entire range of the genus. Subsequent works continued to build upon that taxonomy with the descriptions of recently discovered species (Grismer *et al.* 2013, 2014a, b, 2017, 2018; Nguyen *et al.* 2013, 2014; Sukprasert *et al.* 2018; Guo *et al.* 2015; Cobos *et al.* 2016; Yan *et al.* 2016; Sung *et al.* 2018; Agarwal *et al.* 2019; Elides *et al.* 2019). Among these later works were the first descriptions of new species from Myanmar (Grismer *et al.* 2017, 2018). Smith (1935) was the first to report *Hemiphyllodactylus* from Myanmar based on *H. typus* (not reported in Zug 2010) and a single specimen (BM 1933.7.8.11) collected from “Upper Burma (Lashio)” [=Lashio, Shan State] reported under the name of *H. yunnanensis* (Boulenger 1903). The taxonomy of the latter was followed by subsequent regional works (*e.g.* Taylor 1963:788) and other than the broad ranging parthenogen *H. typus*, this single specimen remained the only record of *Hemiphyllodactylus* for Myanmar until Zug (2010:60)—still following Smith’s (1935) taxonomy—reported on four other specimens (USNM 57032–35) from Pyin Oo Lwin, Mandalay Region, 165 km southwest of Lashio. (Another specimen listed by Zug [2010] as being from Myanmar [USNM 310819], however, is from Kunming, China). Grismer *et al.* (2013) noted that the Pyin Oo Lwin population was not *H. yunnanensis* and described it as *H. uga* (Grismer *et al.* 2018) and placed it in the “eastern Myanmar” clade (*sec.* Grismer *et al.* 2017) with four other previously described species—all endemic to the Shan Plateau of eastern Myanmar (Grismer *et al.* 2018). The specific identity of BM 1933.7.8.11 from Lashio still remains in question.

Based on an integrative taxonomic analysis using morphology, color pattern, and the mitochondrial gene NADH dehydrogenase subunit 2 (ND2) and its flanking tRNA regions, we report here four new species of *Hemiphyllodactylus* from Myanmar, three from the Shan Plateau and another from the isolated karstic mountain Zwegabin—the latter representing the first record of this genus from the Salween Basin (Fig. 1). Surprisingly, only one of the new species from the Shan Plateau belongs to the eastern Myanmar clade that contains the five previously described Shan Plateau endemics (Grismer *et al.* 2017, 2018) whereas the other two new species along with the new species from Zwegabin Mountain, constitute an entirely new unrelated clade. Additionally, these clades come within 46 km of one another in the vicinity of Kalaw, Shan State on the Shan Plateau. The descriptions of these new species and their phylogenetic relationships are presented below.

Material and Methods

Phylogenetic analyses. We obtained 1448 base pairs of NADH dehydrogenase subunit 2 gene (ND2) sequence data and the flanking tRNAs from 149 specimens from GenBank (see Grismer *et al.* 2018) and 29 newly sequenced specimens (Table 1) for phylogenetic analyses. Eight outgroup taxa (*Cyrtodactylus loriae* (Boulenger), *Gekko gekko* Linnaeus, *Gekko swinhonis* Günther, *Gehyra fehmanni* (Taylor), *Gehyra mutilata* (Wiegmann), *Hemidactylus frenatus* Duméril & Bibron, *Lepidodactylus lugubris* (Duméril & Bibron), and *Perochirus ateles* (Duméril)) based on Heinicke *et al.* (2011) were used to root the tree. Total genomic DNA was isolated from liver or skeletal muscle specimens stored in 95% ethanol using a SPRI magnetic bead extraction protocol (<https://github.com/phyletica/lab-protocols/blob/master/extraction-spri.md>). ND2 was amplified using a double-stranded Polymerase Chain Reaction (PCR) under the following conditions: 1.0 µL genomic DNA (~10–30 ng), 1.0 µL light strand primer (10 µM), 1.0 µL heavy strand primer (10 µM), 1.0 µL dinucleotide pairs (1.0 µM), 2.0 µL 5x buffer (2.0 µM), 1.0 MgCl 10x buffer (1.0 µM), 0.10 µL Taq polymerase (5u/µL), and 7.4 µL H₂O. PCR reactions were executed on a Axygen Maxygene II gradient thermocycler under the following conditions: initial denaturation at 95°C for 2 min, followed by a second denaturation at 95°C for 35 s, annealing at 48°C for 35 s, followed by a cycle extension at 72°C for 35 s, for 31 cycles. All PCR products were visualized on a 1.0% agarose electrophoresis gel. Successful targeted PCR products were outsourced to GENEWIZ® for PCR purification, cycle sequencing, and sequencing. Primers used for amplification and sequencing are presented in Table 2.

We used both maximum likelihood (ML) and Bayesian inference (BI) to estimate the phylogenetic relationships among the sampled geckos in our sequence alignment. An ML phylogeny was estimated using the IQ-TREE webserver (Nguyen *et al.* 2015; Trifinopoulos *et al.* 2016) preceded by the selection of substitution models using the Bayesian Information Criterion (BIC) in ModelFinder (Kalyaanamoorthy *et al.* 2017), which supported HKY+F+Γ4 as the best fit model of evolution for the tRNAs and TVM+F+Γ4 for ND2 codon position one, TVM+F+I+Γ4 for

position 2, and GTR+F+I+Γ4 for position 3. One thousand bootstrap pseudoreplicates via the ultrafast bootstrap (UFB; Hoang *et al.* 2018) approximation algorithm were employed and nodes having ML UFB values of 95 and above were considered highly supported (Minh *et al.* 2013). A Bayesian inference (BI) analysis was carried out in MrBayes 3.2.3. (Ronquist *et al.* 2012) on XSEDE using the CIPRES Science Gateway (Cyberinfrastructure for Phylogenetic Research; Miller *et al.* 2010) employing default priors and models of evolution that most closely approximated those selected by the BIC and used in the ML analysis. Two independent Markov chain Monte Carlo (MCMC) analyses were performed each with four chains, three hot and one cold. We ran the MCMC simulation for 50 million generations, sampled every 5000 generations and discarded the first 10% of each run as burn-in. Convergence and stationarity of all parameters from both runs were checked in Tracer v1.6 (Rambaut *et al.* 2014) to ensure effective sample sizes (ESS) were above 200. Post-burn-in sampled trees from both runs were combined and a 50% majority-rule consensus tree was constructed. Nodes with Bayesian posterior probabilities (BPP) of 0.95 and above were considered highly supported (Huelsenbeck *et al.* 2001; Wilcox *et al.* 2002). After removing outgroup taxa, MEGA7 (Kumar *et al.* 2016) was used to calculate uncorrected pairwise sequence divergence among and within species from the north and south lineages (see below).

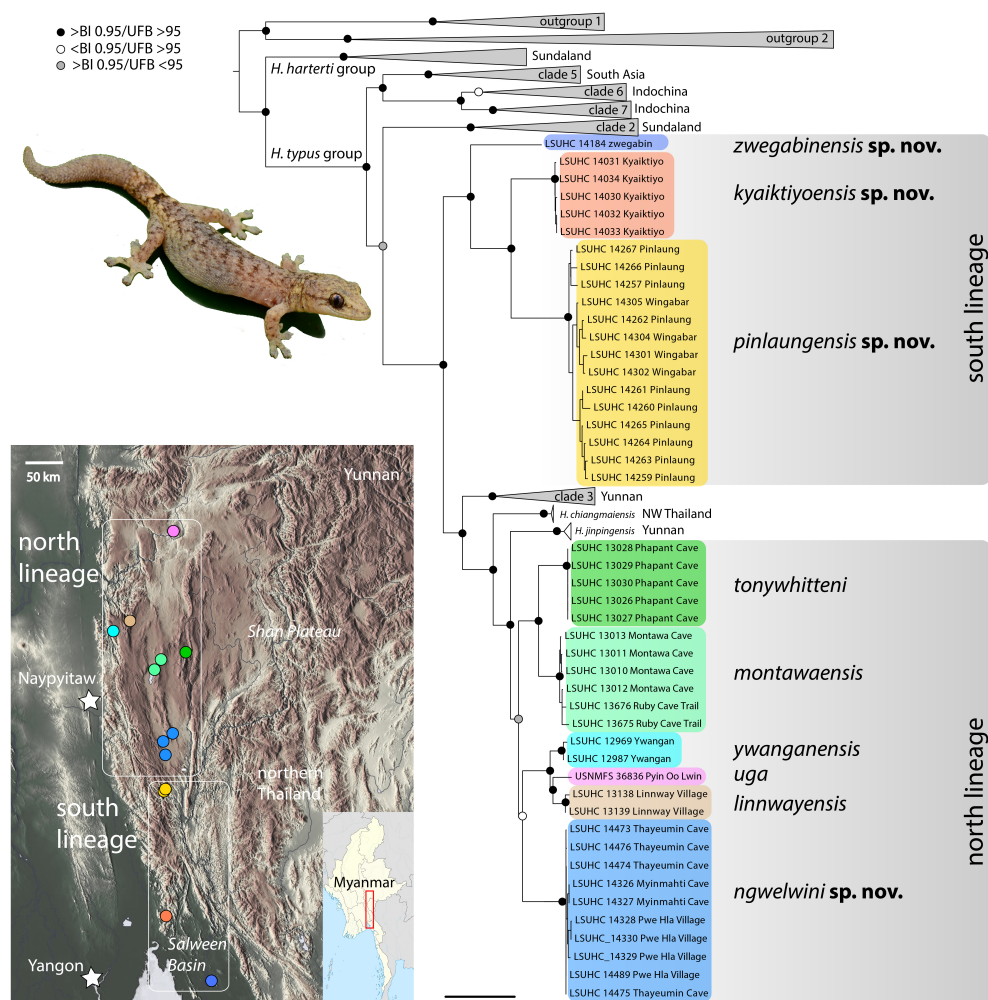


FIGURE 1. Maximum likelihood consensus tree of *Hemiphyllodactylus* clades with UFB and BI support value coding at the nodes. Topographical map showing the distribution of the species in the north and south lineages on the Shan Plateau and in the Salween Basin. Localities of *H. ngwelwini* sp. nov. from north to south are Pwe Hla Village, Thayeumin Cave, and Myintmahati Cave, Shan State.

Morphological analyses. For the descriptive work, color data were taken from digital images of most specimens prior to preservation. For purposes of comparison, the methodology involving the evaluation of mensural and meristic characters follows Zug (2010) and Grismer *et al.* (2018). Mensural data were taken with Mitutoyo dial calipers to the nearest 0.1 mm under a Nikon SMZ 1500 dissecting microscope on the left side of the body where appropriate. Data recovered were snout-vent length (SVL), taken from the tip of the snout to the vent; tail length (TL), taken from the vent to the tip of the tail—original or regenerated; trunk or axillia-groin length (AG), taken from the posterior margin of the forelimb at its insertion point on the body to the anterior margin of the hind limb at its insertion point on the body; head length (HL), measured from the posterior margin of the retroarticular process of the lower jaw to the tip of the snout; head width (HW), measured at the angle of the jaws; eye diameter (ED), the greatest horizontal diameter of the eyeball; snout-eye length (SN), measured from anteriormost margin of the eyeball to the tip of snout; nares-eye length (NE), measured from the anterior margin of the eyeball to the posterior margin of the external nares; and snout width (SW), measured between the external nares. Meristic character states evaluated were the number of scales contacting the nares (circumnasal scales, CN); the number of scales between the supranasals (=postrostrals or intersupranasals, IS); the number of scales contacting the internal edge of the infralabials and mental from the juncture of the second and third infralabials on both sides (CS); the number of supralabial (SL) and infralabial (IL) scales counted from the largest scale immediately posterior to the dorsal inflection of the posterior portion of the upper jaw to the rostral and mental scales, respectively; the number of longitudinal ventral scales at mid-body contained within one eyeball diameter (VS); the number of longitudinal dorsal scales at mid-body contained within one eyeball diameter (DS); the number of subdigital lamellae wider than long on the first finger (FL1) and toe (TL1); lamellar formulae determined as the number of U-shaped, subdigital lamellae (split and single) on the digital pads of digits II–V of the hands and feet; the total number of femoroprecloacal pores (*i.e.* the contiguous rows of femoral and precloacal pore-bearing scales; FP); and the number of cloacal spurs on each side of the hemipenial swelling or immediately posterior to the vent in females. Color pattern characters evaluated were the presence or absence of dark pigmentation in the gonadal tracts and caecum; configuration of the dark markings on the dorsum (dorsal pattern); presence or absence of a dark pre- and/ or postorbital stripe extending to at least the neck; the presence or absence of a linear series of white postorbital and dorsolateral spots on the trunk; and the presence or absence of light-colored, anteriorly projecting arms of the light-colored postsacral marking. Some of the information on character states and their distribution in other species was obtained from Guo *et al.* (2015), Cobos *et al.* (2016), Yan *et al.* (2016), and Sukpraset *et al.* (2018). LSUHC refers to the La Sierra University Herpetological Collection, La Sierra University, Riverside, California, USA. Other acronyms follow Sabaj (2016).

An ANOVA was conducted on characters with statistically similar variances (*i.e.* p values ≤ 0.05 in a Levene's test) to search for the presence of statistically significant mean differences ($p < 0.05$) across the data set. Characters bearing statistical differences were subjected to a TukeyHSD test to ascertain which population pairs differed significantly from each other for those particular characters. Boxplots were generated in order to visualize the range, mean, and degree of differences between pairs of species bearing statistically different mean values for sets of characters.

The morphospacial positions of each species relative to one another and the clustering of the sampled individuals were subsequently visualized using principal component analysis (PCA) from the ADEGENET package in R (Jombart *et al.* 2010) to determine if these parameters were consistent with the putative species boundaries delimited by the molecular phylogenetic analyses and defined by the univariate analyses (see below). PCA is a dimension reducing algorithm that decreases the complexity of a data set by finding a subset of input variables that contain the most relevant information (*i.e.* the greatest variance in the data) while de-emphasizing those characters that do not, thus increasing the overall accuracy of the model by eliminating noise and the potential of overfitting (Agarwal *et al.* 2007). The dimensionality of the data sets was further reduced *a priori* by using only characters that had significantly different mean values between at least one pair of species as determined by the ANOVA and subsequent TukeyHSD tests. PCA was implemented by the `prcomp()` command in R. It is an indiscriminate analysis used to explore morphospacial relationships among the sampled individuals (*i.e.* data points) to each other and how well they form uncoerced clusters that align themselves with the putative species boundaries delimited by the phylogenetic analyses. It is important to note that clusters of conspecific individuals were not pre-defined in the analysis but simply color-coded in the scatter plot in order to observe their positions and morphospacial relationships. Femoroprecloacal pore counts were excluded from the PCA due to their presence in only males. Characters used in the analysis of the north lineage were CS, IL, DS, and HL and those used in the analysis of the south lineage were

CS, IS, and SN. The mensural characters (HL and SN) were scaled to SVL in order to remove any potential effects of allometry using the following equation: $X_{adj} = X - \beta(SVL - SVL_{mean})$, where X_{adj} =adjusted value; X =measured value; β =unstandardized regression coefficient for each OTU; and SVL_{mean} =overall average SVL of all OTU's (Thorpe, 1975, 1983; Turan, 1999; Lleonart *et al.* 2000). Given that the data ranged from 1.0–16, all data were log-transformed prior to analysis in order to normalize their distribution to ensure characters with very large and very low values could not over-leverage the results owing to intervariable nonlinearity. The data were then scaled to their standard deviation to insure they were analyzed on the basis of correlation and not covariance. In order to determine which centroids (*i.e.* means) of the PCA clusters differed significantly from one another, a modified version of the broken stick model (Cangelosi & Goriely 2007) from the VEGAN package in R was implemented using the `bs()` command. This statistical model implements a stopping rule in order to determine the number of interpretable PCs (*i.e.* those that capture the most amount of variation in the data set with the least amount of noise) to retain prior to PC degeneration (*i.e.* the point after which subsequent PCs represent negligible structure in the data and amount mostly to noise). The model produces overlapping curves of eigenvalues and randomly generated broken stick values and proposes that the number of retained PCs should have eigenvalues higher than their corresponding random broken stick component values. For these analyses, PC1–PC3 of the north lineage which accounted for 80.6% of the variation and PC1 and PC2 of the south lineage which accounted for 83.2% of the variation were retained. Their factor loadings were subjected to a Welsh's ANOVA and a Games-Howell test to ascertain which pairs of species centroids differed significantly from one another.

Based on factor loadings from a PCA generated as part of the `dapc()` command in R, a discriminant analysis of principal components (DAPC) was performed on both the north and south lineage data sets. The DAPC places individuals from each predefined population into separate clusters (*i.e.* plots of points) bearing the smallest within-group variance that produce linear combinations of centroids having the greatest between-group variance (*i.e.* linear distance; Jombart *et al.* 2010). DAPC relies on scaled data from its PCA as a prior step to ensure that variables analyzed are not correlated and number fewer than the sample size. Dimension reduction of the DAPC prior to plotting, is accomplished by retaining the first set of PCs that account for approximately 90% of the variation in the data set (Jombart & Collins 2015) as determined from a scree plot generated as part of the analysis. Retaining too many PCs forces false structure to appear in the data while retaining too few, runs the risk of missing true structure (Cangelosi & Goriely 2007).

