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Phylogenetic taxonomy of *Hemiphyllodactylus* Bleeker, 1860 (Squamata: Gekkonidae) with descriptions of three new *species* from Myanmar

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ABSTRACT

A phylogenetic taxonomy of the gekkonid genus *Hemiphyllodactylus* based on molecular, morphological, and ecological data recovered 28 species, including three new species from the upland regions of the Shan Plateau in eastern Myanmar. *Hemiphyllodactylus linnwayensis* sp. nov. is a forest-adapted species that may also be a human commensal and *H. montawaensis* sp. nov. and *H. tonywhitteni* sp. nov. are karst forest-adapted species. The discovery of three new species from montane regions in eastern Myanmar extends the distribution of a larger monophyletic group of *Hemiphyllodactylus* westward to the eastern edge of the Ayeyrawady Basin through a series of semi-contiguous, parallel mountain ranges originating in western China and northern Thailand. The discovery of the karst forest-adapted *H. montawaensis* sp. nov. and *H. tonywhitteni* sp. nov. further emphasizes the unrealized herpetological diversity endemic to karst ecosystems and the need for increased field work throughout such habitats in South-East Asia.

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Phylogenetic taxonomy; new species; Myanmar; karst; *Hemiphyllodactylus*; Gekkonidae

Introduction

The gekkonid genus *Hemiphyllodactylus* Bleeker has a broad range that extends from southern India to the South Pacific (Zug 2010). But because species within this genus are relatively small (SVL < 45 mm), have low densities, localized distributions, and are cryptically coloured, they are never conspicuous components of the environments they inhabit. In fact, with the exception of one wide-ranging parthenogenetic species, their distributions are generally circumscribed and restricted to tropical and sub-tropical montane regions and islands (Grismer et al. 2013). These factors, coupled with data gathering inconsistencies among researchers, misidentifications, and the construction of classifications based on morphological similarity rather than common ancestry, resulted

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in a convoluted nomenclatural history (see Zug 2010). This history was disentangled with the construction of a phylogenetic taxonomy where species 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). The molecular phylogenetic component of that taxonomy indicated that *Hemiphyllodactylus* contained 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. At the time of publication, those groups contained five and 19 species, respectively, 10 of which were revealed as new and unnamed. Subsequent works used that phylogenetic taxonomy as a scaffold upon which to describe some of the unnamed species and to construct taxonomies of other newly discovered species (Nguyen et al. 2013, 2014; Tri et al. 2014; Grismer, Riyanto, et al. 2014; Grismer, Wood, et al. 2014; Grismer et al. 2015; Guo et al. 2015; Cobos et al. 2016; Yan et al. 2016). None of these analyses, however, were genus-wide but instead focused only on specific monophyletic subsets within one or the other major groups. Thus, the discovery of three new species of *Hemiphyllodactylus* from Myanmar reported herein prompted us to construct a new genus-wide phylogeny incorporating the new Burmese species and the 10 additional species described subsequent to Grismer et al. (2013).

The new Burmese species originate from different mountain ranges in the upland regions of the Shan Plateau in eastern Myanmar (Figure 1). Based on a molecular phylogenetic analysis of 1442 base pairs of the mitochondrial gene NADH dehydrogenase subunit 2 (ND2) and its flanking tRNA regions, these species are inferred to form a monophyletic group embedded within clade 4 of the *typus* group (see Grismer et al. 2013, figure 1). One of these species appears to be a forest-dwelling human commensal that may be conspecific

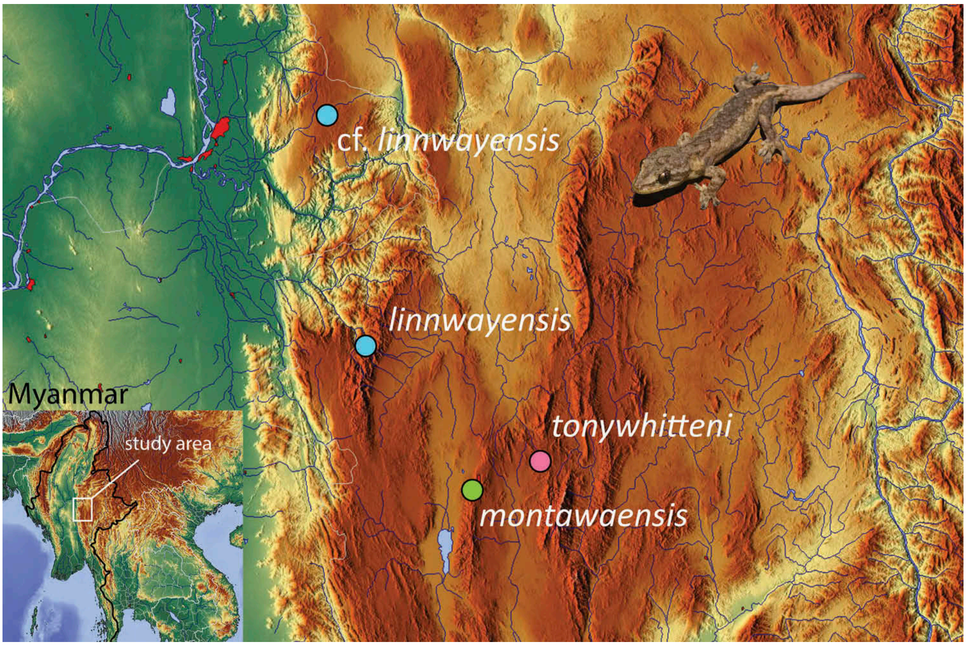

Figure 1. Distribution of *Hemiphyllodactylus montawaensis* sp. nov., *H. tonywhitteni* sp. nov., *H. linnwayensis* sp. nov., and *H.* cf. *linnwayensis* in the Shan Hills of eastern Myanmar.

with the species identified as *H.* sp. nov. 8 by Grismer et al. (2013). The other two species appear to be restricted to karst forest.

Material and methods

Sequences of the mitochondrial NADH dehydrogenase subunit 2 gene (ND2) were obtained from 116 specimens from GenBank. For others, we generated new ND2 sequence data for a 1442 bp fragment including the flanking tRNAs (tRNAmet, tRNAtrp, tRNAala, tRNAsn, tRNAcys, tRNAtyr) gene plus eight outgroup taxa based on Heinicke et al. (2011) (Table 1). Total genomic DNA was isolated from liver or skeletal muscle specimens stored in 95% ethanol using the Qiagen DNeasy^{TM} tissue kit (Valencia, CA, USA). 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 (1.5 µM), 2.0 µl 5× buffer (1.5 µM), 1.0 MgCl 10× buffer (1.5 µM), 0.18 µl Taq polymerase (5 U µl^{-1}), and 7.5 µl H2O. PCR reactions were executed on an Eppendorf Mastercycler gradient thermocycler (Foster City, California, USA) 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 50°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 gel electrophoresis. Successful targeted PCR products were vacuum purified using MANU 30 PCR plates Millipore plates and purified products were re-suspended in DNA grade water. Purified PCR products were sequenced using the ABI Big-Dye Terminator v3.1 Cycle Sequencing Kit (Provo, Utah, USA) in an ABI GeneAmp PCR 9700 thermal cycler. Cycle sequencing reactions were purified with Sephadex G-50 Fine (GE Healthcare) and sequenced on an ABI 3730xl DNA Analyzer at the BYU DNA sequencing centre. Primers used for amplification and sequencing are presented in Table 2.