Species delimitation. The general lineage concept (GLC: de Queiroz 2007) adopted herein proposes that a species constitutes a population of organisms evolving independently from other such populations owing to a lack of gene flow. By “independently,” it is meant that new mutations arising in one species cannot spread readily into another species (Barracough *et al.* 2003; de Queiroz 2007). Integrative studies on the nature and origins of species are using an increasingly wider range of empirical data to delimit species boundaries (Coyne & Orr 1998; Fontaneto *et al.* 2007; Knowles & Carstens 2007; Leaché *et al.* 2009), rather than relying solely on morphology and traditional taxonomic methods. Under the GLC implemented herein, molecular phylogenies were used to recover monophyletic mitochondrial lineages of individuals (populations) in order to develop initial species-level hypotheses—the grouping stage of Hillis (2019). Discrete color pattern data and univariate and multivariate analyses of morphological data were then used to search for characters and morphospacial patterns bearing statistically significant differences that were consistent with the previous designations of the species-level hypotheses—the construction of boundaries representing the hypothesis-testing step of Hillis (2019)—thus providing independent diagnoses to complement the molecular analyses.

Results

The ML and BI analyses recovered trees with identical topologies that corroborate the phylogenetic relationships of the most recent analysis of Burmese *Hemiphyllodactylus* (Grismer *et al.* (2018). Additionally, they recovered a well-supported (BI 1.00/ML 92) north and strongly supported (1.00/100) south lineage that are not sister to one another (Fig. 1). The north lineage contains *H. linnwayensis*, *H. montawaensis*, *H. tonywhitteni*, *H. uga*, and *H. ywanganensis* as well as the strongly supported (1.00/100), newly discovered lineage composed of individuals from Thayeumin Cave, Myinmahti Cave, and Pwe Hla Village (= *H. ngwelwini* **sp. nov.** see below) that is most closely related to a clade composed of *H. ywanganensis* and the sister species *H. uga*, and *H. linnwayensis* (Fig. 1). The

south lineage is composed entirely of newly discovered populations and contain the Zwegabin Mountain individual (= *H. zwegabinensis* **sp. nov.** see below) which is sister to two strongly supported (1.00/100) lineages composed of individuals from Kyaiktiyo Mountain (= *H. kyaiktiyoensis* **sp. nov.** see below) and its sister lineage composed of individuals from Wingabar Cave and Pinlaung City (= *H. pinlaungensis* **sp. nov.** see below; Fig. 1).

The clustering of species in the PCA of the north lineage showed a modest degree of separation with *Hemiphylodactylus linnwayensis*, *H. montawaensis*, and *H. tonywhitteni* clustering separately from *H. ngwelwini* **sp. nov.**, *H. uga*, and *H. ywanganensis* along PC1 which accounted for 38.9% of the variation in the data set and loaded most heavily for CS (Fig. 2, Table 4). All species overlapped with one another along PC2 which accounted for 24.9% of the variation in the data set and loaded most heavily for IS and DS (Fig. 2, Table 4). ANOVA and subsequent TukeyHSD tests demonstrated that the centroid positions based on the combined factor loadings of PC1–3 between the *H. montawaensis* and *H. ywanganensis* were significantly different ($p = 0.024$). The DAPC—based on three retained eigenvalues accounting for 95.2% of the variation—showed better separation of *H. ngwelwini* **sp. nov.** from all other species with little to no overlap in the 95% ellipsoids. ANOVAs and subsequent TukeyHSD tests recovered significantly different mean values among various combinations of species across various combinations of characters (Fig. 2; see comparison sections).

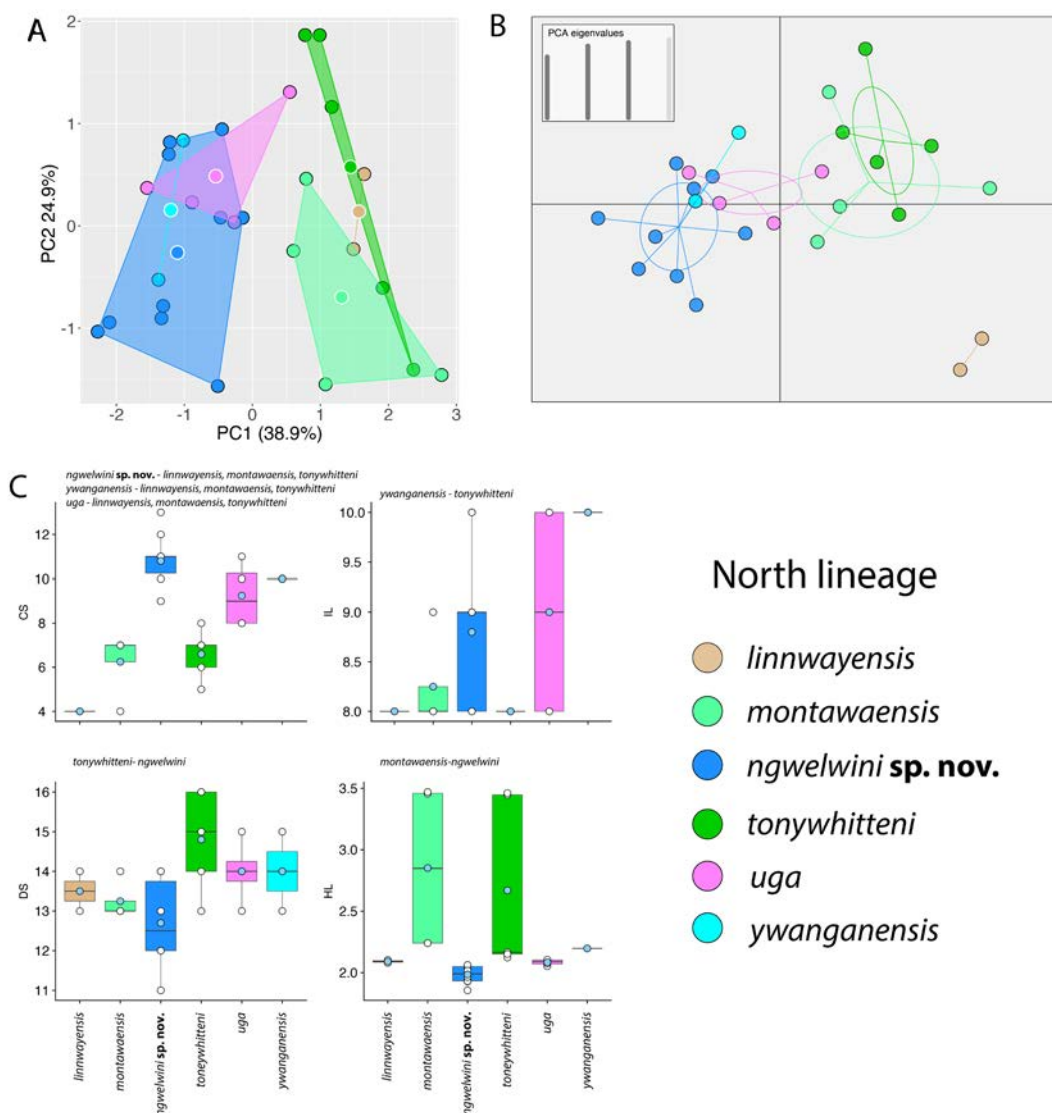


FIGURE 2. Graphics of statistical analyses among species of the north lineage. A. Principal component analysis (PCA). B. Discriminant function of principal components (DAPC). C. Boxplots of characters bearing significantly different mean values. Species pairs bearing significantly different mean values between them are listed above each plot. Abbreviations are in the Materials and methods.

The clustering of species in the PCA of the south lineage showed a modest degree of separation with the individual of *Hemiphyllodactylus zwegabinensis* **sp. nov.** showing little or no overlap with *H. kyaiktiyoensis* **sp. nov.** or *H. pinlaungensis* **sp. nov.** along PC1 which accounted for 52.9% of the variation in the data set and loaded most heavily for SN (Fig. 3, Table 5) and no overlap along PC2, which accounted for 30.1% of the variation in the data set and loaded most heavily for CS (Fig. 3, Table 5). *Hemiphyllodactylus pinlaungensis* **sp. nov.** and *H. kyaiktiyoensis* **sp. nov.** overlapped along both components but clustered fairly separately from one another. ANOVA and subsequent TukeyHSD tests demonstrated that the centroid positions based on the factor loadings of PC1–3 between the *Hemiphyllodactylus zwegabinensis* **sp. nov.** and both *H. pinlaungensis* **sp. nov.** and *H. kyaiktiyoensis* **sp. nov.** were significantly different ($p = 0.002$ and 0.022 , respectively). Separation of all species was much clearer in the DAPC—based on the retention of two eigenvalues accounting for 95.2% of the variation—in that none of the 95% confidence ellipsoids overlapped. ANOVAs and subsequent TukeyHSD tests recovered significantly different mean values between the *H. pinlaungensis* **sp. nov.** and *H. kyaiktiyoensis* **sp. nov.** in CS (11.2 vs 9.2, $p = 0.014$), IS (3.0 vs 3.6 $p = 0.014$), and SN (1.363 vs 1.242, $p = 0.018$) and (Fig. 3; Table 6).

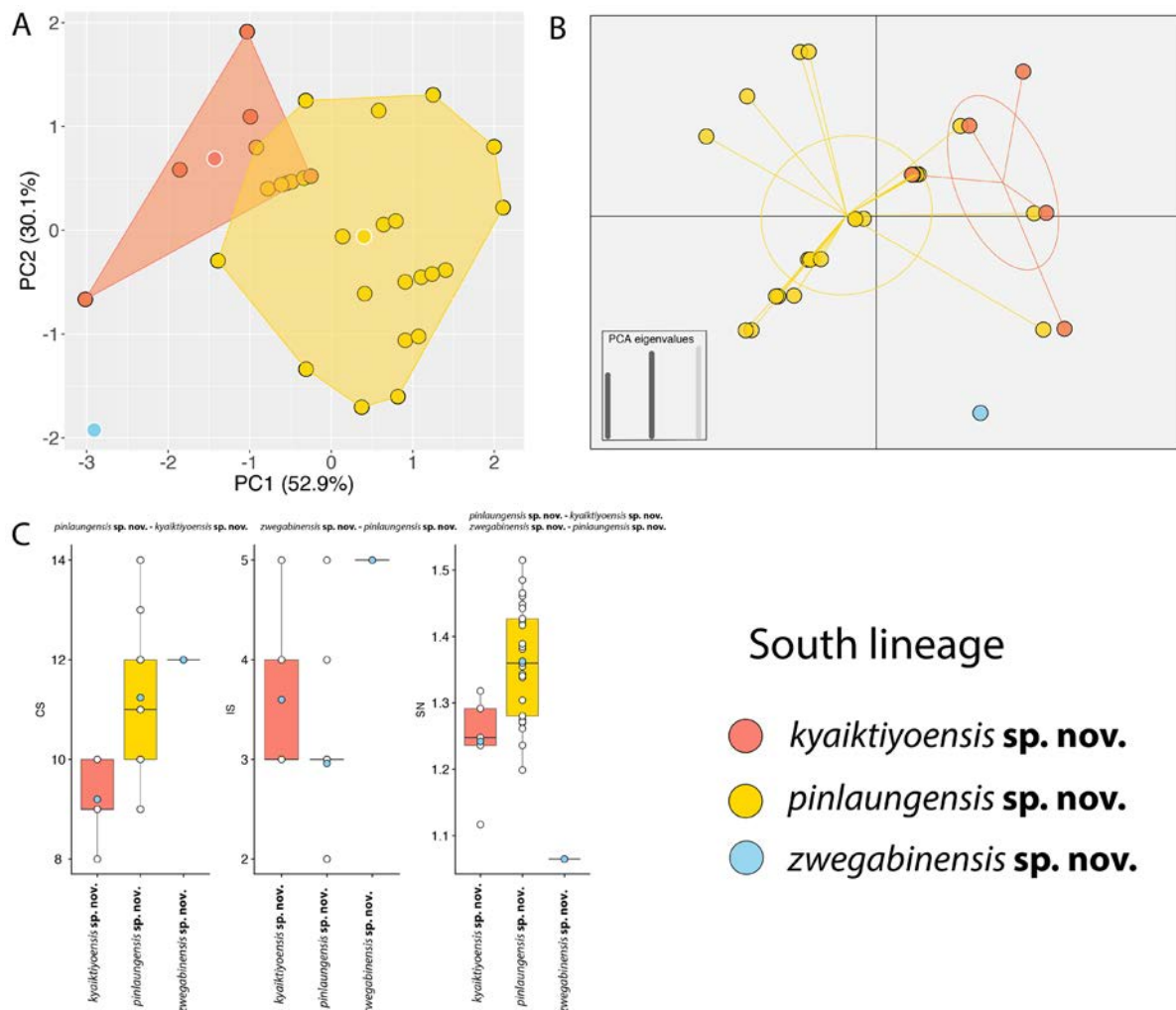


FIGURE 3. Graphics of statistical analyses among species of the south lineage. A. Principal component analysis (PCA). B. Discriminant function of principal components (DAPC). C. Boxplots of characters bearing significantly different mean values. Species pairs bearing significantly different mean values between them are listed above each plot. Abbreviations are in the Materials and methods.

Based on the corroborative lines of evidence among the phylogeny and the PCA, DAPC, and the ANOVAs, we consider *Hemiphyllodactylus ngwelwini* **sp. nov.** of the north lineage and *H. zwegabinensis* **sp. nov.**, *H. pinlaungensis* **sp. nov.**, and *H. kyaiktiyoensis* **sp. nov.** of the south lineage to be consistent with the GLC as outlined above and as such describe each below as new species.

TABLE 1. GenBank accession numbers for the newly recorded specimens *Hemiphyllodactylus* from the north and south lineage.

Taxon	Catalog no.	Locality	GenBank no.
<i>Hemiphyllodactylus kyaiktiyoensis</i> sp. nov.	LSUHC 14030	Mountain trail leading down the northwest facing flank from the Golden Rock Pagoda, Mon State, Myanmar (17.47840°N 97.10042°E WGS; 1057 m in elevation)	MT028146
<i>Hemiphyllodactylus kyaiktiyoensis</i> sp. nov.	LSUHC 14031	Mountain trail leading down the northwest facing flank from the Golden Rock Pagoda, Mon State, Myanmar (17.47840°N 97.10042°E WGS; 1057 m in elevation)	MT028147
<i>Hemiphyllodactylus kyaiktiyoensis</i> sp. nov.	LSUHC 14032	Mountain trail leading down the northwest facing flank from the Golden Rock Pagoda, Mon State, Myanmar (17.47840°N 97.10042°E WGS; 1057 m in elevation)	MT028148
<i>Hemiphyllodactylus kyaiktiyoensis</i> sp. nov.	LSUHC 14033	Mountain trail leading down the northwest facing flank from the Golden Rock Pagoda, Mon State, Myanmar (17.47840°N 97.10042°E WGS; 1057 m in elevation)	MT028149
<i>Hemiphyllodactylus kyaiktiyoensis</i> sp. nov.	LSUHC 14034	Mountain trail leading down the northwest facing flank upon which sits the Golden Rock Pagoda, Mon State, Myanmar (17.47840°N 97.10042°E WGS; 1057 m in elevation)	MT028150
<i>Hemiphyllodactylus ngwelwini</i> sp. nov.	LSUHC 14326	Myintmahati Cave, Shan State, Myanmar (20.59082°N 96.61198°E WGS; 1326 m in elevation)	MT028150
<i>Hemiphyllodactylus ngwelwini</i> sp. nov.	LSUHC 14327	Myintmahati Cave, Shan State, Myanmar (20.59082°N 96.61198°E WGS; 1326 m in elevation)	MT028152
<i>Hemiphyllodactylus ngwelwini</i> sp. nov.	LSUHC 14328	Pwe Hla Village, Shan State, Myanmar (20.84125°N 96.69030°E WGS; 1416 m in elevation)	MT028153
<i>Hemiphyllodactylus ngwelwini</i> sp. nov.	LSUHC 14329	Pwe Hla Village, Shan State, Myanmar (20.84125°N 96.69030°E WGS; 1416 m in elevation)	MT028154
<i>Hemiphyllodactylus ngwelwini</i> sp. nov.	LSUHC 14330	Pwe Hla Village, Shan State, Myanmar (20.84125°N 96.69030°E WGS; 1416 m in elevation)	MT028155
<i>Hemiphyllodactylus ngwelwini</i> sp. nov.	LSUHC 14489	Pwe Hla Village, Shan State, Myanmar (20.84125°N 96.69030°E WGS; 1416 m in elevation)	MT028160
<i>Hemiphyllodactylus ngwelwini</i> sp. nov.	LSUHC 14473	Thayeumin Cave, Shan State, Myanmar (20.72288°N 96.58994°E WGS; 1057 m in elevation).	MT028156
<i>Hemiphyllodactylus ngwelwini</i> sp. nov.	LSUHC 14474	Thayeumin Cave, Shan State, Myanmar (20.72288°N 96.58994°E WGS; 1057 m in elevation).	MT028157
<i>Hemiphyllodactylus ngwelwini</i> sp. nov.	LSUHC 14475	Thayeumin Cave, Shan State, Myanmar (20.72288°N 96.58994°E WGS; 1057 m in elevation).	MT028158
<i>Hemiphyllodactylus ngwelwini</i> sp. nov.	LSUHC 14476	Thayeumin Cave, Shan State, Myanmar (20.72288°N 96.58994°E WGS; 1057 m in elevation).	MT028159
<i>Hemiphyllodactylus pinlaungensis</i> sp. nov.	LSUHC 14257	Pinlaung City, Shan State, Myanmar (20.12869°N 96.78464°E WGS; 1498 m in elevation).	MT028161
<i>Hemiphyllodactylus pinlaungensis</i> sp. nov.	LSUHC 14259	Pinlaung City, Shan State, Myanmar (20.12869°N 96.78464°E WGS; 1498 m in elevation).	MT028162
<i>Hemiphyllodactylus pinlaungensis</i> sp. nov.	LSUHC 14260	Pinlaung City, Shan State, Myanmar (20.12869°N 96.78464°E WGS; 1498 m in elevation).	MT028163
<i>Hemiphyllodactylus pinlaungensis</i> sp. nov.	LSUHC 14261	Pinlaung City, Shan State, Myanmar (20.12869°N 96.78464°E WGS; 1498 m in elevation).	MT028164
<i>Hemiphyllodactylus pinlaungensis</i> sp. nov.	LSUHC 14262	Pinlaung City, Shan State, Myanmar (20.12869°N 96.78464°E WGS; 1498 m in elevation).	MT028165