Phylogenetic analyses

For the phylogenetic analyses, we applied a pluralistic approach using two model-based methods, maximum likelihood (ML) and Bayesian inference (BI). The ML analysis was implemented in IQ-TREE (Nguyen et al. 2015) and using a Bayesian information criterion (BIC), calculated HKY+G4 to be the best-fit model of evolution for the tRNA and TVM+I +G4 for the first codon position, TPM3u+I+G4 for the second position, and TIM3+I+G4 for the third codon position. One-thousand bootstrap pseudoreplicates via the ultrafast bootstrap approximation algorithm were employed and nodes having ML UFboot values (ML) of 95 and above were considered significantly supported (Minh et al. 2013). A codon-partitioned Bayesian analysis was implemented in MrBayes 3.2.3. on XSEDE (Ronquist et al. 2012) using CIPRES (Cyberinfrastructure for Phylogenetic Research; Miller et al. 2010) employing default priors and the closest approximation of the ML model scheme. Two simultaneous runs were performed with four chains, three hot and one cold. The simulation ran for 10,000,000 generations, was sampled every 10,000 generations using Markov chain Monte Carlo (MCMC), and the first 25% of each run was discarded as burn-in. Stationarity and parameter files from each run were checked in Tracer v1.6 to ensure effective sample sizes (ESS) were above 200 for all parameters

Table 1. A list of specimens used for the phylogenetic analyses. Standard museum acronyms follow Frost (2016), non-standard acronyms are as follows: ABTC, Australian Biological Tissue Collection; ACD, Arvin C. Diesmos field collection; AMB, Aaron M. Bauer; DWB, Donald W. Buden; FK, Fred Kraus field series; ITB, Institute of Tropical Biology; LSUHC, La Sierra University Herpetological Collection; RMB, Rafe M. Brown field series; TG, Tony Gamble; USNM-FS, US National Museum, Field Series; and n/a, no voucher number available.

			GenBank accession numbers
Voucher number	Species	Locality	ND2
FK 7709	*Cyrtodactylus loriae*	Milne Bay, Bunis, Papua New Guinea	EU268350
TG 00723	*Gehyra fehlmanni*	Imported from Malaysia	JN393948
ABTC 13940	*Gehyra insulensis*	Krakatau, Indonesia	GQ257784
LSUHC 7379	*Gehyra mutilata*	Pursat Province, Phnom Aural, Cambodia	JN393914
MVZ 215314	*Gekko gecko*	Phuket Island, Thailand	AF114249
ZRC 24847	*Lepidodactylus lugubris*	Singapore	JN393944
ACD 1226	*Lepidodactylus lugubris*	unknown	KF219759
DWB (no number)	*Perochirus ateles*	Pohnpei, Dehpelhi Island, Micronesia	JN393946
LSUHC 12969	***Hemiphyllodactylus linnwayensis* sp. nov.**	Linn-Way Village, Taunggyi District, Shan State, Myanmar	MF576989
LSUHC 12987	***Hemiphyllodactylus linnwayensis* sp. nov.**	Linn-Way Village, Taunggyi District, Shan State, Myanmar	MF576990
USNM-FS 36836	***Hemiphyllodactylus* cf. *linnwayensis***	Mandalay, Pyin Oo Lwin, Myanmar	JN393949
LSUHC 13026	***Hemiphyllodactylus tonywhitteni* sp. nov.**	Phapant Cave 25.2 km northeast of Taunggyi, Taunggyi District, Shan State, Myanmar	MF576991
LSUHC 13027	***Hemiphyllodactylus tonywhitteni* sp. nov.**	Phapant Cave 25.2 km northeast of Taunggyi, Taunggyi District, Shan State, Myanmar	MF576992
LSUHC 13028	***Hemiphyllodactylus tonywhitteni* sp. nov.**	Phapant Cave 25.2 km northeast of Taunggyi, Taunggyi District, Shan State, Myanmar	MF576993
LSUHC 13029	***Hemiphyllodactylus tonywhitteni* sp. nov.**	Phapant Cave 25.2 km northeast of Taunggyi, Taunggyi District, Shan State, Myanmar	MF576994
LSUHC 13030	***Hemiphyllodactylus tonywhitteni* sp. nov.**	Phapant Cave 25.2 km northeast of Taunggyi, Taunggyi District, Shan State, Myanmar	MF576995
LSUHC 10310	***Hemiphyllodactylus montawaensis* sp. nov.**	Montawa Cave 3.7 km southwest of Taunggyi, Taunggyi District, Shan State, Myanmar	MF576996
LSUHC 10311	***Hemiphyllodactylus montawaensis* sp. nov.**	Montawa Cave 3.7 km southwest of Taunggyi, Taunggyi District, Shan State, Myanmar	MF576997
LSUHC 10312	***Hemiphyllodactylus montawaensis* sp. nov.**	Montawa Cave 3.7 km southwest of Taunggyi, Taunggyi District, Shan State, Myanmar	MF576998
LSUHC 10313	***Hemiphyllodactylus montawaensis* sp. nov.**	Montawa Cave 3.7 km southwest of Taunggyi, Taunggyi District, Shan State, Myanmar	MF576999
AMB (no number)	*Hemiphyllodactylus aurantiacus*	Tamil Nadu, Yercaud, India	JN393933
ITB 2450	*Hemiphyllodactylus banaensis*	Ba Na-Nui Chua, Vietnam	KF219783
LSUHC 11216	*Hemiphyllodactylus bintik*	Gunung Tebu, Terengganu, Malaysia	KJ663757
NJNUh 00315	*Hemiphyllodactylus changningensis*	Changning, Yunnan, China	KP732436
NJNUh 00325	*Hemiphyllodactylus changningensis*	Changning, Yunnan, China	KP732437
NJNUh 00326	*Hemiphyllodactylus changningensis*	Changning, Yunnan, China	KP732438
NJNUh00328	*Hemiphyllodactylus changningensis*	Changning, Yunnan, China	KP732439
NJNUh00331	*Hemiphyllodactylus changningensis*	Changning, Yunnan, China	KP732440
NJNUh00334	*Hemiphyllodactylus changningensis*	Changning, Yunnan, China	KP732441
NJNUh00321	*Hemiphyllodactylus changningensis*	Changning, Yunnan, China	KP732442
NJNUh00323	*Hemiphyllodactylus changningensis*	Changning, Yunnan, China	KP732443

(*Continued*)

Table 1. (Continued).