....Continued next page

TABLE 1. (Continued)			
Taxon	Catalog no.	Locality	GenBank no.
<i>Hemiphyllodactylus pinlaungensis</i> sp. nov.	LSUHC 14263	Pinlaung City, Shan State, Myanmar (20.12869°N 96.78464°E WGS; 1498 m in elevation).	MT028166
<i>Hemiphyllodactylus pinlaungensis</i> sp. nov.	LSUHC 14264	Pinlaung City, Shan State, Myanmar (20.12869°N 96.78464°E WGS; 1498 m in elevation).	MT028167
<i>Hemiphyllodactylus pinlaungensis</i> sp. nov.	LSUHC 14265	Pinlaung City, Shan State, Myanmar (20.12869°N 96.78464°E WGS; 1498 m in elevation).	MT028168
<i>Hemiphyllodactylus pinlaungensis</i> sp. nov.	LSUHC 14266	Pinlaung City, Shan State, Myanmar (20.12869°N 96.78464°E WGS; 1498 m in elevation).	MT028169
<i>Hemiphyllodactylus pinlaungensis</i> sp. nov.	LSUHC 14267	Pinlaung City, Shan State, Myanmar (20.12869°N 96.78464°E WGS; 1498 m in elevation).	MT028170
<i>Hemiphyllodactylus pinlaungensis</i> sp. nov.	LSUHC 14301	Wingabar Cave approximately 7 km southwest of Pinlaung City, Shan State, Myanmar (20.06936°N 96.76988°E WGS; 1464 m in elevation)	MT028171
<i>Hemiphyllodactylus pinlaungensis</i> sp. nov.	LSUHC 14302	Wingabar Cave approximately 7 km southwest of Pinlaung City, Shan State, Myanmar (20.06936°N 96.76988°E WGS; 1464 m in elevation)	MT028172
<i>Hemiphyllodactylus pinlaungensis</i> sp. nov.	LSUHC 14305	Wingabar Cave approximately 7 km southwest of Pinlaung City, Shan State, Myanmar (20.06936°N 96.76988°E WGS; 1464 m in elevation)	MT028173
<i>Hemiphyllodactylus zwegabinensis</i> sp. nov.	LSUHC 14184	top of Zwegabin Mountain, Kayin State, Myanmar (16.82407°N 97.66810°E WGS; 710 m in elevation).	MT028174

TABLE 2. A list of primers used for PCR amplification and sequencing reaction. For specific amplification conditions see materials and methods.

Primer name	Primer citation		Sequence
L4437b	(Macey <i>et al.</i> 1997)	External	5'-AAGCAGTTGGGCCCATACC-3'
CyrtintF1	(Siler <i>et al.</i> 2010)	Internal	5'-TAGCCYTCTCYTCYATYGCCC-3'
CyrtintR1	(Siler <i>et al.</i> 2010)	Internal	5'-ATTGTKAGDGTRGCGYAGGSTKGG-3'
H5934	(Macey <i>et al.</i> 1997)	External	5'-AGRGTGCCAATGTCTTTGTGRTT-3'

TABLE 3. Summary statistics of meristic and scaled mensural characters among species of the north lineage.

	<i>ngwelwini</i> sp. nov.	<i>montawaensis</i>	<i>tonywhitteni</i>	<i>linnwayensis</i>	<i>uga</i>	<i>ywanganensis</i>
chin scales (CS)						
range	9–13	4–7	5–8	4–6	8–11	10
mean (±sd)	10.8 (±1.23)	6.3 (±1.50)	6.6 (±1.14)	5.0 (±1.00)	9.3 (±1.5)	10.0 (±0.00)
n	10	4	5	2	4	2
circumnasal scales (CN)						
range	5	4–6	3–5	5	5	5
mean (±sd)	5.0 (±0.00)	5.0 (±0.82)	4.6 (±0.89)	5.0 (±0.00)	5.0 (±0.00)	5.0 (±0.00)
n	10	4	5	2	4	2

....Continued next page

TABLE 3. (Continued)

	<i>ngwelwini</i> sp. nov.	<i>montawaensis</i>	<i>tonywhitteni</i>	<i>linnwayensis</i>	<i>uga</i>	<i>ywanganensis</i>
intersupranasals (IS)						
range	1–3	1–4	2–4	2	2 or 3	2 or 3
mean (\pm sd)	2.0 (\pm 0.47)	1.5 (\pm 0.58)	2.8 (\pm 0.84)	2.0 (\pm 0.00)	2.3 (\pm 0.58)	2.5 (\pm 0.71)
n	10	4	5	2	4	2
supralabial scales (SL)						
range	8–11	8–10	8 or 9	9 or 10	9 or 10	9 or 10
mean (\pm sd)	9.1 (\pm 0.88)	8.5 (\pm 1.00)	8.6 (\pm 0.55)	9.5 (\pm 0.71)	9.5 (\pm 0.58)	9.5 (\pm 0.71)
n	10	4	5	2	4	2
infralabial scales (IL)						
range	8–10	8 or 9	8	8	8–10	10
mean (\pm sd)	8.8 (\pm 0.79)	8.25 (\pm 0.50)	8.0 (\pm 0.00)	8.0 (\pm 0.00)	9.0 (\pm 1.15)	10.0 (\pm 0.00)
n	10	4	5	2	4	2
dorsal scales (DS)						
range	11–14	13 or 14	13–16	13 or 14	13–15	13–15
mean (\pm sd)	12.7 (\pm 1.04)	13.3 (\pm 0.50)	14.8 (\pm 1.30)	13.5 (\pm 0.71)	14.0 (\pm 0.82)	14.0 (\pm 1.41)
n	10	4	5	2	4	2
ventral scales (VS)						
range	7 or 8	7 or 8	7–9	8	6–8	7 or 8
mean (\pm sd)	7.7 (\pm 0.48)	7.3 (0.50)	8.0 (\pm 0.71)	8.0 (\pm 0.00)	7.3 (\pm 0.96)	7.5 (\pm 0.71)
n	10	4	5	4	4	2
first finger lamellae (FL1)						
range	4	3 or 4	3	3 or 4	2 or 3	3
mean (\pm sd)	4.0 (\pm 0.00)	3.8 (\pm 0.50)	3.0 (\pm 0.00)	3.5 (\pm 0.71)	2.3 (\pm 0.50)	3.0 (\pm 0.00)
n	10	4	5	2	4	2
first toe lamellae (TL1)						
range	4	3 or 4	3 or 4	4 or 5	2 or 3	2 or 3
mean (\pm sd)	4.0 (\pm 0.00)	3.3 (\pm 0.50)	3.6 (\pm 0.55)	4.5 (\pm 0.71)	2.3 (\pm 0.50)	2.3 (\pm 0.71)
n	10	4	5	2	4	2
femoroprecloacal pores (FP)						
range	15–22	19–21	20–26	/	18–22	26
mean (\pm sd)	19.3 (\pm 3.79)	21.0 (\pm 0.50)	22.0 (\pm 2.83)	/	20.0 (\pm 2.83)	26.0 (\pm 0.0)
n	3	2	4	/	2	1
scaled trunk length (AG)						
range	2.447–2.821	2.693–3.618	2.698–3.558	2.649–2.679	2.750– 2.826	2.708
mean (\pm sd)	2.617 (\pm 0.106)	3.138 (\pm 0.515)	3.062 (\pm 0.44)	2.664 (\pm 0.021)	2.803 (\pm 0.036)	2.708 (\pm 0.000)
n	10	4	5	2	4	2

....Continued next page

TABLE 3. (Continued)

	<i>ngwelwini</i> sp. nov.	<i>montawaensis</i>	<i>tonywhitteni</i>	<i>linnwayensis</i>	<i>uga</i>	<i>ywanganensis</i>
scaled head length (HL)						
range	1.856–2.063	2.240–3.470	2.123–3.461	2.079— 2.103	2.053– 2.105	2.197
mean (±sd)	1.985 (±0.071)	2.852 (±0.706)	2.67 (±0.716)	2.091 (±0.017)	2.084 (±0.025)	2.197 (±0.000)
n	10	4	4	2	4	2
scaled snout to eye length (SN)						
range	1.134–1.315	1.309–3.528	1.211–3.445	1.192–1.296	1.181– 1.273	1.224
mean (±sd)	1.223 (±0.063)	2.396 (±1.256)	2.133 (±1.189)	1.244 (±0.073)	1.238 (±0.042)	1.224 (±0.000)
n	10	4	4	2	4	2

TABLE 4. Summary statistics and principal component analysis scores for the species of *Hemiphyllodactylus* of the north lineage. Abbreviations are listed in the Materials and methods.

	PC1	PC2	PC3	PC4	PC5
Standard deviation	1.39540	1.11478	0.91662	0.80103	0.57296
Proportion of variance	0.38943	0.24855	0.16804	0.12833	0.06566
Cumulative proportion	0.38943	0.63798	0.80602	0.93434	1.00000
Eigenvalue	1.94714	1.24274	0.84019	0.64164	0.32828
CS	-0.63744	0.03820	0.13224	-0.10777	0.75040
IL	-0.53523	0.04589	-0.48135	-0.52820	-0.44803
IS	-0.11789	-0.69049	-0.53340	0.46437	0.09571
DS	0.19824	-0.69047	0.32929	-0.61006	0.05790
HL	0.50398	0.20713	-0.59822	-0.34868	0.47292

TABLE 5. Summary statistics and principal component analysis scores for the species of *Hemiphyllodactylus* of the south lineage. Abbreviations are listed in the Materials and methods.

	PC1	PC2	PC3
Standard deviation	1.25930	0.95330	0.71091
Proportion of variance	0.52861	0.30292	0.16847
Cumulative proportion	0.52861	0.83153	1.00000
Eigenvalue	1.58583	0.90877	0.50540
CS	0.38925	-0.90572	-0.16781
IS	-0.63205	-0.39515	0.66661
SN	0.67007	0.15341	0.72627

TABLE 6. Summary statistics of meristic, scaled mensural, and diagnostic color pattern characters among species of the south lineage.

	<i>pinlaungensis</i> sp. nov.	<i>kyaiktiyoensis</i> sp. nov.	<i>zwegabinensis</i> sp. nov.
chin scales (CS)			
range	9–14	8–10	12

....Continued next page

TABLE 6. (Continued)

	<i>pinlaungensis</i> sp. nov.	<i>kyaiaktiyoensis</i> sp. nov.	<i>zwegabinensis</i> sp. nov.
chin scales (CS)			
mean (\pm sd)	11.2 (\pm 1.45)	9.2 (\pm 0.83)	12.0 (\pm 0.00)
n	25	5	1
circumnasal scales (CN)			
range	5 or 6	5	5
mean (\pm sd)	5.0 (\pm 0.20)	5.0 (\pm 0.00)	5.0 (\pm 0.00)
n	25	5	1
intersupranasals (IS)			
range	2–5	3–5	5
mean (\pm sd)	3.0 (\pm 0.61)	3.6 (\pm 0.89)	5.0 (\pm 0.00)
n	25	5	1
supralabial scales (SL)			
range	7–10	7–10	9
mean (\pm sd)	9.1 (\pm 0.91)	8.8 (\pm 1.30)	9.0 (\pm 0.00)
n	25	5	1
infralabial scales (IL)			
range	8–11	8 or 9	10
mean (\pm sd)	9.4 (\pm 0.77)	8.6 (\pm 0.54)	10 (\pm 0.00)
n	25	5	1
dorsal scales (DS)			
range	12–19	12–16	16
mean (\pm sd)	15.0 (\pm 1.98)	14.0 (\pm 0.1.87)	16.0 (\pm 0.00)
n	25	5	1
ventral scales (VS)			
range	7–12	8 or 9	7
mean (\pm sd)	8.2 (\pm 0.65)	8.2 (\pm 0.45)	7.0 (\pm 0.00)
n	25	5	1
first finger lamellae (FL1)			
range	3 or 4	4	4
mean (\pm sd)	3.3 (\pm 0.46)	4.0 (\pm 0.00)	4.0 (\pm 0.00)
n	25	5	1
first toe lamellae (TL1)			
range	3 or 4	4 or 5	4
mean (\pm sd)	3.3 (\pm 0.48)	4.2 (\pm 0.50)	4.0 (\pm 0.00)
n	25	5	1
femoroprecloacal pores (FP)			
range	17–24	/	/
mean (\pm sd)	20.9 (\pm 2.39)	/	/
n	11	/	/
scaled trunk length (AG)			
range	2.707–3.497	2.903–2.955	2.912

....Continued next page

TABLE 6. (Continued)

	<i>pinlaungensis</i> sp. nov.	<i>kyaiktiyoensis</i> sp. nov.	<i>zwegabinensis</i> sp. nov.
mean (\pm sd)	2.958 (\pm 0.159)	2.928 (\pm 0.019)	2.912 (\pm 0.000)
n	25	25	1
scaled head length (HL)			
range	2.029–2.296	2.007–2.131	1.980
mean (\pm sd)	2.154 (\pm 0.086)	2.067 (\pm 0.047)	1.980 (\pm 0.000)
n	15	25	1
scaled snout to eye length (SN)			
range	1.199–1.515	1.117–1.318	1.065
mean (\pm sd)	1.363 (\pm 0.085)	1.242 (\pm 0.077)	1.065 (\pm 0.000)
n	25	25	1
dark ventrolateral stripe on trunk	yes	yes	no
dark paravertebral markings on trunk	yes	no	yes

Taxonomy

Hemiphyllodactylus ngwelwini sp. nov.

Ngwe Lwin's Slender Gecko

(Figs. 4, 5)

Holotype. Adult male (LSUHC 14473) collected on 2 August 2019 at 1955 hrs by L. Lee Grismer, Perry L. Wood Jr., Myint Kyaw Thura, and Aung Lin at the Thayeumin Cave, State, Myanmar (20.72288°N 96.58994°E WGS; 1057 m in elevation).

Paratypes. Females and juvenile LSUHC 14474–76 bear the same collection data as the holotype. Females LSUHC 14328–29 and male 14330 were collected from Pwe Hla Village, Shan State (20.84125°N 96.69030°E WGS; 1416 m in elevation) by L. Lee Grismer, Perry L. Wood, Jr, Evan S. H. Quah, Myint Kyaw Thura, Jamie R. Oaks, and Aung Lin on 14 November 2018 and female LSUHC 14489 bears the same collecting locality but was collected by L. Lee Grismer, Perry L. Wood Jr., Myint Kyaw Thura, and Aung Lin on 3 August 2019. Female LSUHC 14326 and male 14327 from the Myintmahati Cave, Shan State (20.59082°N 96.61198°E WGS; 1326 m in elevation) were collected by L. Lee Grismer, Perry L. Wood, Jr, Evan S. H. Quah, Myint Kyaw Thura, Jamie R. Oaks, and Aung Lin on 15 November 2018.

Diagnosis. *Hemiphyllodactylus ngwelwini* sp. nov. can be separated from all other species of *Hemiphyllodactylus* by possessing the unique combination of having a maximum SVL of 40.2 mm; 9–13 chin scales; enlarged postmentals; five circumnasal scales; 1–3 intersupranasals (=postrostrals); 8–11 supralabials; 8–10 infralabials; 11–14 longitudinally arranged dorsal scales at midbody contained within one eye diameter and seven or eight ventral scales; four subdigital lamellae on the first finger and toe; 15–22 continuous, pore-bearing, femoroprecloacal scales in males; no plate-like subcaudal scales; adult females variably yellow; a dark postorbital stripe extending to at least base of neck; dorsolateral light-colored spots usually present on trunk; no dark, dorsolateral or ventrolateral stripe on trunk; dark zig-zag of paravertebral markings on trunk variable; light-colored postsacral marking variably bearing anteriorly projecting arms; and caecum and gonads unpigmented. These characters are scored across all Burmese species in Tables 3 and 6 and from all other species of *Hemiphyllodactylus* from southern China and western Thailand (clades 3 and 4 in Grismer *et al.* (2017:Table 3)).