Voucher number	Species	Locality	GenBank accession numbers
			ND2
NJNUh00349	*Hemiphyllodactylus changningensis*	Changning, Yunnan, China	KP732444
LSUHC 9503	*Hemiphyllodactylus chiangmaiensis*	Chang Mai, Thailand	KF219781
LSUHC 9504	*Hemiphyllodactylus chiangmaiensis*	Chang Mai, Thailand	KF219782
LSUHC 11762	*Hemiphyllodactylus cicak*	Penang Hill, Penang, Malaysia	KU845548
LSUHC 11763	*Hemiphyllodactylus cicak*	Penang Hill, Penang, Malaysia	KU845549
LSUHC 11764	*Hemiphyllodactylus cicak*	Penang Hill, Penang, Malaysia	KU845550
n/a	*Hemiphyllodactylus dushanensis*	Guizhou, China	FJ971017
n/a	*Hemiphyllodactylus dushanensis*	Guizhou, China	FJ971016
MVZ 239346	*Hemiphyllodactylus engganoensis*	Pulau Enggano, Sumatra	KF219776
USNM 563671	*Hemiphyllodactylus ganoklonis*	Ngercheu, Palau	JN393950
LSUHC 10383	*Hemiphyllodactylus harterti*	Bukit Larut, Malaysia	KF219761
LSUHC 10384	*Hemiphyllodactylus harterti*	Bukit Larut, Malaysia	KF219760
NJNUh00729-739	*Hemiphyllodactylus huishuiensis*	Huishui, Guizhou, China	KU519707
NJNUh00741-746	*Hemiphyllodactylus huishuiensis*	Huishui, Guizhou, China	KU519708
NJNUh00748	*Hemiphyllodactylus huishuiensis*	Huishui, Guizhou, China	KU519709
NJNUh00851-859	*Hemiphyllodactylus huishuiensis*	Huishui, Guizhou, China	KU519710
NJNUh	*Hemiphyllodactylus huishuiensis*	Huishui, Guizhou, China	KU519711
n/a	*Hemiphyllodactylus jinpingensis*	Yunnan, China	FJ971045
n/a	*Hemiphyllodactylus jinpingensis*	Yunnan, China	FJ971048
n/a	*Hemiphyllodactylus jinpingensis*	Yunnan, China	FJ971046
n/a	*Hemiphyllodactylus jinpingensis*	Yunnan, China	FJ971047
IEBR A.2014.3	*Hemiphyllodactylus kiziriani*	Luang Prabang, Laos	KJ676800
IEBR A.2014.4	*Hemiphyllodactylus kiziriani*	Luang Prabang, Laos	KJ676801
IEBR A.2014.5	*Hemiphyllodactylus kiziriani*	Luang Prabang, Laos	KJ676802
LSUHC 11295	*Hemiphyllodactylus larutensis*	Bukit Larut, Malaysia	KJ663758
KU 314962	*Hemiphyllodactylus insularis*	Mindanao, Philippines	KF219762
n/a	*Hemiphyllodactylus longlingensis*	Yunnan, China	FJ971042
n/a	*Hemiphyllodactylus longlingensis*	Yunnan, China	FJ971038
n/a	*Hemiphyllodactylus longlingensis*	Yunnan, China	FJ971041
n/a	*Hemiphyllodactylus longlingensis incertae sedis*	Yunnan, China	FJ971049
n/a	*Hemiphyllodactylus longlingensis*	Yunnan, China	FJ971040
LSUHC 5707	*Hemiphyllodactylus* sp. nov. 2	Pulau Sibu, Malaysia	JN393936
KU 331843	*Hemiphyllodactylus* sp. nov. 4	Cebu Island, Philippines	KF219777
RMB 4262	*Hemiphyllodactylus* sp. nov. 5	Palaui Island, Philippines	KF219778
KU 314090	*Hemiphyllodactylus* sp. nov. 6	Mindanao, Philippines	KF219779

(*Continued*)

Table 1. (Continued).

Voucher number	Species	Locality	GenBank accession numbers
			ND2
KU 314091	*Hemiphyllodactylus* sp. nov. 6	Mindanao, Philippines	KF219780
FMNH 258695	*Hemiphyllodactylus* sp. nov. 9	Champasak, Pakxong, Laos	JN393935
LSUHC 10904	*Hemiphyllodactylus tehtarik*	Gunung Tebu, Terengganu, Malaysia	KF219784
LSUHC 10717	*Hemiphyllodactylus titiwangsaensis*	Cameron Highlands, Malaysia	KF219785
LSUHC 10713	*Hemiphyllodactylus titiwangsaensis*	Cameron Highlands, Malaysia	KF219786
LSUHC 10714	*Hemiphyllodactylus titiwangsaensis*	Cameron Highlands, Malaysia	KF219787
LSUHC 10722	*Hemiphyllodactylus titiwangsaensis*	Cameron Highlands, Malaysia	KF219788
LSUHC 10723	*Hemiphyllodactylus titiwangsaensis*	Cameron Highlands, Malaysia	KF219789
LSUHC 10718	*Hemiphyllodactylus titiwangsaensis*	Cameron Highlands, Malaysia	KF219790
LSUHC 7208	*Hemiphyllodactylus titiwangsaensis*	Cameron Highlands, Malaysia	KF219791
LSUHC 10721	*Hemiphyllodactylus titiwangsaensis*	Cameron Highlands, Malaysia	KF219792
LSUHC 10716	*Hemiphyllodactylus titiwangsaensis*	Cameron Highlands, Malaysia	KF219793
LSUHC 10720	*Hemiphyllodactylus titiwangsaensis*	Cameron Highlands, Malaysia	KF219794
LSUHC 10715	*Hemiphyllodactylus titiwangsaensis*	Cameron Highlands, Malaysia	KF219795
LSUHC 10693	*Hemiphyllodactylus* cf. *titiwangsaensis*	Genting Highlands, Malaysia	KF219763
LSUHC 10700	*Hemiphyllodactylus* cf. *titiwangsaensis*	Genting Highlands, Malaysia	KF219763
LSUHC 10699	*Hemiphyllodactylus* cf. *titiwangsaensis*	Genting Highlands, Malaysia	KF219765
LSUHC 10694	*Hemiphyllodactylus* cf. *titiwangsaensis*	Genting Highlands, Malaysia	KF219766
LSUHC 6487	*Hemiphyllodactylus* cf. *titiwangsaensis*	Fraser’s Hill, Malaysia	KF219767
LSUHC 6488	*Hemiphyllodactylus* cf. *titiwangsaensis*	Fraser’s Hill, Malaysia	KF219768
LSUHC 6489	*Hemiphyllodactylus* cf. *titiwangsaensis*	Fraser’s Hill, Malaysia	KF219769
LSUHC 6477	*Hemiphyllodactylus* cf. *titiwangsaensis*	Fraser’s Hill, Malaysia	KF219770
LSUHC 8055	*Hemiphyllodactylus* cf. *titiwangsaensis*	Fraser’s Hill, Malaysia	KF219771
LSUHC 8056	*Hemiphyllodactylus* cf. *titiwangsaensis*	Fraser’s Hill, Malaysia	KF219772
LSUHC 8080	*Hemiphyllodactylus* cf. *titiwangsaensis*	Fraser’s Hill, Malaysia	KF219773
LSUHC 8092	*Hemiphyllodactylus* cf. *titiwangsaensis*	Fraser’s Hill, Malaysia	KF21977
ABTC 49760	*Hemiphyllodactylus typus*	Papua New Guinea	GQ257744
ABTC 32736	*Hemiphyllodactylus typus*	Fiji Suva	GQ257745
LSUHC 10340	*Hemiphyllodactylus typus*	Pulau Pinang, Malaysia	KF219796
LSUHC 8751	*Hemiphyllodactylus typus*	Tasik Chini, Malaysia	KF219797
MVZ 226500	*Hemiphyllodactylus typus*	Vinh Phu, Vietnam	KF219798
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971044
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971039
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971036
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971032

(*Continued*)

Table 1. (Continued).

Voucher number	Species	Locality	GenBank accession numbers
			ND2
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971027
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971031
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971030
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971043
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971035
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971022
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971020
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971019
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971018
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971028
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971026
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971023
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971029
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971025
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971024
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971021
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971034
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971037
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971033
IEBRA.2013.20	*Hemiphyllodactylus zugi*	Ha Lang, Cao Bang, Vietnam	KF575151
IEBRA.2013.21	*Hemiphyllodactylus zugi*	Ha Lang, Cao Bang, Vietnam	KF575152
ZFMK 94782	*Hemiphyllodactylus zugi*	Ha Lang, Cao Bang, Vietnam	KF575153

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 et al. (1997)	External	5′-AAGCAGTTGGGCCCATACC-3′
CyrtintF1	Siler et al. (2010)	Internal	5′-TAGCCYTCTCYTCYATYGCCC-3′
CyrtintR1	Siler et al. (2010)	Internal	5′-ATTGTKAGDGTRGCYAGGSTKGG-3′
H5934	Macey et al. (1997)	External	5′-AGRGTGCCAATGTCTTTGTGRTT-3′

(Rambaut et al. 2014). Nodes with Bayesian posterior probabilities (BPP) of 0.95 and above were considered well supported (Huelsenbeck et al. 2001; Wilcox et al. 2002).