Description of holotype. Adult male, SVL 34.4 mm; head triangular in dorsal profile, depressed, distinct from neck; lores flat; rostrum moderate in length (SN/SVL 0.10); prefrontal region weakly concave; canthus rostralis smoothly rounded, barely discernible; snout moderate, rounded in dorsal profile; eye large; ear opening elliptical, small; eye to ear distance greater than diameter of eye; rostral wider than high, bordered posteriorly by large supra-



FIGURE 4. Color pattern variation in *Hemiphyllodactylus ngwelwini* **sp. nov.** from Shan State, Myanmar. A. Adult male holotype (LSUHC 14473) from Thayeumin Cave. Photo by L. Lee Grismer. B. Adult female paratype (LSUHC 14326) from Myintmahati Cave. Photo by Evan S. H. Quah. C. Adult male paratype (LSUHC 14327) from Myintmahati Cave. Photo by Evan S. H. Quah. D. Adult female paratype (LSUHC 14328) from Pwe Hla Village. Photo by Evan S. H. Quah. E. Juvenile paratype (LSUHC 14329) from Pwe Hla Village. Photo by Evan S. H. Quah.



FIGURE 5. Type series of *Hemiphyllodactylus ngwelwini* **sp. nov.** from Shan State, Myanmar. Top row: adult male holotype (LSUHC 14473), adult female paratypes (LSUHC 14474–75), and juvenile (LSUHC 14476) from Thayeumin Cave. Middle row: adult female paratypes (LSUHC 14328, 14330, 14489) and juvenile female paratype (LSUHC 14329) from Pwe Hla Village. Bottom row: Adult female paratype (LSUHC 14326) and adult male paratype (LSUHC 14327) from Myintmahati Cave

nasals; two differently sized intersupranasals (=postnasals); external nares bordered anteriorly by rostral, dorsally by supranasal, posteriorly by two postnasals, ventrally by first supralabial (=circumnasals); eight (R, L) rectangular supralabials tapering to below posterior margin of eye; 9, 10 (R, L) rectangular infralabials tapering to below posterior margin of eye; scales of rostrum, lores, top of head, and occiput small, granular, those of rostrum largest and slightly raised; dorsal superciliaries flat, mostly square, subimbricate, largest anteriorly; mental triangular, bordered laterally by first infralabials, posteriorly by two large nearly square postmentals; each postmental in contact with first infralabial, bordered laterally by single slightly enlarged sublabial; 10 chin scales; gular scales small, subimbricate, grading posteriorly into slightly larger, subimbricate throat and even larger pectoral scales which grade into slightly larger, subimbricate ventrals.

Body somewhat elongate (AG/SVL 0.49), dorsoventrally compressed; ventrolateral folds absent; dorsal scales small, granular, 12 dorsal scales at midbody contained within one eye diameter; ventral scales flat, subimbricate much larger than dorsal scales, eight ventral scales contained within one eye diameter; precloacal scales slightly

larger than abdominal scales; pore-bearing precloacal scales continuous with pore-bearing femoral scales, totaling 21 pore-bearing femoroprecloacal scales; single enlarged tubercle on anterior margin of hemipenial swelling; forelimbs short, robust in stature, covered with flat, subimbricate scales dorsally and ventrally; palmar scales flat, subimbricate; all digits except digit I well-developed; digit I vestigial, clawless; distal subdigital lamellae of digits II–V undivided, angular and U-shaped, lamellae proximal to these transversely expanded; distal lamellar formula of digits II–V 3-3-3-3 (R, L); four transversely expanded lamellae on digit I; claws on digits II–V well developed, unsheathed; distal portions of digits strongly curved, terminal joint free, arising from central portion of lamellar pad; hind limbs short, more robust than forelimbs, covered with flat, juxtaposed scales dorsally and larger, flat subimbricate scales ventrally; plantar scales low, flat, subimbricate; all digits except digit I well-developed; digit I vestigial, clawless; distal subdigital lamellae of digits II–V undivided, angular and U-shaped, lamellae proximal to these transversely expanded; distal lamellar formula of digits II–V 3-3-3-3 (R, L); four transversely expanded lamellae on digit I; claws on digits II–V well-developed, unsheathed; distal portions of digits strongly curved, terminal joint free, arising from central portion of lamellar pad; caudal scales not occurring in whorls; dorsal caudal scales of original tail larger than dorsal body scales, flat, subcycloid, subimbricate; subcaudals slightly larger than dorsal caudals, not plate-like. Raw and ratiometric mensural data are presented in Table 7.

TABLE 7. Meristic, mensural (in mm), and color pattern data from the type series of *Hemiphyllodactylus ngwelwini* sp. nov. R = right, L = left, m = adult male, f = adult female, j = juvenile, / = data unobtainable or not applicable, r = regenerated.

	Theyumin				Myintmahati		Pwe Hla			
	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC
	14473	14475	14474	14476	14326	14327	14489	14330	14329	14328
	holotype	paratype	paratype	paratype	paratype	paratype	paratype	paratype	paratype	paratype
sex and age class	m	f	f	j	f	m	f	m	j	f
chin scales (CS)	10	11	11	11	11	11	13	9	12	9
postmentals distinctly enlarged	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
circumnasal scales (CN)	5	5	5	5	5	5	5	5	5	5
intersupranasals (IS)	2	2	1	2	2	3	2	2	2	2
supralabial scales (SL)	8	9	9	8	11	10	9	9	9	9
infralabial scales (IL)	9	9	8	8	10	9	10	8	9	8
dorsal scales (DS)	12	12	14	13	12	14	12	11	14	13
ventral scales (VS)	8	8	8	8	8	8	7	7	7	8
lamellar formula on hand	3333	3343	3333	3444	3333	3333	3333	3333	3333	3333
lamellar formula on foot	3333	4444	3333	3333	3333	3443	3333	3333	3333	3444
subdigital lamellae on first finger	4	4	4	4	4	4	4	4	4	4
subdigital lamellae on first toe	4	4	4	4	4	4	4	4	4	4
precloacal and femoral pore series continuous	yes	/	/	/	/	yes	/	yes	/	/
femoroprecloacal pores	21	/	/	/	/	15	/	22	/	/
cloacal spurs on each side	1	1	1	1	1	1	1	1	1	1
subcaudals enlarged, plate-like	no	no	no	/	no	no	no	no	no	no

....Continued next page

TABLE 7. (Continued)

	Theyumin				Myintmahati		Pwe Hla			
	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC
	14473	14475	14474	14476	14326	14327	14489	14330	14329	14328
	holotype	paratype	paratype	paratype	paratype	paratype	paratype	paratype	paratype	paratype
dark postorbital stripe	yes	yes	yes	yes	yes	/	yes	yes	yes	yes
adult females yellow	/	no	no	no	yes	yes	yes	/	/	yes
dorsolateral light-colored spots on trunk	yes	yes	yes	yes	variable	variable	yes	yes	yes	yes
dark dorsolateral stripe on trunk	no	no	no	no	no	no	no	no	no	no
dark ventrolateral stripe on trunk	no	no	no	no	no	no	no	no	no	no
wide vertebral area generally unicolor	no	no	no	no	no	no	no	no	no	no
dark dorsal transverse blotches/bands	no	no	no	no	no	no	no	no	no	no
dark reticulate pattern on dorsum	no	no	no	no	no	no	no	no	no	no
dark transverse zig-zag pattern on dorsum	no	no	no	no	yes	yes	no	no	no	no
dark paravertebral markings on trunk	yes	yes	yes	yes	no	no	yes	yes	yes	yes
postsacral marking bearing light-colored anteriorly projecting arms	no	no	no	no	yes	yes	yes	yes	yes	yes
caecum pigmented	no	no	no	no	no	no	no	no	no	no
gonads pigmented	no	no	no	no	no	no	no	no	no	no
SVL	34.4	38.4	38.6	26.4	36.9	33.0	39.8	33.0	28.2	40.2
AG	16.7	18.5	19.9	5.8	18.9	16.2	21.4	14.8	12.7	20.4
HL	7.2	8.8	7.8	6.8	7.6	6.4	8.8	7.9	6.4	8.7
SN	3.3	3.9	4.2	2.8	3.7	3.2	4.1	3.5	3.3	4.5
HW	6.3	7.1	6.9	5.5	6.7	6.0	7.6	6.8	5.3	8.2
NE	2.5	3.0	3.1	1.9	2.7	2.6	3.2	2.4	2.4	3.2
ED	1.9	2.0	2.0	1.6	2.0	2.0	2.1	2.0	1.5	2.3
SW	1.3	1.3	1.1	1.0	1.2	1.1	1.4	1.3	0.9	1.5
AG/SVL	0.49	0.48	0.52	0.22	0.51	0.49	0.54	0.45	0.45	0.51
HL/SVL	0.21	0.23	0.20	0.92	0.21	0.20	0.22	0.24	0.23	0.22
SN/SVL	0.10	0.10	0.11	0.10	0.10	0.10	0.10	0.10	0.12	0.11
HW/SVL	0.18	0.19	0.18	0.21	0.18	0.18	0.19	0.21	0.19	0.20
NE/HL	0.35	0.34	0.39	0.27	0.36	0.40	0.37	0.31	0.38	0.37
ED/HL	0.26	0.22	0.26	0.24	0.26	0.31	0.24	0.25	0.23	0.26
SW/HL	0.18	0.14	0.14	0.15	0.15	0.17	0.16	0.17	0.14	0.17

Coloration in life (Fig. 4). All *Hemiphyllodactylus* are capable of considerable change in the intensity and boldness of their coloration and pattern. The description below was taken when the holotype was photographed the morning after capture, approximately 12 hours following the time of collection while during its light-phase. Ground color of top of head, body, and limbs, gray and densely mottled with darker markings; top of head overlain with dark, semi-reticulate pattern; broad, dark, diffuse pre- and postorbital stripe extends from the external nares, through eye to just posterior of forelimb insertion on the body; pairs of diffuse, dark, paravertebral markings counter-shaded posteriorly with diffuse white spots extend from nape to base of tail transforming into a distinct, dark (nearly

black), post-sacral band; immaculate, beige post-sacral marking immediately posterior to black post-sacral band not bearing light-colored, anteriorly projecting arms; dorsum and flanks faintly mottled with diffuse speckling; limbs bearing irregularly shaped, diffuse, dark markings; original tail bearing eight dark bands; gular region generally immaculate, except for darker lateral areas and faint stippling in scales; pigmentation density increases posteriorly with abdomen being generally gray; ground color of dorsal caudal region beige, bearing nine black diffuse bands not encircling tail; median subcaudal region faintly orange, generally immaculate.

Variation (Figs. 4, 5). The color patterns of the paratypes generally match that of the holotype and no inter-populational differences were observed (Table 6). The dark, dorsal pattern of LSUHC 14326, 14328, 14330, 14489 is not as bold as that of the holotype. LSUHC 14476 is a juvenile with a broken tail. The tails of LSUHC 14326–28, 14330, and 14489 are regenerated and generally unicolor gray. Variation in scales counts, mensural data, and additional minor aspects in coloration are presented in Table 7.

Distribution. *Hemiphyllodactylus ngwelwini* **sp. nov.** is known from three localities across a distance of approximately 29 km from Pwe Hla Village in the north to the Thayeumin and Myintmahati caves in the south, Shan State (Fig. 1).

Natural History. All individuals from Pwe Hla Village were found on man-made structures in highly disturbed forest. LSUHC 14328–29 and LSUHC 14489 were collected on the walls of cement water tanks and LSUHC 14330 was collected from the underside of a wooden roof from a nearby rest shelter along the road. Both specimens from the Myintmahati Cave population (LSUHC 14326–27) were collected on cement structures immediately outside of a limestone cave in highly disturbed forest. LSUHC 14473 (the holotype) and LSUHC 14474–76 from the Thayeumin Cave population were found outside the limestone cave on corrugated tin shacks, cement buildings, and other man-made structures (Fig. 6) between a rice paddy and an isolated tract of highly disturbed forest.



FIGURE 6. Natural and man-made habitat of *Hemiphyllodactylus ngwelwini* **sp. nov.** from Thayeumin Cave, Shan State, Myanmar.

Etymology. The specific epithet recognizes and honors Mr. Ngwe Lwin, northern Program Manager of Fauna

and Flora International in Myanmar. Mr. Ngwe Lwin has been supportive and invaluable instrumental in facilitating our field work in Myanmar since October of 2017.

Comparisons. The molecular analyses indicate that *Hemiphyllodactylus ngwelwini* **sp. nov.** is a genetically distinct member of the north lineage composed of three, putatively, interbreeding populations being that the intrapopulation uncorrected pairwise sequence divergence across 29 km is only 1.0% and that individuals from the three populations are polyphyletic with respect to one another (Fig. 1, Table 8). *Hemiphyllodactylus ngwelwini* **sp. nov.** is the sister species to a clade composed of *H. ywanganensis* and the sister species *H. uga*, and *H. linnwayensis* (Fig. 1) from which it bears an uncorrected pairwise sequence divergence of 8.4% from *H. linnwayensis*, 9.0% from *H. uga*, and 8.5% from *H. ywanganensis* (Table 8). *H. ngwelwini* **sp. nov.** differs significantly from *H. linnwayensis*, *H. montawaensis*, and *H. tonywhitteni* in mean values of CS (10.8 vs 5.0, $p = 7.42^{-06}$; 10.8 vs 6.3, $p = 4.93^{-05}$; and 10.8 vs. 6.6, $p = 5.14^{-05}$; respectively; Table 3); differs significantly from *H. tonywhitteni* in mean values of DS (12.7 vs 14.8, $p = 0.014$; Table 3); and from *H. montawaensis* it differs significantly in adjusted mean values of HL (1.985 vs 2.852, $p = 0.021$; Fig. 2, Table 3). *Hemiphyllodactylus ngwelwini* **sp. nov.** differs from *H. uga* and *H. ywanganensis* ($n = 2$) by having four subdigital lamellae on the first finger as opposed to two or three in *H. uga* and three in *H. ywanganensis* and four subdigital lamellae on the first toe as opposed to two or three in the latter two species. However, the sample sizes of the latter two species ($n = 4$ and $n = 2$, respectively) are so small that these values are likely to change with the addition of more samples. Owing to the high intraspecific variability of color pattern characters in *H. ngwelwini* **sp. nov.** (Figs. 4, 5), no interspecific differences between it and other members of the north lineage were found.

TABLE 8. Uncorrected pairwise sequence divergences between the mitochondrial ND2 lineages among the species of the north lineage. Bold values are intraspecific values.

	<i>linnwayensis</i>	<i>montawaensis</i>	<i>ngwelwini</i> sp. nov.	<i>tonywhitteni</i>	<i>uga</i>	<i>ywanganensis</i>
<i>linnwayensis</i>	0.005					
<i>montawaensis</i>	0.085	0.007				
<i>ngwelwini</i> sp. nov.	0.084	0.093	0.010			
<i>tonywhitteni</i>	0.080	0.049	0.092	0.000		
<i>uga</i>	0.039	0.092	0.090	0.087	0.000	
<i>ywanganensis</i>	0.032	0.088	0.085	0.087	0.042	0.005

Hemiphyllodactylus zwegabinensis **sp. nov.**

Zwegabin Mountain Slender Gecko

(Figs. 7A, 8)

Holotype. Adult female (LSUHC 14184) collected on 8 August 2019 at 1830 hrs by L. Lee Grismer, Evan S. H. Quah, Perry L. Wood Jr., Myint Kyaw Thura, Jamie R. Oaks, and Aung Lin at the top of Zwegabin Mountain, Kayin State, Myanmar (16.82407°N 97.66810°E WGS; 710 m in elevation).

Diagnosis. *Hemiphyllodactylus zwegabinensis* **sp. nov.** can be separated from all other species of *Hemiphyllodactylus* by possessing the unique combination of having a maximum SVL of 36.9 mm; 12 chin scales; enlarged postmentals; five circumnasal scales; five intersupranasals (=postrostrals); nine supralabials; 10 infralabials; 16 longitudinally arranged dorsal scales at midbody contained within one eye diameter and seven ventral scales; varied digital formulae on hands and feet; four subdigital lamellae on the first finger and toe; no pore-bearing, femoropre-cloacal scales; no plate-like subcaudal scales; adult females not yellow; a dark postorbital stripe extending to at least base of neck; dorsolateral light-colored spots on trunk; no dark dorsolateral or ventrolateral stripe on trunk; dark paravertebral markings on trunk; light-colored postsacral marking bearing anteriorly projecting arms; and caecum and gonads unpigmented. These characters are scored across all Burmese species in Tables 3 and 6 and from all other species of *Hemiphyllodactylus* from southern China and western Thailand (clades 3 and 4 in Grismer *et al.* (2017:Table 3)).

Description of holotype. Adult female SVL 36.9 mm; head triangular in dorsal profile, depressed, distinct from neck; lores flat; rostrum moderate in length (SN/SVL 0.09); prefrontal region weakly concave; canthus rostralis

smoothly rounded, barely discernable; snout moderate, rounded in dorsal profile; eye large; ear opening elliptical, small; eye to ear distance greater than diameter of eye; rostral wider than high, bordered posteriorly by large supranasals; five equally sized intersupranasals (=postnasals); external nares bordered anteriorly by rostral, dorsally by supranasal, posteriorly by two postnasals, ventrally by first supralabial (=circumnasals); 9, 10 (R, L) rectangular supralabials tapering to below posterior margin of eye; 10, 10 (R, L) rectangular infralabials tapering to below posterior margin of eye; scales of rostrum, lores, top of head, and occiput small, raised, those of rostrum largest; dorsal superciliaries flat, mostly square, subimbricate, largest anteriorly; mental triangular, bordered laterally by first infralabials and posteriorly by two differently sized, square-shaped postmentals; each postmental in contact with first infralabial and bordered laterally by a smaller sublabial; 12 chin scales; gular scales small, subimbricate, grading posteriorly into slightly larger, subimbricate throat and even larger pectoral scales which grade into slightly larger, subimbricate ventrals.

Body somewhat elongate (AG/SVL 0.51), dorsoventrally compressed; ventrolateral folds absent; dorsal scales small, granular, 16 dorsal scales at midbody contained within one eye diameter; ventral scales flat, subimbricate much larger than dorsal scales, seven ventral scales contained within one eye diameter; precloacal scales larger than abdominal scales; no pore-bearing femoroprecloacal scales; single enlarged tubercle on lateral margin of tail base; forelimbs short, robust in stature, covered with flat, subimbricate scales dorsally and ventrally; palmar scales slightly raised, subimbricate; all digits except digit I well-developed; digit I vestigial, clawless; distal subdigital lamellae of digits II–V undivided, angular and U-shaped, lamellae proximal to these transversely expanded; distal lamellar formula of digits II–V 4-4-4-4 (R, L); four transversely expanded lamellae on digit I; claws on digits II–V well developed, unsheathed; distal portions of digits strongly curved, terminal joint free, arising from central portion of lamellar pad; hind limbs short, more robust than forelimbs, covered with slightly raised, juxtaposed scales dorsally and by larger, flat subimbricate scales anteriorly and ventrally; plantar scales slightly raised, subimbricate; all digits except digit I well-developed; digit I vestigial, clawless; distal subdigital lamellae of digits II–V undivided, angular and U-shaped, lamellae proximal to these transversely expanded; distal lamellar formula of digits II–V 4-5-5-4 (R, L); four transversely expanded lamellae on digit I; claws on digits II–V well-developed, unsheathed; distal portions of digits strongly curved, terminal joint free, arising from central portion of lamellar pad; tail original, complete; caudal scales occurring in whorls; dorsal caudal scales larger than dorsal body scales, flat, subcycloid, subimbricate; ventrolateral caudals slightly enlarged, weakly flared anteriorly giving a fringe-like appearance; subcaudals flat, slightly larger than dorsal caudals, not plate-like. Morphometric data are presented in Table 9.

TABLE 9. Meristic, mensural (in mm), and color pattern data from the type series of *Hemiphyllodactylus kyaiktiyoensis* **sp. nov.** and *H. zwegabinensis* **sp. nov.** R = right, L = left, m = adult male, f = adult female, j = juvenile, / = data unobtainable or not applicable, r = regenerated.

	<i>kyaiktiyoensis</i> sp. nov.					<i>zwegabinensis</i> sp. nov.
	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC
	14032	14033	14030	14031	14034	14184
	holotype	paratype	paratype	paratype	paratype	holotype
Sex and age class	f	f	f	f	f	f
chin scales (CS)	10	8	9	9	10	12
postmentals distinctly enlarged	yes	yes	yes	yes	yes	yes
circumnasal scales (CN)	5	5	5	5	5	5
intersupranasals (IS)	3	3	3	4	5	5
supralabial scales (SL)	9	10	8	7	10	9
infralabial scales (IL)	8	9	9	8	9	10
dorsal scales (DS)	13	12	16	16	13	16
ventral scales (VS)	8	8	9	8	8	7
lamellar formula on hand	3343	3444	3333	3343	3444	4444
lamellar formula on foot	3444	3454	3343	3444	4454	4554
subdigital lamellae on first finger	4	4	4	4	4	4

....Continued next page

TABLE 9. (Continued)

	<i>kyaiktiyoensis</i> sp. nov.					<i>zwegabinensis</i> sp. nov.
	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC
	14032	14033	14030	14031	14034	14184
	holotype	paratype	paratype	paratype	paratype	holotype
subdigital lamellae on first toe	5	4	4	4	4	4
precloacal and femoral pore series continuous	/	/	/	/	/	/
femoroprecloacal pores	/	/	/	/	/	/
cloacal spurs on each side	1	1	1	1	1	1
subcaudals enlarged, plate-like	no	no	no	/	no	no
dark postorbital stripe	yes	yes	yes	yes	yes	yes
adult females yellow	no	no	no	no	no	no
dorsolateral light-colored spots on trunk	yes	yes	yes	yes	yes	yes
dark dorsolateral stripe on trunk	no	no	no	no	no	no
dark ventrolateral stripe on trunk	faint	faint	faint	faint	faint	no
wide vertebral area generally unicolor	yes	yes	yes	yes	yes	no
dark dorsal transverse blotches/bands	no	no	no	no	no	no
dark reticulate pattern on dorsum	no	no	no	no	no	no
dark transverse zig-zag pattern on dorsum	no	no	no	no	no	no
dark paravertebral markings on trunk	no	no	no	no	no	yes
postsacral marking bearing light-colored anteriorly projecting arms	yes	yes	yes	yes	yes	yes
caecum pigmented	no	no	no	no	no	no
gonads pigmented	no	no	no	no	no	no
SVL	43.4	37.0	32.3	41.1	40.7	36.9
AG	23.6	19.0	16.0	21.5	22.2	18.9
HL	9.6	7.6	7.1	9.6	8.9	7.8
SN	4.6	3.7	3.0	4.0	3.6	3.5
HW	7.1	6.8	6.0	7.2	7.1	6.5
NE	3.5	2.8	2.3	2.9	2.9	3.0
ED	2.6	2.1	2.1	2.3	2.2	2.1
SW	1.5	1.2	0.0	1.6	1.3	1.2
AG/SVL	0.54	0.51	0.50	0.52	0.55	0.51
HL/SVL	0.22	0.21	0.22	0.23	0.22	0.21
SN/SVL	0.11	0.10	0.09	0.10	0.09	0.09
HW/SVL	0.16	0.18	0.19	0.17	0.17	0.18
NE/HL	0.36	0.37	0.33	0.30	0.33	0.38
ED/HL	0.27	0.28	0.29	0.24	0.25	0.27
SW/HL	0.15	0.16	0.01	0.17	0.14	0.15



FIGURE 7. A. Adult female holotype of *Hemiphyllodactylus zwegabinensis* **sp. nov.** (LSUHC 14184) from Zwegabin Mountain, Kayin State, Myanmar. Color pattern variation in B. Adult female paratype (LSUHC 14033) *H. kyaiktiyoensis* **sp. nov.** from Kyaiktiyo Mountain, Mon State, Myanmar and C. Adult female paratype (LSUHC 14030) *H. kyaiktiyoensis* **sp. nov.** from Kyaiktiyo Mountain, Mon State, Myanmar. Photos by L. Lee Grismer.

Coloration in life (Fig. 7). All *Hemiphyllodactylus* are capable of considerable change in the intensity and boldness of their coloration and pattern. The description below is of that when the holotype was photographed the morning after capture, approximately 12 hours after the time of collection when in its light-phase. Ground color of top of head, body, and limbs, light-brown and densely mottled with darker markings; top of head overlain with dark, semi-reticulate pattern; broad, dark, diffuse pre- and postorbital stripe extends from the external nares, through the eye to forelimb insertion; pairs of diffuse, dark, paravertebral markings counter-shaded posteriorly with diffuse white markings extend from nape to base of tail transforming into a distinct black, post-sacral marking; light-colored counter shaded areas appear as dorsolateral spots along the trunk; faint yellow post-sacral marking bears light-colored anteriorly projecting arms (most obvious on left side); dorsum and flanks heavily mottled with faint, dark, diffuse speckling; limbs bearing irregularly shaped diffuse dark markings and bands; gular region generally immaculate, except for darker lateral areas, scales faintly stippled, and pigmentation density increases posteriorly with abdomen being generally gray; ground color of dorsal caudal region dull-yellow, bearing three faint diffuse bands anteriorly that do not encircle the tail and irregular dark mottling posteriorly; median subcaudal region heavily stippled.

Distribution. *Hemiphyllodactylus zwegabinensis* **sp. nov.** is known only from the type locality of Zwegabin Mountain, Kayin State (Fig. 1).

Natural History. The holotype was collected on a metal building in stunted, wind-blown, primary forest at the crest of Zwegabin Mountain (Fig. 8).



FIGURE 8. Natural wind-blown upland karst habitat of *Hemiphyllodactylus zwegabinensis* **sp. nov.** from the peak of Zwegabin Mountain, Kayin State, Myanmar.

TABLE 10. Uncorrected pairwise sequence divergences between the mitochondrial ND2 lineages among the species of the south lineage. Bold values are intraspecific values.

	<i>kyaiktiyoensis</i> sp. nov.	<i>pinlaungensis</i> sp. nov.	<i>zwegabinensis</i> sp. nov.
<i>kyaiktiyoensis</i> sp. nov.	0.003		
<i>pinlaungensis</i> sp. nov.	0.095	0.017	
<i>zwegabinensis</i> sp. nov.	0.137	0.141	0.000

Etymology. The specific epithet is a toponym referring to the type locality of Zwegabin Mountain.

Comparisons. The molecular analyses indicate that *Hemiphyllodactylus zwegabinensis* **sp. nov.** is a genetically

distinct member of the south lineage and is the sister species to a clade composed of the sister species *H. kyaiktiyoensis* **sp. nov.**, and *H. pinlaungensis* **sp. nov.** (Fig. 1) from which it bears an uncorrected pairwise sequence divergence of 13.7% and 14.1%, respectively (Table 10). *Hemiphyllodactylus zwegabinensis* **sp. nov.** differs from *H. pinlaungensis* **sp. nov.** and *H. kyaiktiyoensis* **sp. nov.** by having significantly different centroid position based on the factor loadings of the PC1–3 ($p = 0.002$ and 0.022 , respectively). *Hemiphyllodactylus zwegabinensis* **sp. nov.** differs from *H. kyaiktiyoensis* **sp. nov.** by having 12 as opposed to 8–10 chin scales (CS), 10 as opposed to eight or nine infralabials, seven as opposed to eight or nine ventral scales (VS) (Fig. 3, Table 6), and lacking as opposed to having a nearly dorsum-wide, brown vertebral stripe (Fig. 7). *Hemiphyllodactylus zwegabinensis* **sp. nov.** differs from *H. pinlaungensis* **sp. nov.** by having significantly shorter adjusted SN (1.065 vs 1.363 , $p = 0.005$; Fig. 3, Table 6).

***Hemiphyllodactylus kyaiktiyoensis* sp. nov.**

Kyaiktiyo Mountain Slender Gecko

(Figs. 7, 9)

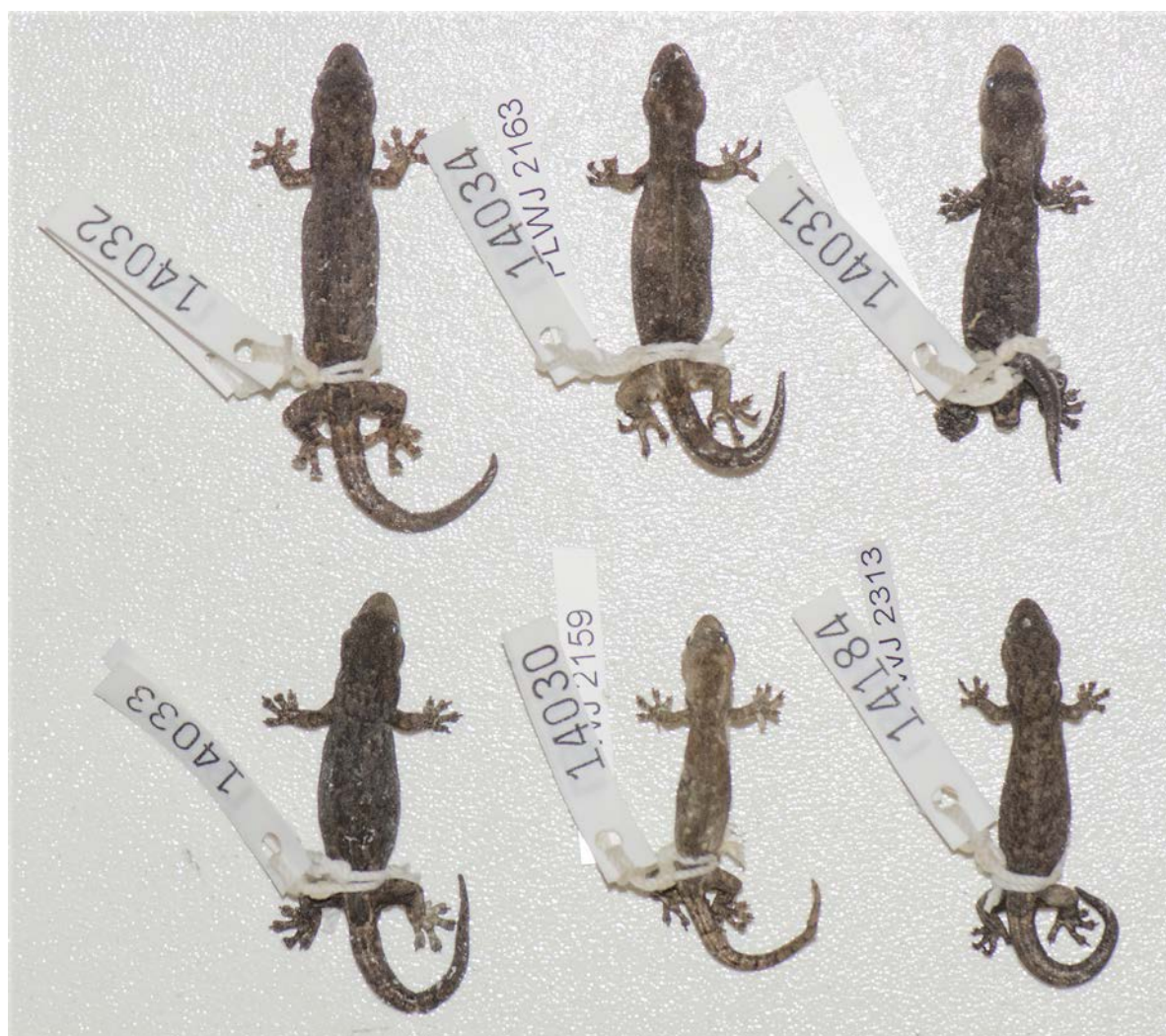


FIGURE 9. Type series of adult female holotype (LSUHC 14032) adult female paratypes (LSUHC 14030–31, 14033–34) of *Hemiphyllodactylus kyaiktiyoensis* **sp. nov.** from Kyaiktiyo Mountain, Mon State, Myanmar. Adult female holotype (LSUHC 14184) of *H. zwegabinensis* **sp. nov.**, from Zwegabin Mountain, Kayin State, Myanmar.

Holotype. Adult female (LSUHC 14032) collected on 4 November 2018 at 1900 hrs by Evan S. H. Quah, L. Lee Grismer, Perry L. Wood Jr., Myint Kyaw Thura, Jamie R. Oaks, and Aung Lin along a trail leading down the north-west facing flank of the mountain from the Golden Rock Pagoda, Mon State, Myanmar (17.47840°N 97.10042°E WGS; 1057 m in elevation).

Paratypes. Female paratypes (LSUHC 14030–31, 14033–34) bear the same collection data as the holotype.

Diagnosis. *Hemiphyllodactylus kyaiktiyoensis* **sp. nov.** can be separated from all other species of *Hemiphyllodactylus* by possessing the unique combination of having a maximum SVL of 43.4 mm; 8–10 chin scales; enlarged postmentals; five circumnasal scales; 3–5 intersupranasals (=postrostrals); 7–10 supralabials; eight or nine infralabials; 12–16 longitudinally arranged dorsal scales at midbody contained within one eye diameter and eight or nine ventral scales; four subdigital lamellae on the first finger and four or five on first toe; no plate-like subcaudal scales; adult females not yellow; a dark postorbital stripe extending to at least base of neck; dorsolateral light-colored spots on trunk; no dark, dorsolateral stripe on trunk; faint, dark, ventrolateral stripe on trunk; no dark-colored pattern on trunk; wide, light-brown, nearly unicolor, vertebral region on trunk; beige, postsacral marking bearing anteriorly projecting arms; and caecum and gonads unpigmented. These characters are scored across all Burmese species in Tables 3 and 6 and from all other species of *Hemiphyllodactylus* from southern China and western Thailand (clades 3 and 4 in Grismer *et al.* [2017:Table 3]).