Morphological analyses

For the descriptive work, colour notes were taken using digital images of specimens prior to preservation. For purposes of comparison, the terminology and methodology involving the evaluation of mensural and meristic characters generally follows Zug (2010) and Grismer et al. (2013). Mensural data were taken with Mitutoyo dial callipers to the nearest 0.1 mm under a Nikon SMZ 1500 dissecting microscope on the left side of the body where appropriate: snout–vent length (SVL), taken from the tip of snout to the vent; tail length (TailL), taken from the vent to the tip of the tail, original or regenerated; trunk length (TrunkL), 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 (HeadL), the distance from the posterior margin of the retroarticular process of the lower jaw to the tip of the snout; head width (HeadW), measured at the angle of the jaws; eye diameter (EyeD), the greatest horizontal diameter of the eyeball; snout–eye length (SnEye), measured from anteriormost margin of the eyeball to the tip of snout; nares–eye length (NarEye), measured from the anterior margin of the eyeball to the posterior margin of the external nares; and internarial width (SnW), measured between the nares across the rostrum. Meristic character states evaluated were the number of scales contacting the nares (circumnasal scales); the number of scales between the supranasals (postrostrals); the numbers of supralabial and infralabial 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 eye diameter; the number of longitudinal dorsal scales at mid-body contained within one eye diameter; the number of subdigital lamellae wider than long on the first finger and toe; lamellar formulae determined as the number of U-shaped, subdigital lamellae (split and single) on the digital pads on digits II–V of the hands and feet; the total number of femoroprecloacal pores (i.e. the contiguous femoral and precloacal scales bearing pores); and the number of cloacal spurs on each side. Colour pattern characters evaluated were the presence or absence of dark pigmentation in the gonadal tracts and caecum; dorsal pattern; presence or absence of a dark postorbital stripe extending to at least the neck; the presence of absence of a linear series of white postorbital and trunk spots above a dark stripe; and the presence or absence of anteriorly projecting arms of the postsacral marking. Some of the information on character states and their distribution in other species was obtained from Guo et al. (2015) and Yan et al. (2016). LSUHC refers to the La Sierra University Herpetological Collection, La Sierra University, Riverside, CA, USA; and LSUDPC refers to the La Sierra University Digital Photo Collection. Other acronyms follow Frost (2016). Specimens examined are listed in the Appendix.

Principal component analysis (PCA) and discriminant analysis of principal components (DAPC) were used to determine if the new species occupied unique positions in morphospace and the degree to which their variation in morphospace coincided with their species boundaries delimited by the molecular phylogenetic analyses. PCA, implemented by the prcomp command in R v 3.2.1 (R Core Team 2015), searches for the best overall low-dimensional representation of significant morphological variation in the data. Femoroprecloacal pore counts were excluded from the PCA due their presence in only males. We used a concatenated dataset composed of the discrete meristic data from the scale counts chin scales, circumnasal scales, supranasals, supralabials, infralabials, dorsal scales, ventral scales, subdigital lamellae of the first finger, and subdigital lamellae of the first toe and the continuous mensural data from TrunkL, HeadL, HeadW, SnEye, NarEye and ED. To remove the effects of body size from the mensural data, we used the following equation: $Xadj = X - \beta(SVL - SVLmean)$, where Xadj = adjusted value; X = measured value; β = unstandardized regression coefficient for each OTU; SVL = measured SVL; SVLmean = overall average SVL of all OTUs (Thorpe 1975, 1983; Turan 1999; Lleonart et al. 2000). All PCA data were log-transformed prior to analysis and scaled to their standard deviation in order to normalize their distribution so as to ensure characters with very large and very low values did not over-leverage the results owing to intervariable nonlinearity. To characterize clustering and separation in morphospace, a DAPC was performed to search for linear combinations of morphological variables having the greatest between-group variance and the smallest within-group variance (Jombart et al. 2010). DAPC relies on log transformed data from the PCA as a prior step to ensure that variables analysed are not correlated and number fewer than the sample size. Principal components with eigenvalues greater than one were retained for the DAPC analysis according to the criterion of Kaiser (1960), thus further reducing the dimensionality of the dataset. All statistical analyses were performed using the platform R v 3.2.1 (R Core Team 2015).

Results

The ML and BI analyses returned trees with the identical topologies and strong branch support at all nodes (Figure 2). The topology matched that of Grismer et al. (2013), confirming the designation of the *harterti* and *typus* groups and the relationships of the seven clades within the latter. The phylogeny supports the relationships of *H. changningensis* reported by Guo et al. (2015) and of *H. huishuiensis* and *H. zugi* reported by Yan et al. (2016). It differs from Nguyen et al. (2014) by placing *H. kiziriani* as the sister species to *H. yunnanensis* as opposed to its weakly supported placement as the sister species of *H. zugi*, and it differs from Yan et al. (2016) who placed *H. kiziriani* at the base of clade 6. The resolution and strong support for these nodes herein is likely due to the sampling of all species throughout the genus as opposed to just a subset of samples within a species group. Within the *harterti* group, the phylogeny confirms the results of Grismer et al. (2013) in placing *H. bintik* as the sister species of *H. harterti* and corroborates the placement of *H. cicak* as the sister lineage to the sister species *H. bintik* and *H. harterti*