Description of holotype Adult female SVL 43.4 mm; head triangular in dorsal profile, depressed, distinct from neck; lores flat; rostrum moderate in length (SN/SVL 0.11); prefrontal region weakly concave; canthus rostralis smoothly rounded, barely discernable; snout moderate, rounded in dorsal profile; eye large; ear opening elliptical, small; eye to ear distance greater than diameter of eye; rostral wider than high, bordered posteriorly by large supranasals; three equally sized intersupranasals (=postnasals); external nares bordered anteriorly by rostral, dorsally by supranasal, posteriorly by two postnasals, ventrally by first supralabial (=circumnasals); nine (R, L) rectangular supralabials tapering to below posterior margin of eye; 8 (R, L) rectangular infralabials tapering to below posterior margin of eye; scales of rostrum, lores, top of head, and occiput small, granular, those of rostrum largest, slightly raised; dorsal superciliaries flat, mostly square, subimbricate, largest anteriorly; mental triangular, bordered laterally by first infralabials and posteriorly by two rectangular postmentals; each postmental in contact with first infralabial and bordered laterally by slightly smaller sublabial; 10 chin scales; gular scales small, subimbricate, grading posteriorly into slightly larger, subimbricate throat and even larger pectoral scales which grade into slightly larger, subimbricate ventrals.

Body somewhat elongate (AG/SVL 0.54), dorsoventrally compressed; ventrolateral folds absent; dorsal scales small, granular, 13 dorsal scales at midbody contained within one eye diameter; ventral scales flat, subimbricate much larger than dorsal scales, eight ventral scales contained within one eye diameter; precloacal scales larger than abdominal scales; no pore-bearing femoroprecloacal scales; single enlarged tubercle on lateral margin of tail base; forelimbs short, robust in stature, covered with flat, subimbricate scales dorsally and ventrally; palmar scales flat, subimbricate; all digits except digit I well-developed; digit I vestigial, clawless; distal subdigital lamellae of digits II–V undivided, angular, U-shaped, lamellae proximal to these transversely expanded; distal lamellar formula of digits II–V 3-3-4-3 (R, L); four transversely expanded lamellae on digit I; claws on digits II–V well developed, unsheathed; distal portions of digits strongly curved, terminal joint free, arising from central portion of lamellar pad; hind limbs short, more robust than forelimbs, covered with raised, juxtaposed scales dorsally and by larger, flat, subimbricate scales anteriorly and ventrally; plantar scales slightly raised, subimbricate; all digits except digit I well-developed; digit I vestigial, clawless; distal subdigital lamellae of digits II–V undivided, angular, and U-shaped, lamellae proximal to these transversely expanded; distal lamellar formula of digits II–V 3-4-4-4 (R, L); five transversely expanded lamellae on digit I; claws on digits II–V well-developed, unsheathed; distal portions of digits strongly curved, terminal joint free, arising from central portion of lamellar pad; caudal scales occurring in whorls; dorsal caudal scales of original tail larger than dorsal body scales, flat, subcycloid, subimbricate; ventrolateral caudals enlarged, weakly flared giving a fringe-like appearance punctuated every five or six scales by even larger, raised scales; subcaudals flat slightly larger than dorsal caudals, not plate-like; posterior one-half of tail regenerated; dorsal caudals of regenerated portion smaller, more irregular in shape; other caudal scales generally same shape as those in original tail. Morphometric data are presented in Table 9.

Coloration in life (Fig. 7). All *Hemiphyllodactylus* are capable of considerable change in the intensity and boldness of their coloration and pattern. The description below is of that when the holotype was photographed the morning after capture, approximately 12 hours after the time of collection when in its light-phase. Ground color of top of head, body, limbs, and tail dull-yellow or straw; top of head overlain with a dense dark-brown mottling giving top of head a brownish appearance; brown, semi-reticulate pattern on top of head; broad, dark, diffuse pre- and postorbital stripe extends from external nares, through eye to forelimb, preorbital portion very faint; wide, nearly immaculate, light-brown stripe with crenulated margins extends from nape to base of tail, nearly covering entire

dorsum; invaginations of crenulated margins contain a diffuse, light-colored spot that collectively appear as regularly spaced, dorsolateral spots along trunk; faint, dark, ventrolateral stripe on trunk; immaculate, beige, postsacral marking bears light-colored, anteriorly projecting arms; flanks faintly mottled with diffuse brown speckling; limbs bearing irregularly shaped, diffuse, brown bands and markings; base of toes bearing a faintly orange spot; gular region mottled with brown and faint stippling in scales; pigmentation density in scales decreases posteriorly with the abdomen being generally beige with faint stippling; original portion of tail bearing four faint, irregularly shaped, brown bands and heavily mottled interspaces; enlarged scales of ventrolateral fringe highlighted in white; subcaudal region densely stippled; regenerated portion of tail brownish with faint, dark markings.

Variation (Figs. 7, 9). The color pattern of the paratypes (LSUHC 14030–31, 14033–34) generally match that of the holotype. The dark, dorsal patterns of LSUHC 14031 and 14033 are slightly bolder. LSUHC 14030 has a more lightly colored dorsal pattern overall and the dorsolateral trunk spots are more obvious. Variation in scales counts, mensural data, and additional minor aspects in coloration are presented in Table 9.

Distribution. *Hemiphyllodactylus kyaiktiyoensis* **sp. nov.** is known only from the type locality on Kyaiktiyo Mountain in Mon State, Myanmar but is expected to occur in other, nearby upland areas (Fig. 1).

Natural History. All individuals of the type series were found on the brick wall of a house at night beneath a neon light approximately 2.5 meters above the ground in disturbed hill forest (Fig. 10). No other geckos were found on the wall but *Hemidactylus garnotii*, *Hemidactylus brookii*, *Gehyra mutilata*, and *Cyrtodactylus aequalis* were abundant on all other nearby vegetation and human-made structures. Specimens LSUHC 14032–34 were gravid with two eggs indicating the month of November falls within the reproductive season of this species. Although no males were found, we cannot determine if this species is parthenogenetic or not.

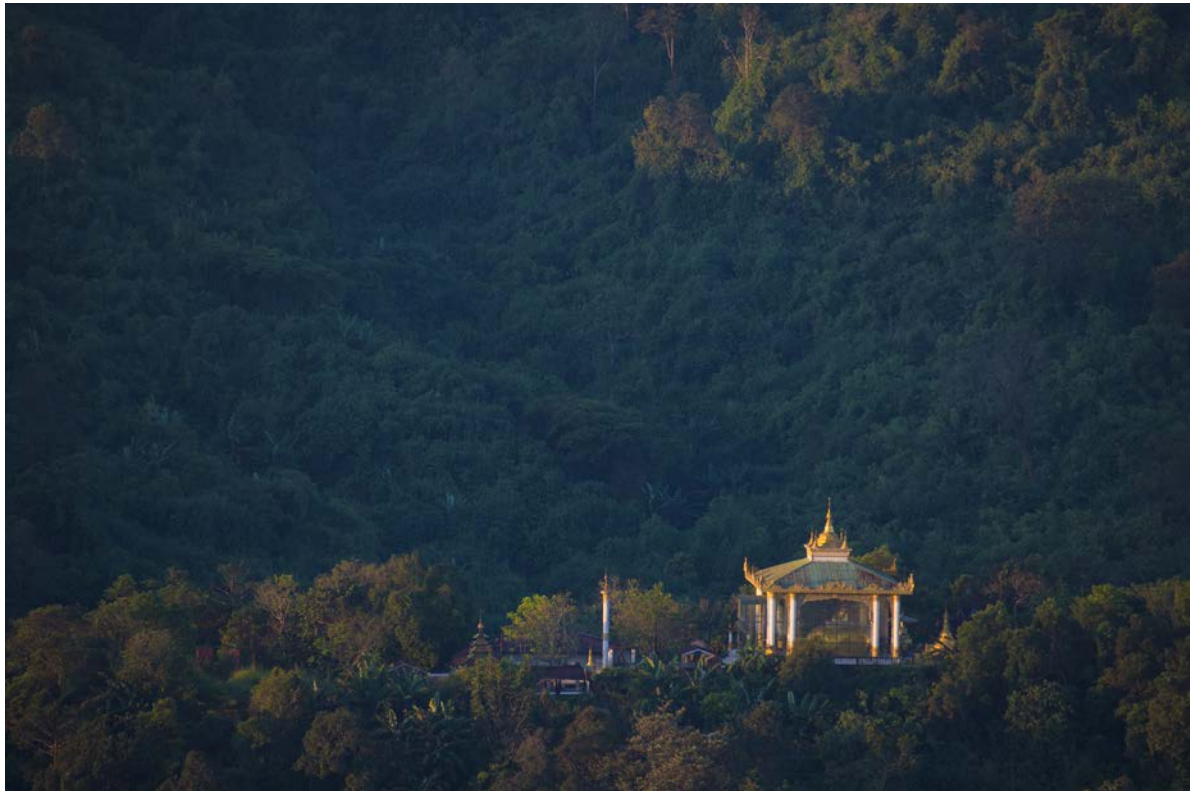


FIGURE 10. Natural and man-made microhabitat habitat of *Hemiphyllodactylus kyaiktiyoensis* **sp. nov.** from Kyaiktiyo Mountain, Mon State, Myanmar.

Etymology. The specific epithet is a toponym referring to the type locality of Kyaiktiyo Mountain, Mon State, Myanmar.

Comparisons. The molecular analyses indicate that *Hemiphyllodactylus kyaiktiyoensis* **sp. nov.** is a genetically distinct member of the south lineage and is the sister species to *H. pinlaungensis* **sp. nov.** (Fig. 1) from which it bears an uncorrected pairwise sequence divergence of 9.5% (Table 10). *Hemiphyllodactylus kyaiktiyoensis* **sp. nov.** differs significantly from *H. pinlaungensis* **sp. nov.** in having a lower mean value of CS (9.2 vs 11.2, $p = 0.014$) and

a lower adjusted mean value of SN (1.242 vs 1.363) $p = 0.018$, respectively; Table 6, Fig. 3). It differs further from *H. pinlaungensis* **sp. nov.** by having a significantly different centroid position based on the factor loadings of the PC1–3 ($p = 0.002$; Fig. 3). This latter metric can not be considered a diagnostic character but serves as a measure of the quantitative difference between these two species in multivariate space. Its differences from *H. zwegabinensis* **sp. nov.** are listed above in the comparisons section for that species.

***Hemiphyllodactylus pinlaungensis* sp. nov.**

Pinlaung Slender Gecko

(Figs. 11, 12)



FIGURE 11. Color pattern variation among holotype, selected paratypes and a hatchling of *Hemiphyllodactylus pinlaungensis* **sp. nov.** from Pinlaung City, Shan State, Myanmar. A. Adult male holotype (LSUHC 14274). B. Adult female (LSUHC 14266). C. Adult female (LSUHC 14273). D. Adult female (LSUHC 14265). E. Adult female (LSUHC 14277). F. Hatchling (LSUHC 14258). Photographs by L. Lee Grismer.

Holotype. Adult male (LSUHC 14274) collected on 12 November 2018 at 1900 hrs by Jamie R. Oaks, L. Lee Grismer, Perry L. Wood Jr., Myint Kyaw Thura, Evan S. H. Quah, and Aung Lin from Pinlaung City, Shan State, Myanmar (20.12869°N 96.78464°E WGS; 1498 m in elevation).

Paratypes. Paratypes (LSUHC 14257, 14259–73, 14275–77) bear the same collection data as the holotype.

Additional specimens. Additional specimens (LSUHC 14301–05) were collected from Wingabar Cave approximately 7 km southwest of Pinlaung City, Shan State, Myanmar (20.06936°N 96.76988°E WGS; 1464 m in elevation) by Jamie R. Oaks, L. Lee Grismer, Perry L. Wood Jr., Myint Kyaw Thura, Evan S. H. Quah, and Aung Lin on 13 November 2018.

Diagnosis. *Hemiphyllodactylus pinlaungensis* **sp. nov.** can be separated from all other species of *Hemiphyllodactylus* by possessing the unique combination of having a maximum SVL of 43.0 mm; 9–14 chin scales; enlarged postmentals; five or six circumnasal scales; 2–5 intersupranasals (=postrostrals); 7–10 supralabials; 8–11 infralabi-

als; 12–19 longitudinally arranged dorsal scales at midbody contained within one eye diameter and 7–12 ventral scales; 17–24 pore-bearing femoroprecloacal scales in males; three or four subdigital lamellae on first finger and first toe; no plate-like subcaudal scales; adult females not yellow; a dark postorbital stripe extending to at least base of neck; dorsolateral light-colored spots on trunk variable; no dark, dorsolateral stripe on trunk; dark ventrolateral stripe on trunk; dark paravertebral markings on trunk; light-colored postsacral marking bearing anteriorly projecting arms; and caecum and gonads unpigmented. These characters are scored across all Burmese species in Tables 3 and 6 and from all other species of *Hemiphyllodactylus* from southern China and western Thailand (clades 3 and 4 in Grismer *et al.* (2017:Table 3)).

Description of holotype Adult male SVL 38.9 mm; head triangular in dorsal profile, depressed, distinct from neck; lores flat; rostrum moderate in length (SN/SVL 0.10); prefrontal region weakly concave; canthus rostralis smoothly rounded, barely discernable; snout moderate, rounded in dorsal profile; eye large; ear opening circular, small; eye to ear distance greater than diameter of eye; rostral wider than high, bordered posteriorly by large supranasals; five equally sized intersupranasals (=postnasals); external nares bordered anteriorly by rostral, dorsally by supranasal, posteriorly by two postnasals, ventrally by first supralabial (=circumnasals); 10 (R, L) rectangular supralabials tapering to below posterior margin of eye; 8 (R, L) rectangular infralabials tapering to below posterior margin of eye; scales of rostrum, lores, top of head, and occiput small, granular, raised, those of rostrum largest; dorsal superciliaries flat, mostly square, subimbricate, largest anteriorly; mental triangular, bordered laterally by first infralabials, posteriorly by two trapezoidal postmentals; each postmental in contact with first infralabial, bordered laterally by slightly smaller sublabial; 10 chin scales; gular scales small, subimbricate to slightly raised, grading posteriorly into slightly larger, subimbricate throat and larger pectoral scales which grade into slightly larger, subimbricate ventrals.

Body somewhat elongate (AG/SVL 0.48), dorsoventrally compressed; ventrolateral folds absent; dorsal scales small, granular, 14 dorsal scales at midbody contained within one eye diameter; ventral scales flat, subimbricate much larger than dorsal scales, eight ventral scales contained within one eye diameter; precloacal scales larger than abdominal scales; 19 pore-bearing femoroprecloacal scales; single enlarged tubercle on lateral margin of tail base; forelimbs short, robust in stature, covered with flat, subimbricate scales dorsally and ventrally; palmar scales flat, subimbricate; all digits except digit I well-developed; digit I vestigial, clawless; distal subdigital lamellae of digits II–V undivided, angular, U-shaped, lamellae proximal to these transversely expanded; distal lamellar formula of digits II–V 3-4-4-3 (R, L); three transversely expanded lamellae on digit I; claws on digits II–V well developed, unsheathed; distal portions of digits strongly curved, terminal joint free, arising from central portion of lamellar pad; hind limbs short, more robust than forelimbs, covered with raised, juxtaposed scales dorsally and by larger, flat, subimbricate scales anteriorly and ventrally; plantar scales slightly raised, subimbricate; all digits except digit I well-developed; digit I vestigial, clawless; distal subdigital lamellae of digits II–V undivided, angular, and U-shaped, lamellae proximal to these transversely expanded; distal lamellar formula of digits II–V 3-4-4-4 (R, L); three transversely expanded lamellae on digit I; claws on digits II–V well-developed, unsheathed; distal portions of digits strongly curved, terminal joint free, arising from central portion of lamellar pad; caudal scales not occurring in distinct whorls; dorsal caudal scales of original tail larger than dorsal body scales, flat, subcycloid, subimbricate; ventrolateral caudals enlarged, weakly flared giving a weak fringe-like appearance punctuated every 4–6 scales by slightly larger, raised scales; subcaudals flat, slightly larger than dorsal caudals, not plate-like. Morphometric data are presented in Table 11.

TABLE 11. Meristic, mensural (in mm), and color pattern data from the type series and additional specimens from the two populations of *Hemiphyllodactylus pinlaungensis* **sp. nov.** R = right, L = left, m = adult male, f = adult female, j = juvenile, / = data unobtainable or not applicable, r = regenerated.