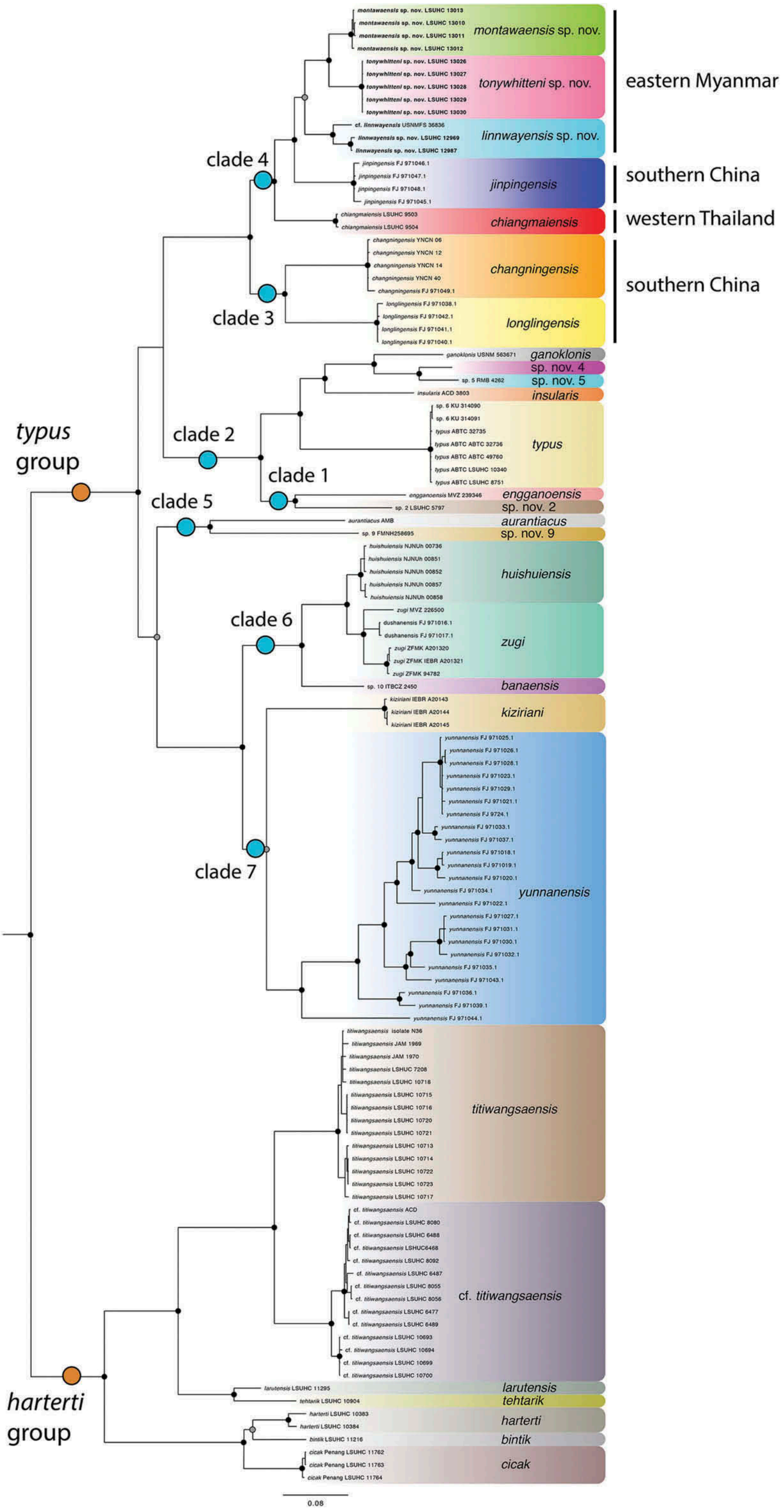

Figure 2. A Bayesian inference topology illustrating the phylogenetic relationships of the 28 species of *Hemiphyllodactylus*. Black circles are nodes supported by BPP and ML values of 0.95 and 95 or greater, respectively. Grey circles are nodes supported only by ML values 95 or greater.

(Cobos et al. 2016). The three new Burmese species form a monophyletic group within clade 4 and compose the sister lineage to *Hemiphyllodactylus jinpingensis*. The morphological analyses corroborate the lineage delineation of molecular analyses in that each new species is diagnosable from one another and all other species in clade 4 and its sister lineage clade 5 (Tables 3 and 4) and are well separated from each other in morphospace (Figures 3 and 4). They are described below herein.

Taxonomy

Hemiphyllodactylus tonywhitteni sp. nov.
Phapant dwarf gecko
(Figures 5 and 6)

Holotype

Adult male (LSUHC 13026) collected on 18 October 2016 at 1600 hours by Evan S. H. Quah, Perry L. Wood, Jr., Matthew L. Murdoch, Thaw Zin, Myint Kyaw Thura, Htet Kyaw, Marta S. Grismer, and L. Lee Grismer from Phapant Cave, 25.2 km north-east of Taunggyi, Taunggyi District, Shan State, Myanmar (21°11.472N, 96°33.214E; 1270 m).

Paratypes

Adult females (LSUHC 13027 and 13030) and juvenile female (LSUHC 13028) and juvenile male (LSUHC 13029) bear the same data as the holotype.

Diagnosis

Hemiphyllodactylus tonywhitteni sp. nov. can be separated from all other species of *Hemiphyllodactylus* by possessing the unique combination of having a maximum SVL of 38.8 mm; 5–8 chin scales; enlarged postmentals; 3–5 circumnasal scales; 2–4 scales between supranasals (=postrostrals); eight or nine supralabials; eight infralabials; 13–16 longitudinally arranged dorsal scales at midbody contained within one eye diameter and 7–9 ventral scales; varied digital formulae (Table 3); three subdigital lamellae on the first finger; three or four subdigital lamellae on the first toe; 20–26 continuous pore-bearing femoroprecloacal scales; no plate-like subcaudal scales; dark postorbital stripe not extending onto trunk; pairs of paravertebral light spots on trunk; dorsal body pattern not unicolour; postsacral marking bearing light-coloured anteriorly projecting arms; and caecum and gonads unpigmented. These characters are scored across all species of *Hemiphyllodactylus* from clades 3 and 4 (Table 3).

Description of holotype

Adult male; head triangular in dorsal profile, depressed, distinct from neck; lores and interorbital regions flat; rostrum moderate in length (NarEye/HeadL 0.33); prefrontal region flat to weakly concave; canthus rostralis smoothly rounded, barely discernible; snout moderate, rounded in dorsal profile; eye large; ear opening round, small; eye to ear distance greater than diameter of eye; rostral wider than high, bordered posteriorly by small supranasals; three internasals (=postnasal); external nares bordered anteriorly by rostral, dorsally by supranasal, posteriorly by two postnasals, ventrally by first supralabial (=circumnasals); 8 (R,L) rectangular

Table 3. Descriptive characters among species of clade 4 of Grismer et al. (2013). Shaded cells identify characters that are potentially diagnostic between one or more species.

	montawaensis sp. nov.	*tonywhitteni* sp. nov.	*linnwayensis* sp. nov.	*jinpingensis*	*chiangmaiensis*	*changningensis*	*longlingensis*
Chin scales	4–7	5–8	4–6	7–9	8–12	7 or 8	7–9
Postmentals distinctly enlarged	yes	yes	yes	yes	yes	yes	yes
Circumnasal scales	4–6	3–5	5	3 or 4	3 or 4	3 or 4	4 or 5
Scales between supranasals	1–4	2–4	2	2 or 3	1–3	2 or 3	1–3
Supralabial scales	8–10	8 or 9	9 or 10	9–11	9–11	8–11	9 or 10
Infralabial scales	8 or 9	8	8	9–11	9–12	8–10	8–10
Dorsal scales	13 or 14	13–16	13 or 14	11 or 12	11–21	11–15	10–14
Ventral scales	7 or 8	7–9	8	5–7	6–10	6–8	6 or 7
Variation in lamellar formula on hand	3–4–4–3 3–3–3–3	4–4–4–4 4–5–5–5 4–4–5–4	4–4–4–4	3–4–4–4 4–4–4–4 3–3–4–4	3–3–3–3 3–4–4–4	3–4–4–4 3–3–3–3	?
Variation in lamellar formula on foot	3–4–4–4 3–5–5–5 4–4–4–4	4–4–4–4 4–5–5–4 4–5–5–5 3–4–4–4	4–5–5–4 4–5–4–4	4–4–4–4	3–3–3–3 3–4–4–4	3–4–4–4	3–4–4–4 3–3–3–3
Subdigital lamellae on first finger	3 or 4	3	3 or 4	4	3 or 4	3 or 4	4 or 5
Subdigital lamellae on first toe	3 or 4	3 or 4	4 or 5	4 or 5	3 or 4	3 or 4	4 – 6
Femoral pores present	yes	yes	/	yes	yes	yes	yes
Precloacal and femoral pore series continuous	yes	yes	/	yes	yes	yes	yes
Femoroprecloacal pores	19–21	20–26	/	20–24	17–25	19–22	16–27
Cloacal spurs on each side	1	1	1	1	1	1 or 2	1 or 2
Subcaudals enlarged, plate-like	no	no	no	no	no	no	no
Adult females yellow	yes	no	no	no	no	no	no
Dark postorbital stripe	yes	variable	yes	yes	yes	yes	yes
Pairs of light-coloured paravertebral spots on trunk	no	yes	yes	/	no	/	yes
Dark dorsolateral stripe on trunk	no	no	no	yes	yes	yes	yes
Dorsal pattern unicolour	no	no	no	no	no	no	no
Dark dorsal transverse blotches/bands	no	no	no	yes	yes	yes	yes
Dark reticulate pattern on dorsum	yes	no	no	no	no	no	no
Postsacral marking bearing light-coloured anteriorly projecting arms	variable	yes	no	yes	no	no	yes
Caecum pigmented	no	no	no	no	yes	No	no
Gonads pigmented	no	no	no	no	yes	No	no
Maximum SVL (mm)	40.1	38.8	41.5	39.6	41.2	43.8	45.7
Trunk/SVL	0.48–0.42	0.43–0.52	0.48–0.49	0.47–0.51	0.46–0.56	0.46–0.51	0.47–0.52
HeadL/SVL	0.23–0.26	0.24–0.27	0.23–0.25	0.23–0.24	0.25–0.43	0.22–0.25	0.22–0.24
HeadW/SVL	0.16–0.17	0.17–0.19	0.17	0.17	0.18–0.23	0.17–0.18	0.17–0.19
SnEye/HeadL	0.41–0.44	0.41–0.50	0.40–0.42	0.41–0.43	0.23–0.49	0.41–0.49	0.42–0.45
NarEye/HeadL	0.29–0.34	0.29–0.34	0.300.31	0.29–0.32	0.17–0.33	0.30–0.37	0.29–0.34
EyeD/HeadL	0.22–0.24	0.21–0.23	0.22–0.25	0.22–0.26	0.13–0.24	0.21–0.25	0.22–0.25
SnW/HeadL	0.13–0.15	0.13–0.14	0.14	0.13–0.15	0.08–0.23	0.12–0.16	0.12–0.14

Table 4. Summary statistics of meristic characters in *Hemiphyllodactylus montawaensis* sp. nov., *H. tonywhitteni* sp. nov., and *H. linnwayensis* sp. nov.

	montawaensis sp. nov.	*tonywhitteni* sp. nov.	*linnwayensis* sp. nov.
Chin scales			
Mean	6.3	6.6	5.0
SD	1.50	1.14	1.00
Range	4–7	5–8	4–6
N	4	5	2
Postmentals distinctly enlarged	yes	yes	yes
Circumnasal scales			
Mean	5.0	4.6	5.0
SD	0.82	0.89	0
Range	4–6	3–5	5
N	4	5	2
Scales between supranasals			
Mean	1.5	2.8	2.0
SD	0.58	0.84	0
Range	1–4	2–4	2
N	4	5	2
Supralabial scales			
Mean	8.5	8.6	9.5
SD	1.00	0.55	0.71
Range	8–10	8 or 9	9 or 10
N	4	5	2
Infralabial scales			
Mean	8.25	8.0	8.0
SD	0.50	0.00	0
Range	8 or 9	8	8
N	4	5	2
Dorsal scales			
Mean	13.3	14.8	13.5
SD	0.50	1.30	0.71
Range	13 or 14	13–16	13 or 14
N	4	5	2
Ventral scales			
Mean	7.3	8.0	8.0
SD	0.50	0.71	0
Range	7 or 8	7–9	8
N	4	5	2
Subdigital lamellae on first finger			
Mean	3.8	3.0	3.5
SD	0.50	0.00	0.71
Range	3 or 4	3	3 or 4
N	4	5	2
Subdigital lamellae on first toe			
Mean	3.3	3.6	4.5
SD	0.50	0.55	0.71
Range	3 or 4	3 or 4	4 or 5
N	4	5	2
Femoroprecloacal pores			
Mean	21.0	22.0	/
SD	0.50	2.83	/
Range	19–21	20–26	/
N	2	4	/

supralabials tapering to below posterior margin of orbit; 8 (R,L) rectangular infralabials tapering to below posterior margin of orbit; 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 and posteriorly by two large postmentals; each postmental bordered laterally by a single large,

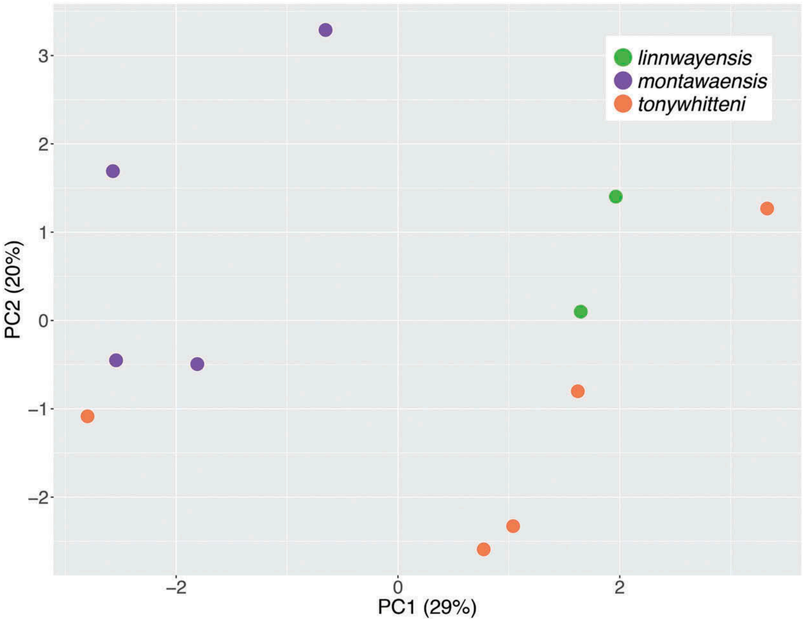

Figure 3. Principal component analysis (PCA) of the species *Hemiphyllodactylus montawaensis* sp. nov., *H. tonywhitteni* sp. nov., and *H. linnwayensis* sp. nov., showing their distribution in morphospace along the first two principal components.

sublabial; seven chin scales; gular scales small, subimbricate, grading posteriorly into slightly larger, subimbricate, throat and pectoral scales which grade into slightly larger, subimbricate ventrals.

Body somewhat elongate (Trunk/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, seven ventral scales contained within one eye diameter; precloacal scales slightly larger than abdominal scales; pore-bearing precloacal scales continuous with pore-bearing femoral scales, totalling 26; 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; lamellar formula of digits II–V 4-4-4-4 (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; hind limbs short, more robust than forelimbs, covered with flat, juxtaposed scales dorsally and by 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; lamellar formula of digits II–V 4-4-4-4 (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; dorsal caudal scales small, square, subimbricate; tail

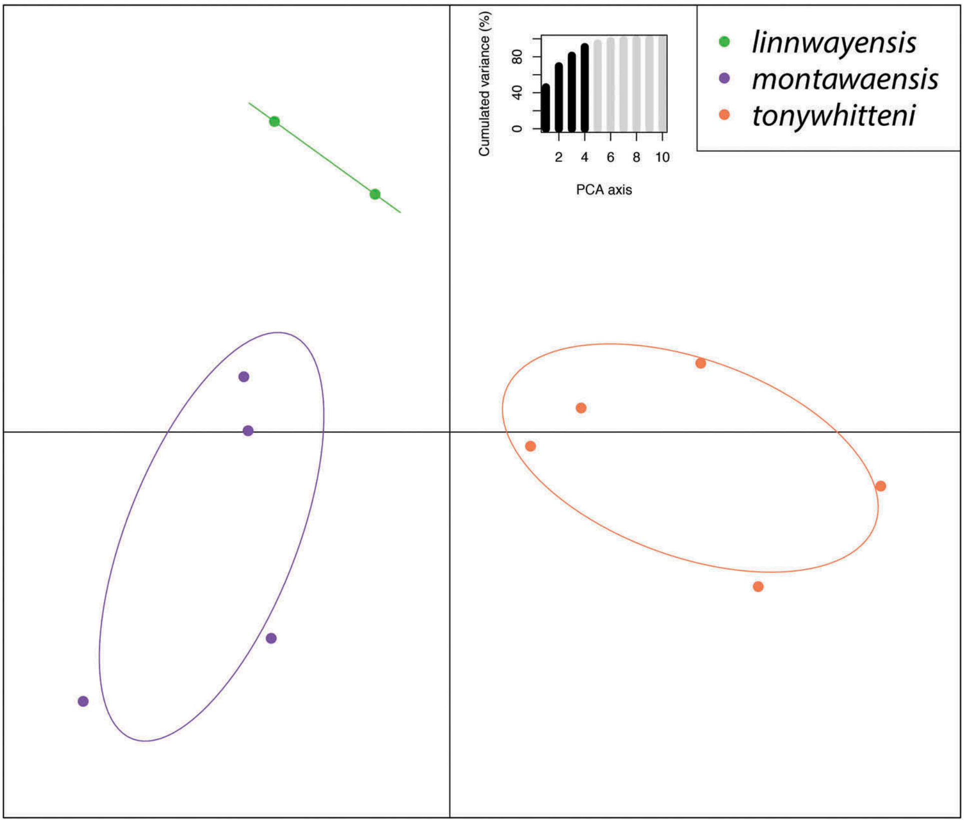

Figure 4. Discriminant analysis of principal components (DAPC) of the species *Hemiphyllodactylus montawaensis* sp. nov., *H. tonywhitteni* sp. nov., *H. linnwayensis* sp. nov. emphasizing between-group variance and minimizing within-group variance based on retention of the first four components.

regenerated, covered with flat imbricate scales. Morphometric data are presented in Table 5.