Pinlaung City	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC
	14274	14261	14270	14262	14259	14265	14273	14263	14272	14277
	holotype	paratype	paratype	paratype	paratype	paratype	paratype	paratype	paratype	paratype
Sex and age class	m	m	m	f	m	f	f	m	m	f
chin scales (CS)	10	10	10	14	11	9	11	10	10	12
postmentals										
distinctly enlarged	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes

.....Continued next page

TABLE 11. (Continued)

Pinlaung City	LSUHC 14274 holotype	LSUHC 14261 paratype	LSUHC 14270 paratype	LSUHC 14262 paratype	LSUHC 14259 paratype	LSUHC 14265 paratype	LSUHC 14273 paratype	LSUHC 14263 paratype	LSUHC 14272 paratype	LSUHC 14277 paratype
circumnasal scales (CN)	5	5	5	5	5	5	5	5	5	5
intersupranasals (IS)	5	2	2	3	3	3	3	3	3	3
supralabial scales (SL)	10	10	9	10	10	10	9	10	9	9
infralabial scales (IL)	8	10	9	10	9	10	8	10	10	11
dorsal scales (DS)	14	12	16	18	17	13	15	14	14	15
ventral scales (VS)	8	8	9	10	9	7	7	8	8	8
lamellar formula on hand	3443	3444	3444	3333	3443	3344	3333	3333	3333	3333
lamellar formula on foot	3444	3344	4444	4444	3344	3444	3443	3444	3433	3444
subdigital lamellae on first finger (FL1)	3	4	3	3	3	3	3	3	3	4
subdigital lamellae on first toe (TL1)	3	4	3	3	4	3	3	3	3	4
precloacal and femoral pore series continuous	yes	yes	yes	/	yes	/	/	yes	yes	/
femoroprecloacal pores (FP)	19	17	23	/	21	/	/	22	23	/
cloacal spurs on each side	1	1	1	1	1	0	1	1	1	1
subcaudals enlarged, plate-like	no	/	/	no	no	no	no	no	no	no
dark postorbital stripe	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
adult females yellow	no	no	no	no	no	no	no	no	no	no
pairs of paravertebral light spots on trunk	variable	variable	variable	variable	variable	variable	variable	variable	variable	variable
dark dorsolateral stripe on trunk	no	no	no	no	no	no	no	no	no	no
dark ventrolateral stripe on trunk	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
dorsal pattern unicolor	no	no	no	no	no	no	no	no	no	no
dark dorsal transverse blotches/bands	no	no	no	no	no	no	no	no	no	no
dark reticulate pattern on dorsum	no	no	no	no	no	no	no	no	no	no
dark transverse zig-zag pattern on dorsum	no	no	no	no	no	no	no	no	no	no
dark paravertebral markings on trunk	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes

.....Continued next page

TABLE 11. (Continued)

Pinlaung City	LSUHC 14274 holotype	LSUHC 14261 paratype	LSUHC 14270 paratype	LSUHC 14262 paratype	LSUHC 14259 paratype	LSUHC 14265 paratype	LSUHC 14273 paratype	LSUHC 14263 paratype	LSUHC 14272 paratype	LSUHC 14277 paratype
postsacral marking										
bearing light- colored anteriorly										
projecting arms	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
caecum pigmented	no	no	no	no	no	no	no	no	no	no
gonads pigmented	no	no	no	no	no	no	no	no	no	no
SVL	38.9	35.1	39.3	31.1	35.4	38.1	39.3	35.5	40.9	37.5
AGL	18.6	16.3	19.9	14.0	18.2	0.5	21.4	18.0	19.7	18.7
HL	8.3	9.2	9.4	8.0	8.7	9.6	10.0	8.1	8.1	8.1
SN	4.0	4.0	3.7	3.4	3.8	3.9	4.2	4.0	4.4	3.5
HW	7.1	7.0	7.7	5.7	7.3	6.8	7.9	6.2	7.6	6.9
NE	2.9	2.9	2.6	2.5	2.7	2.8	3.2	2.7	0.1	2.4
ED	2.3	2.3	2.5	2.2	2.4	2.3	2.6	2.4	2.4	2.2
SW	1.4	1.2	1.4	1.4	1.3	1.3	1.3	1.2	1.6	1.1
AG/SVL	0.48	0.46	0.51	0.45	0.51	0.01	0.48	0.45	0.51	0.54
HL/SVL	0.21	0.26	0.24	0.26	0.24	0.25	0.21	0.24	0.27	0.23
SN/SVL	0.10	0.11	0.09	0.11	0.11	0.10	0.11	0.10	0.10	0.11
HW/SVL	0.18	0.20	0.20	0.18	0.21	0.18	0.19	0.19	0.19	0.17
NE/HL	0.35	0.32	0.28	0.31	0.31	0.30	0.35	0.34	0.26	0.34
ED/HL	0.28	0.25	0.27	0.27	0.27	0.24	0.28	0.23	0.22	0.25
SW/HL	0.17	0.13	0.15	0.17	0.15	0.14	0.14	0.17	0.15	0.16
SN/SVL	0.10	0.11	0.09	0.11	0.11	0.10	0.11	0.10	0.10	0.11
HW/SVL	0.18	0.20	0.20	0.18	0.21	0.18	0.19	0.19	0.19	0.17
NE/HL	0.35	0.32	0.28	0.31	0.31	0.30	0.35	0.34	0.26	0.34
ED/HL	0.28	0.25	0.27	0.27	0.27	0.24	0.28	0.23	0.22	0.25
SW/HL	0.17	0.13	0.15	0.17	0.15	0.14	0.14	0.17	0.15	0.16

TABLE 11. (Continued)

Pinlaung City	LSUHC 14260 paratype	LSUHC 14275 paratype	LSUHC 14266 paratype	LSUHC 14267 paratype	LSUHC 14264 paratype	LSUHC 14268 paratype	LSUHC 14257 paratype	LSUHC 14276 paratype	LSUHC 14269 paratype	LSUHC 14271 paratype
Sex and age class	m	f	f	f	f	f	f	f	m	f
chin scales (CS)	12	13	11	10	13	12	10	12	10	9
postmentals										
distinctly enlarged	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
circumnasal scales (CN)	5	6	5	5	5	5	5	5	5	5
intersupranasals (IS)	3	3	3	3	3	3	3	3	3	4
supralabial scales (SL)	9	10	8	10	8	9	7	8	9	9
infralabial scales (IL)	9	9	9	11	9	9	9	9	9	10
dorsal scales (DS)	15	18	12	14	13	14	16	14	19	13
ventral scales (VS)	8	10	7	8	9	8	6	8	9	9

.....Continued next page

TABLE 11. (Continued)

Pinlaung City	LSUHC 14260 paratype	LSUHC 14275 paratype	LSUHC 14266 paratype	LSUHC 14267 paratype	LSUHC 14264 paratype	LSUHC 14268 paratype	LSUHC 14257 paratype	LSUHC 14276 paratype	LSUHC 14269 paratype	LSUHC 14271 paratype
lamellar formula on hand	3333	3333	3333	3333	3333	3334	4444	3333	3333	3343
lamellar formula on foot	3343	3333	3344	3333	4444	3444	4444	3443	3444	3333
subdigital lamellae on first finger (FL1)	3	3	3	3	3	3	3	4	3	3
subdigital lamellae on first toe (TL1)	3	3	3	3	3	3	3	3	4	3
precloacal and femoral pore series continuous	yes	/	/	/	/	/	/	/	yes	/
femoroprecloacal pores (FP)	20	/	/	/	/	/	/	/	22	/
cloacal spurs on each side	1	1	1	1	1	1	1	1	1	0
subcaudals enlarged, plate-like	no	no	no	no	no	no	/	/	no	no
dark postorbital stripe	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
adult females yellow	no	no	no	no	no	no	no	no	no	no
pairs of paravertebral light spots on trunk	variable	variable	variable	variable	variable	variable	variable	variable	variable	variable
dark dorsolateral stripe on trunk	no	no	no	no	no	no	no	no	no	no
dark ventrolateral stripe on trunk	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
dorsal pattern unicolor	no	no	no	no	no	no	no	no	no	no
dark dorsal transverse blotches/bands	no	no	no	no	no	no	no	no	no	no
dark reticulate pattern on dorsum	no	no	no	no	no	no	no	no	no	no
dark transverse zig-zag pattern on dorsum	no	no	no	no	no	no	no	no	no	no
dark paravertebral markings on trunk	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
postsacral marking bearing light-colored anteriorly	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
projecting arms	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
caecum pigmented	no	no	no	no	no	no	no	no	no	no
gonads pigmented	no	no	no	no	no	no	no	no	no	no
SVL	39.34	35.47	40.91	37.45	43.01	41.57	39.94	2.45	33.76	43.0
AGL	21.41	17.99	19.68	18.65	23.09	20.63	20.7	16.87	16.7	23.1
HL	9.95	8.12	8.12	8.13	8.08	8.43	9.83	7.26	7.47	8.1

.....Continued next page

TABLE 11. (Continued)

Pinlaung City	LSUHC 14260	LSUHC 14275	LSUHC 14266	LSUHC 14267	LSUHC 14264	LSUHC 14268	LSUHC 14257	LSUHC 14276	LSUHC 14269	LSUHC 14271
	paratype	paratype	paratype	paratype	paratype	paratype	paratype	paratype	paratype	paratype
SN	4.24	3.99	4.37	3.47	4.29	4.44	3.62	3.57	3.62	4.3
HW	7.91	6.24	7.57	6.85	7.9	7.5	7.18	6.45	6.34	7.9
NE	3.19	2.68	0.12	2.44	3	3.03	3.03	2.4	2.47	3.0
ED	2.6	2.4	2.4	2.2	2.4	2.4	2.3	1.9	2.2	2.4
SW	1.27	1.19	1.56	1.14	1.12	1.28	1.67	1.27	1.16	1.1
AG/SVL	0.54	0.51	0.48	0.50	0.54	0.50	0.52	6.89	0.49	0.61
HL/SVL	0.25	0.23	0.20	0.22	0.19	0.20	0.25	2.96	0.22	0.22
SN/SVL	0.11	0.11	0.11	0.09	0.10	0.11	0.09	1.46	0.11	0.11
HW/SVL	0.20	0.18	0.19	0.18	0.18	0.18	0.18	2.63	0.19	0.19
NE/HL	0.32	0.33	0.01	0.30	0.37	0.36	0.31	0.33	0.33	0.35
ED/HL	0.26	0.30	0.30	0.27	0.30	0.28	0.23	0.26	0.29	0.29
SW/HL	0.13	0.15	0.19	0.14	0.14	0.15	0.17	0.17	0.16	0.14

TABLE 11. (Continued)

Wingabar Cave	LSUHC 14302	LSUHC 14301	LSUHC 14303	LSUHC 14305	LSUHC 14304
	additional specimen	additional specimen	additional specimen	additional specimen	additional specimen
Sex and age class	f	m	m	m	f
chin scales (CS)	12	13	12	14	11
postmentals distinctly enlarged	yes	yes	yes	yes	yes
circumnasal scales (CN)	5	5	5	5	5
intersupranasals (IS)	3	3	2	3	2
supralabial scales (SL)	8	10	10	8	8
infralabial scales (IL)	9	10	10	10	9
dorsal scales (DS)	14	19	15	16	15
ventral scales (VS)	7	12	8	10	8
lamellar formula on hand	3333	3333	3333	3333	3333
lamellar formula on foot	3444	4444	4444	4444	3444
subdigital lamellae on first finger (FL1)	4	4	4	4	3
subdigital lamellae on first toe (TL1)	4	4	4	4	3
precloacal and femoral pore series continuous	/	yes	yes	yes	/
femoroprecloacal pores (FP)	/	17	22	24	/
cloacal spurs on each side	1	1	1	1	1
subcaudals enlarged, plate-like	no	/	no	no	no
dark postorbital stripe	yes	yes	yes	yes	yes
adult females yellow	no	/	no	no	/
pairs of paravertebral light spots on trunk	variable	variable	variable	variable	variable
dark dorsolateral stripe on trunk	no	no	no	no	no
dark ventrolateral stripe on trunk	yes	yes	yes	yes	yes
dorsal pattern unicolor	no	no	no	no	no
dark dorsal transverse blotches/bands	no	no	no	no	no
dark reticulate pattern on dorsum	no	no	no	no	no

....Continued next page

TABLE 11. (Continued)

Wingabar Cave	LSUHC 14302 additional specimen	LSUHC 14301 additional specimen	LSUHC 14303 additional specimen	LSUHC 14305 additional specimen	LSUHC 14304 additional specimen
dark transverse zig-zag pattern on dorsum	no	no	no	no	no
dark paravertebral markings on trunk	yes	yes	yes	yes	yes
postsacral marking bearing light-colored anteriorly projecting arms	yes	yes	yes	yes	yes
caecum pigmented	no	no	no	no	no
gonads pigmented	no	no	no	no	no
SVL	40.3	30.1	40.7	37.1	39.2
AGL	20.0	14.5	18.9	33.2	20.7
HL	8.1	7.3	10.2	9.0	8.9
SN	3.9	3.2	4.3	3.8	4.4
HW	7.5	5.7	7.7	7.2	7.4
NE	2.7	2.3	3.3	2.7	2.8
ED	2.4	1.9	2.2	2.4	2.5
SW	1.3	1.1	1.5	1.2	1.3
AG/SVL	0.50	0.48	0.46	0.89	0.53
HL/SVL	0.20	0.24	0.25	0.24	0.23
SN/SVL	0.10	0.11	0.11	0.10	0.11
HW/SVL	0.19	0.19	0.19	0.19	0.19
NE/HL	0.33	0.31	0.32	0.30	0.31
ED/HL	0.30	0.26	0.22	0.27	0.28
SW/HL	0.16	0.15	0.15	0.13	0.14

Coloration in life. All *Hemiphyllodactylus* are capable of considerable change in the intensity and boldness of their coloration and pattern. The description below is of that when the holotype was photographed the morning after capture, approximately 12 hours after the time of collection when in its light-phase. Ground color of top of head, body, limbs, and tail straw-colored but heavily mottled with dark-brown markings; top of head overlain with a light-colored mottling and small, dark-brown reticulations on occiput; broad, faint, diffuse pre- and postorbital stripe extends from external nares, through eye to forelimb, preorbital portion very faint; dorsolateral row of faint, diffuse, dark, paravertebral markings extend from nape to base of tail, countershaded posteriorly by diffuse light-colored spots composing a dorsolateral row; faint, wide dark, ventrolateral stripe on trunk; beige, postsacral marking bears light-colored, anteriorly projecting arms; flanks faintly mottled with diffuse, brown speckling; limbs bearing faint, dark, irregularly shaped markings; base of toes bearing a single faint, orange spot; gular region mottled with brown, dense stippling in most scales; stippling density increases posteriorly with the abdomen being generally darker, especially laterally; original tail bearing 10 faint, irregularly shaped, brown bands and heavily mottled interspaces; enlarged scales of ventrolateral fringe highlighted in white; subcaudal region densely stippled.

Variation (Figs. 11, 12). Given the large sample size (25) across all ages classes and both sexes coupled with the ability of this species to change the intensity and boldness of its color pattern, dorsal color pattern characteristics vary considerably ranging from nearly unicolor gray-brown (Fig. 11A) to boldly contrasted patterns being offset by lightly colored areas (Figs. 11B, D). Other specimens have dorsal patterns that are more lightly colored overall and overlain with relatively faint, diffuse darker markings (Figs. 11C, E). The single hatchling had a nearly uniform gray dorsal coloration and pattern (Fig. 11F). Caudal pattern of original tails is especially variable, ranging from light-yellow to dull-white with bold, dark-colored bands (Figs. 11B, D) to having wide, faint, diffuse bands (Fig. 11C) or thin, dark, dorsal, transverse markings (Fig. 11E). There are no consistent differences in color pattern variation between individuals from the Pinlaung City (n=20) population and those from the Wingabar Cave population (n=5).

Variation in scales counts, mensural data, and additional minor aspects in coloration are presented in Table 11.

Distribution. *Hemiphyllodactylus pinlaungensis* **sp. nov.** is known from the type locality of Pinlaung City and from Wingabar Cave approximately 7 km to the southwest, Shan State and is expected to occur in other nearby areas (Fig. 1).

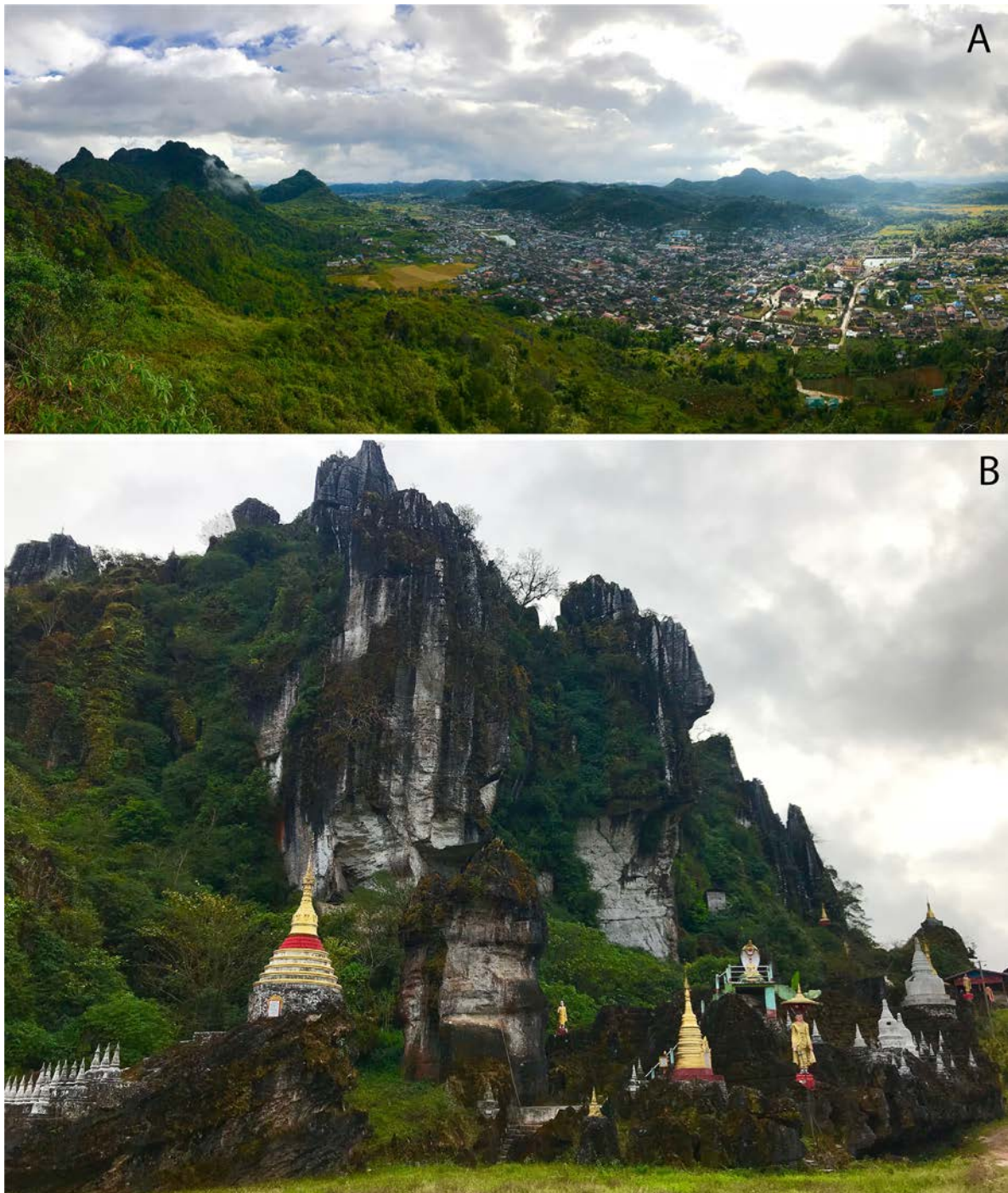


FIGURE 12. Natural and man-made microhabitat habitat of *Hemiphyllodactylus pinlaungensis* **sp. nov.** A. Pinlaung City, Shan State, Myanmar. B. Wingabar Cave, Shan State, Myanmar.

Natural History. During the evening from 1800–2400 hrs, we observed dozens of individuals on the cement and brick walls of nearly every building on the outskirts of the city but none in the surrounding upland forest (Fig. 12). Many of the females were gravid with two eggs and we also found hatchlings (SVL < 22 mm). This indicates that November is within the reproductive season of this species. Given the small area of urban habitat through which we walked on our route to forested areas (~0.5 km), we suspect individuals of this species in Pinlaung City number

well into the thousands if not more. We also observed several individuals on the following evening during the same hours on the walls of buildings and karst tower formations at Wingabar Cave (Fig. 13). Here too, we found gravid females but no hatchlings.

Etymology. The specific epithet is a toponym referring to the type locality of Pinlaung City, Shan State, Myanmar.

Comparisons. The molecular analyses indicate that *Hemiphyllodactylus pinlaungensis* **sp. nov.** is a genetically distinct member of the south lineage and is the sister species to *H. kyaiktiyoensis* **sp. nov.** (Fig. 1) from which it bears an uncorrected pairwise sequence divergence of 9.5% (Table 10). Its differences from *H. kyaiktiyoensis* **sp. nov.** and *H. zwegabinensis* **sp. nov.** are listed in the comparisons sections for those species.

Discussion

The description of these four new species of *Hemiphyllodactylus* from Myanmar brings the country total to 10, perhaps 11 given that the Lashio specimen remains unstudied. This number is undoubtedly a gross underestimate of the true diversity of this genus given that cement or wooden structures on nearly every mountain top we survey in the Shan Plateau has a new species on it. The discovery of the south lineage extends the distribution of the endemic species in this genus 345 km to the south from *H. montawaensis* at Montawa Cave in the north, Shan State to *H. zwegabinensis* **sp. nov.**, Kayin State in the south. Even though the south and north lineages come within approximately 46 km to one another in the vicinity of Kalaw, Shan State they are not sister lineages. The south lineage is sequentially related to clade 3 from Yunnan, *H. chiangmaiensis* from northwestern Thailand, *H. jinpingsensis* from Yunnan, and the north lineage, respectively (Fig. 1). In the absence of an ancestral area reconstruction analysis, this leaves multiple, competing biogeographic hypotheses as to the origin(s) of the endemic *Hemiphyllodactylus* in eastern Myanmar. This issue is currently being addressed (Grismer et al. in prep).

Acknowledgments

We wish to thank Mr. Win Naing Thaw of the Ministry of Natural Resources and Environmental Conservation Forest Department for the collection and export permits. LLG thanks the College of Arts and Sciences of La Sierra University and Fauna & Flora International for partial funding. JRO was supported by funding from the National Science Foundation of the USA (DEB 1656004). This paper is contribution number 913 of the Auburn University Museum of Natural History.

References

- Agarwal, A., El-Ghazawi, T., El-Askary, H. & Le-Moigne, J. (2007) Efficient hierarchical-PCA dimension reduction for hyperspectral imagery. *2007 IEEE International Symposium on Signal Processing and Information Technology, Giza, Egypt*, 15–18 December 2007, 9863589.
<https://doi.org/10.1109/ISSPIT.2007.4458191>
- Agarwal, I., Khandekar, A., Varad, B.G. & Ramakrishnan, U. & Karanth, K.P. (2019) The hills are alive with geckos! A radiation of a dozen species on sky islands across peninsular India (Squamata: Gekkonidae, *Hemiphyllodactylus*) with the description of three new species. *Organisms, Diversity, & Evolution*, 19, 341–361.
<https://doi.org/10.1007/s13127-019-00392-5>
- Barracough, T.G., Birky, C.W. Jr. & Burt, A. (2003) Diversification in sexual and asexual organisms. *Evolution*, 57, 2166–2172.
<https://doi.org/10.1554/02-339>
- Boulenger, G.A. (1903) Descriptions of new lizards in the collection of the British Museum. *The Annals and Magazine of Natural History*, Series 7, 12 (70), 429–435.
<https://doi.org/10.1080/00222930308678877>
- Cangelosi, R. & Goriely, A. (2007) Component retention in principal component analysis with application of cDNA microarray data. *Biology Direct*, 2 (2), 1–21.
<https://doi.org/10.1186/1745-6150-2-2>
- Cobos, A.L., 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.
<https://doi.org/10.11646/zootaxa.4107.3.5>
- Coyne, J.A. & Orr, H.A. (1998) The evolutionary genetics of speciation. *Philosophical Transactions of the Royal Society of London B*, 353, 287–305.
<https://doi.org/10.1098/rstb.1998.0210>
- De Queiroz, K. (2007) Species concepts and species delimitation. *Systemic Biology*, 56, 879–886.
<https://doi.org/10.1080/10635150701701083>
- Fontaneto, D., Herniou, E.A., Boschetti, C., Caprioli, M., Melone, G., Ricci, C. & Barraclough, T.G. (2007) Independently evolving species in asexual bdelloid rotifers. *PLoS Biology*, 5, e87.
<https://doi.org/10.1371/journal.pbio.0050087>
- Eliades, S.J., Phimmachak, S., Sivongxay, N., Siler, C.D. & Stuart, B.L. (2019) Two new species of *Hemiphyllodactylus* (Reptilia: Gekkonidae) from Laos. *Zootaxa*, 4577 (1), 131–147.
<https://doi.org/10.11646/zootaxa.4577.1.8>
- Grismer, L.L., Wood Jr., P.L., Anuar, S., Muin, M.A., Quah, E.S.H., McGuire, J.A., Brown, R.A., Ngo, V.T. & Pham, H.T. (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., Djoko, I.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), 67–68.
<https://doi.org/10.11646/zootaxa.3760.1.4>
- Grismer, L.L., Wood Jr., P.L., Zug, G.R., Thura, M.K., Grismer, M.S., Murdoch, M.L., Quah, E.S.H. & Lin, A. (2018) Two more new species of *Hemiphyllodactylus* Bleeker (Squamata: Gekkonidae) from the Shan Hills of eastern Myanmar (Burma). *Zootaxa*, 4483 (2), 295–316.
<https://doi.org/10.11646/zootaxa.4483.2.4>
- Grismer, L.L., Wood Jr., P.L., Thura, M.K., Zin, T., Quah, E.S.H., Murdoch, M.L., Grismer, M.S., Li, A., Kyaw, H. & Ngwe, L. (2017b) Phylogenetic taxonomy of *Hemiphyllodactylus* Bleeker, 1860 (Squamata: Gekkonidae) with descriptions of three new species from Myanmar. *Journal of Natural History*, 52 (13–16), 881–915.
<https://doi.org/10.1080/00222933.2017.1367045>
- Guo, W., Kaiya, Z., Jie, Y. & Peng, L. (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>
- Hillis, D.M. (2019) Species delimitation in herpetology. *Journal of Herpetology*, 53, 3–12.
<https://doi.org/10.1670/18-123>
- Hoang, D.T., Chernomor, O., von Haeseler, A., Minh, B.Q. & Le, S.V. (2017) UFBoot2: Improving the Ultrafast Bootstrap Approximation. *Molecular Biology and Evolution*, 35, 518–522.
<https://doi.org/10.1093/molbev/msx281>
- Huelsenbeck, J.P., Ronquist, F., Nielsen, R. & Bollback, J.P. (2001) Bayesian Inference of Phylogeny and Its Impact on Evolutionary Biology. *Science*, 294, 2310–2314.
<https://doi.org/10.1126/science.1065889>
- 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, 94.
<https://doi.org/10.1186/1471-2156-11-94>
- Jombart, T., Collins, C. 2015. A tutorial for discriminant analysis of principal components (DAPC) using adegenet 2.0.0. Available from: <http://adegenet.r-forge.r-project.org/files/tutorial-dapc-pdf> (accessed 11 February 2020)
- Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K., von Haeseler, A. & Jermini, L.S. (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods*, 14, 587.
<https://doi.org/10.1038/nmeth.4285>
- Knowles, L.L. & Carstens, B.C. (2007) Delimiting species without monophyletic gene trees. *Systematic Biology*, 56, 887–895.
<https://doi.org/10.1080/10635150701701091>
- Kumar, S., Stecher, G. & Tamura, K. (2016) MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution*, 33, 1870–1874.
<https://doi.org/10.1093/molbev/msw054>
- Leaché, A.D., Koo, M.S., Spencer, C.L., Papenfuss, T.J., Fisher, R.N. & McGuire, J.A. (2009) Quantifying ecological, morpho-

- logical, and genetic variation to delimit species in the coast horned lizard species complex (*Phrynosoma*). *Proceedings of the National Academy of Sciences*, 106, 12418–12423.
<https://doi.org/10.1073/pnas.0906380106>
- Lleonart, J., Salat, J. & Torres, G.J. (2000) Removing allometric effects of body size in morphological analysis. *Journal of Theoretical Biology*, 205, 85–93.
- Macey, J.J., Larson, A., Ananjeva, N.B., Fang, Z. & Papenfuss, T.J. (1997) Two novel gene orders and the role of light-strand replication in rearrangement of the vertebrate mitochondrial genome. *Molecular Biology and Evolution*, 14, 91–104.
<https://doi.org/10.1093/oxfordjournals.molbev.a025706>
- Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *Proceedings of the Gateway Computing Environments Workshop (GCE)*, New Orleans, Louisiana, 14 November 2010, pp. 1–8.
<https://doi.org/10.1109/GCE.2010.5676129>
- Minh, Q., Nguyen, M.A.T. & von Haeseler, A. (2013) Ultrafast approximation for phylogenetic bootstrap. *Molecular Biology and Evolution*, 30, 1188–1195.
<https://doi.org/10.1093/molbev/mst024>
- Ngo, V.T., Grismer, L.L., Thai, P.H. & Wood Jr., P.L. (2014) A new species of *Hemiphyllodactylus* Bleeker, 1860 (Squamata: Gekkonidae) from Ba Na-Nui Nature reserve, central Vietnam. *Zootaxa*, 3760 (4), 539–552.
<https://doi.org/10.11646/zootaxa.3760.4.3>
- 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, 268–274.
<https://doi.org/10.1093/molbev/msu300>
- Nguyen, T.Q., Botoc, 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>
- Nguyen, T.Q., Tanja, L., Minh, D.L., Ha, T.D., Michael, B. & 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>
- Rambaut, A., Suchard, M.A., Xie, D. & Drummond, A.J. (2014) Tracer. Version 1.6. Available from: <http://beast.bio.ed.ac.uk/Tracer/> (accessed 19 November 2019)
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, B., Larget, L., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) Mr. Bayes 3.2: Efficient Bayesian phylogenetic Inference and model choice across a large model space. *Systematic Biology*, 61, 539–542.
<https://doi.org/10.1093/sysbio/sys029>
- Sabaj, M.H. (2016) Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an Online Reference. Version 6.5. Available from: <http://www.asih.org/> (accessed 23 November 2019)
- Siler, C.D., Oaks, J.R., Esselstyn, J.A., Diesmos, A.C. & Brown, R.M. (2010) Phylogeny and biogeography of Philippine bent-toed geckos (Gekkonidae: *Cyrtodactylus*) contradict a prevailing model of Pleistocene diversification. *Molecular Phylogenetics and Evolution*, 55, 699–710.
<https://doi.org/10.1016/j.ympev.2010.01.027>
- Smith, M.A. (1935) *Fauna of British India, including Ceylon and Burma. Reptilia and Amphibia. Vol. II Sauria*. Taylor & Francis Ltd, London, 440 pp.
<https://doi.org/10.2307/1436417>
- Sukprasert, A., Sutthiwiwes S., Lauhachinda V. & Taksintum W. (2018) Two new species of *Hemiphyllodactylus* (Squamata: Gekkonidae) from Thailand. *Zootaxa*, 4369 (3), 363–376.
<https://doi.org/10.11646/zootaxa.4369.3.4>
- Sung, Y-H., Wing-Ho, L., Ng, N.-H., Zhang, Y. & Yang, J-H (2018) A new species of *Hemiphyllodactylus* (Squamata: Gekkonidae) from Hong Kong. *Zootaxa*, 4392 (2), 361–373.
<https://doi.org/10.11646/zootaxa.4392.2.8>
- Taylor, E.H. (1963) The lizards of Thailand. *The University of Kansas Science Bulletin*, 44, 687–1077.
- Thorpe, R.S. (1975) Quantitative handling of characters useful in snake systematics with particular reference to interspecific variation in the Ringed Snake *Matrix natrix* (L.). *Biological Journal of the Linnean Society*, 7, 27–43.
<https://doi.org/10.1111/j.1095-8312.1975.tb00732.x>
- Thorpe, R.S. (1983) A review of the numerical methods for recognizing and analyzing racial differentiation. In: Felsenstein, J. (Ed.), *Numerical Taxonomy. NATO ASI Series. Series G: Ecological Sciences. Vol. 1*. Springer-Verlag, Berlin, pp. 404–423.
https://doi.org/10.1007/978-3-642-69024-2_43
- Trifinopoulos, J., Nguyen, L.-T., von Haeseler, A. & Minh, B.Q. (2016) W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research*, 44, W232–W235.
<https://doi.org/10.1093/nar/gkw256>
- Turan, C. (1999) A note on the examination of morphometric differentiation among fish populations: The Truss System. *Turkish*

Journal of Zoology, 23, 259–263.

- Wilcox, T.P., Zwickl, D.J., Heath, T.A. & Hillis, D.M. (2002) Phylogenetic relationships of the Dwarf Boas and a comparison of Bayesian and bootstrap measures of phylogenetic support. *Molecular Phylogenetics and Evolution*, 25, 361–371. [https://doi.org/10.1016/S1055-7903\(02\)00244-0](https://doi.org/10.1016/S1055-7903(02)00244-0)
- Yan, J., Yubo, L., Guo, W., Peng, Li. & Kaiya, Z. (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. & Yang, G.-P. (1981) Three new subspecies of *Hemiphyllodactylus yunnanensis* (Boulenger) from China. *Acta Zootaxonomica Sinica*, 6, 202–209. [in Chinese, English translation by H. Ota (1996) in Smithsonian Herpetological Information Service, 110, 1–8, 1 pl.]
- 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>