Coloration before preservation (Figure 5)

Top of head, body, limbs, and tail grey, overlain with darker, broken bands on trunk appearing as paravertebral markings highlighted posteriorly by light-coloured, diffuse blotches; poorly defined dark, lineate markings extend from occipital region to shoulder; spotting or striping on trunk absent; diffuse, dark, preorbital stripe; dark, postorbital stripe irregularly shaped, extending to shoulder region; limbs bearing irregularly shaped, dark markings; tail generally unicolour; gular region generally immaculate, except for darker lateral areas and faint stippling in scales; and pigmentation density increases posteriorly with the abdomen being generally grey.

Variation (Figures 5 and 6)

The colour patterns of the paratypes generally match that of the holotype. LSUHC 13027 is darker overall and the colour pattern is less distinct. The light-coloured, paravertebral blotches in LSUHC 13029 are salmon coloured. The dark dorsal pattern of LSUHC 13028

Figure 5. (a) Juvenile male paratype (LSUHC 13029) of *Hemiphyllodactylus tonywhitteni* sp. nov. from the type locality of Phapant Cave 25.2 km north-east of Taunggyi, Taunggyi District, Shan State, Myanmar. (b) Adult female paratype (LSUHC 13030) from the type locality.

is more speckled and that of the adult female LSUHC 13030 is more reticulate. LSUHC 13030 has an original tail lacking enlarged subcaudal plates and bearing a weak, ventrolateral fringe and a distinct banding pattern. The tail is oval in cross-section and the underside is dull orange. The intensity of coloration and contrast in pattern changes with mood and activity. Differences in scales counts are presented in Table 5.

Distribution

Hemiphyllodactylus tonywhitteni sp. nov. is known only from the type locality of Phapant Cave, Taunggyi District, Shan State, Myanmar (Figure 1).

Figure 6. Type series of *Hemiphyllodactylus tonywhitteni* sp. nov. from the type locality of Phapant Cave 25.2 km north-east of Taunggyi, Taunggyi District, Shan State, Myanmar.

Natural history

Phapant Cave is a complex of three caves situated around a small depression along a narrow river. The karstic ridge and outcroppings surround a small monastery which incorporates the caves for worship. The hilly area connecting the caves is composed of highly eroded limestone walls bearing many cracks and pores. Large limestone boulders that have broken away from the cliff face line the base of the shallow escarpment (Figure 7). We believe *Hemiphyllodactylus tonywhitteni* sp. nov. is a karst-adapted species. A specimen of *H. tonywhitteni* sp. nov. was found just inside a small opening of one of the caves nearly 4 m above the cave entrance. More specimens were found on the boulders at the base of the cliff and one on one of the cement buildings of the monastery. Syntopic with *H. tonywhitteni* sp. nov. on both the karst outcroppings and the cement building was an undescribed species of *Hemidactylus*. *Hemidactylus* sp. nov. was also found on wooden structures and vegetation where *H. tonywhitteni* sp. nov. was absent.

Etymology

This specific epithet '*tonywhitteni*' honours Dr Tony Whitten of Fauna & Flora International who has championed a broad range of conservation efforts in Indonesia and the Asia Pacific for well over a quarter of a century. His tireless efforts to conserve and help manage karst ecosystems have been a great inspiration to the senior author (LLG) herein.

Comparisons

The molecular analyses indicate that *Hemiphyllodactylus tonywhitteni* sp. nov. is embedded within clade 4 of the *typus* group and is the sister species of *H. montawaensis* sp. nov. It can be distinguished from *H. jinpingensis*, *H. chiangmaiensis* and the species of clade 3 by lacking dark, dorsolateral stripes on the trunk and transverse, dorsal blotches. The PCA analysis shows that it occupies a unique morphospace

Table 5. Type series of *Hemiphyllodactylus tonywhitteni* sp. nov. / = data unavailable.

	LSUHC 13026 holotype m	LSUHC 13027 paratype f	LSUHC 13028 paratype f	LSUHC 13029 paratype m	LSUHC 13030 paratype f
Chin scales	7	5	6	7	8
Postmentals distinctly enlarged	yes	yes	yes	yes	yes
Circumnasal scales	5	5	5	3	5
Scales between supranasals	3	2	3	2	4
Supralabial scales	8	9	9	9	8
Infralabial scales	8	8	8	8	8
Dorsal scales	14	13	15	16	16
Ventral scales	7	9	8	8	8
Lamellar formula on hand	4-4-4-4	4-4-4-4	4-5-5-5	4-4-4-4	4-4-5-4
Lamellar formula on foot	4-4-4-4	4-5-5-4	4-5-5-5	3-4-4-4	4-4-4-4
Subdigital lamellae on first finger	3	3	3	3	3
Subdigital lamellae on first toe	3	4	4	3	4
Femoroprecloacal pores	26	20	/	22	20
Cloacal spurs on each side	1	1	1	1	1
Subcaudals enlarged, plate-like	no	no	no	no	no
Dark postorbital stripe	yes	yes	yes	no	yes
Adult females yellow	/	no	/	/	no
Pairs of paravertebral light spots on trunk	yes	yes	yes	yes	yes
Dark dorsolateral stripe on trunk	no	no	no	no	no
Dorsal pattern unicolour	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
Postsacral marking bearing light-coloured anteriorly projecting arms	yes	yes	yes	yes	yes
Caecum pigmented	no	no	no	no	no
gonads pigmented	no	no	no	no	no
SVL	36.2	37.2	31.5	32.1	38.8
Trunk	17.4	19.2	14.9	13.7	19
HeadL	9.3	9.1	8.4	7.9	9.2
HeadW	6.7	6.6	5.2	5.6	6.8
SnEye	3.9	4.2	3.6	3.2	4.6
NarEye	3.1	3.1	2.4	2.3	3
EyeD	2	2.1	1.8	1.7	2
SnW	1.2	1.2	1.2	1	1.3
Trunk/SVL	0.48	0.52	0.47	0.43	0.49
HeadL/SVL	0.26	0.24	0.27	0.25	0.24
HeadW/SVL	0.19	0.18	0.17	0.17	0.18
SnEye/HeadL	0.42	0.46	0.43	0.41	0.50
NarEye/HeadL	0.33	0.34	0.29	0.29	0.33
EyeD/HeadL	0.22	0.23	0.21	0.22	0.22

with respect to *H. montawaensis* sp. nov. and *H. linnwayensis* sp. nov. with PC1 and PC2 accounting for 49% of the variation in the concatenated dataset (Figure 3). PC1 accounted for 29% of the variation and loaded most heavily for trunk length and the number of subdigital lamellae on the first toe (Table 6). PC2 accounted for an additional 20% of the variation and loaded most heavily for the number of dorsal scales. The first four components of the PCA were retained for the DAPC which shows that not only are all three species distinct but all individuals of each species fall very close to or within the 95% confidence ellipses (Figure 4). Uncorrected pair-wise sequence divergence between *H. tonywhitteni* sp. nov. and all other species of clades 3 and 4 ranges from 6.4–18.7% (Table 7). *Hemiphyllodactylus tonywhitteni* sp. nov. is most similar to its sister species *H. montawaensis* sp. nov. but differs in having more

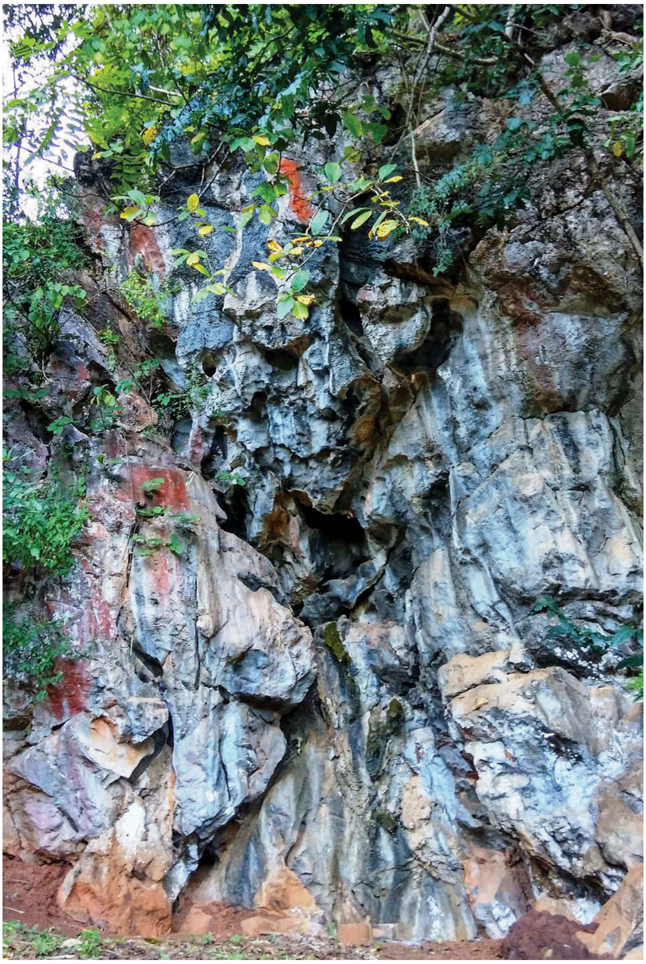

Figure 7. Karst wall microhabitat of *Hemiphyllodactylus tonywhitteni* sp. nov. from the type locality.

femoroprecloacal pores (20–26 versus 19–21) and a relatively wider head (0.17–0.19 versus 0.16–0.17) throughout its growth trajectory (Figure 8) and a statistically significantly wider head ($p < 0.24$, $n = 5$) as an adult.

Hemiphyllodactylus montawaensis sp. nov.

Montawa dwarf gecko

(Figures 9 and 10)

Holotype

Adult male (LSUHC 13010) collected on 17 October 2016 at 1600 hours by Evan S. H. Quah, Perry L. Wood, Jr., Matthew L. Murdoch, Thaw Zin, Myint Kyaw Thura, Htet Kyaw, Marta S. Grismer, and L. Lee Grismer from Montawa, Cave 3.7 km south-west of Taunggyi, Taunggyi District, Shan State, Myanmar (20°47.521N, 97°01.222E; 1171 m).

Table 6. Summary statistics and principal component analysis scores for *Hemiphyllodactylus linnwayensis* sp. nov., *H. montawaensis* sp. nov., and *H. tonywhitteni* sp. nov. Abbreviations are listed in the Materials and methods.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11
Standard deviation	2.157940	1.779671	1.559294	1.273633	1.203946	1.012170	0.947366	0.626729	0.493023	0.339397	0.000000
Proportion of variance	0.291040	0.197950	0.151960	0.101380	0.090590	0.064030	0.056090	0.024550	0.015190	0.007200	0.000000
Cumulative proportion	0.291040	0.489000	0.640960	0.742340	0.832930	0.896970	0.953060	0.977610	0.992800	1.000000	1.000000
Eigenvalue	4.656706	3.167229	2.431399	1.622141	1.449485	1.024488	0.897502	0.392790	0.243071	0.115190	0.000000
Chin scales	−0.148314	−0.287171	0.256611	0.291001	−0.145190	−0.495888	0.061530	0.118869	0.327434	0.431150	−0.234871
Circumnasals	−0.034626	0.128182	−0.377335	0.510465	0.100847	−0.322998	0.206325	−0.094720	−0.203535	0.026118	0.247419
Internasals	0.116043	−0.339999	−0.103996	−0.003223	0.551867	0.104580	0.248237	0.208468	0.260508	0.169824	0.155119
Supralabials	0.288826	0.299020	0.206789	0.218203	−0.144543	0.278485	−0.144693	0.090768	0.248821	0.053238	0.411638
Infralabials	−0.046511	0.344486	0.398984	0.295475	−0.099127	−0.186725	0.154711	0.109195	0.071608	−0.263909	−0.198112
Dorsal scales	0.087242	−0.476615	0.256987	−0.011066	0.011951	0.025099	0.033307	−0.264777	0.246776	−0.590175	−0.116556
Ventral scales	0.370568	−0.115556	−0.100733	−0.157315	−0.153022	−0.191594	−0.159774	−0.604698	−0.110723	0.327582	−0.117109
1st finger lamellae	−0.211009	0.134501	−0.392445	−0.159053	−0.343884	0.228945	0.091143	0.025524	0.590777	0.138250	−0.168650
1st toe lamellae	0.347451	0.187914	−0.049698	0.286869	0.072347	0.179632	0.274057	−0.366383	0.325139	0.012830	−0.124641
Trunk	0.353355	0.201224	−0.027951	−0.204926	−0.145258	−0.416392	−0.060214	0.033090	0.122227	−0.203543	0.131890
HeadL	−0.119104	0.284472	0.088735	−0.473296	0.269773	−0.397555	−0.089578	0.006972	0.290226	0.009848	0.189396
HeadW	−0.393999	0.164159	−0.256558	0.060967	−0.013365	0.002175	−0.103334	−0.159693	−0.041496	−0.216735	−0.320194
SnEye	−0.245543	0.017735	0.477566	−0.083367	−0.195242	0.239828	0.078352	−0.190587	−0.148360	0.337694	0.161090
NarEye	−0.089255	0.177093	0.114952	0.225725	0.498779	0.085761	−0.634857	−0.175907	0.149071	0.108840	−0.194969
EyeD	−0.282884	0.211138	0.146691	−0.156143	0.269557	−0.016475	0.492722	−0.424568	0.001642	0.002733	0.107816
SnW	−0.353572	−0.242658	−0.095144	0.188016	−0.181128	−0.088362	−0.250627	−0.261635	0.208416	−0.151062	0.590091

Table 7. Per cent uncorrected pairwise sequence divergence between the species of clades 3 and 4.

	1	2	3	4	5	6	7
1. *changningensis*	**0.007**	**	**	**	**	**	**
2. *chiangmaiensis*	0.188	**0.002**	**	**	**	**	**
3. *jinpingensis*	0.169	0.146	**0.009**	**	**	**	**
4. *linnwayensis*	0.199	0.149	0.111	**0.005**	**	**	**
5. *longlingensis*	0.177	0.182	0.179	0.185	**0.006**	**	**
6. *montawaensis*	0.179	0.137	0.117	0.118	0.193	**0.002**	**
7. *tonywhitteni*	0.182	0.135	0.123	0.108	0.187	0.064	**

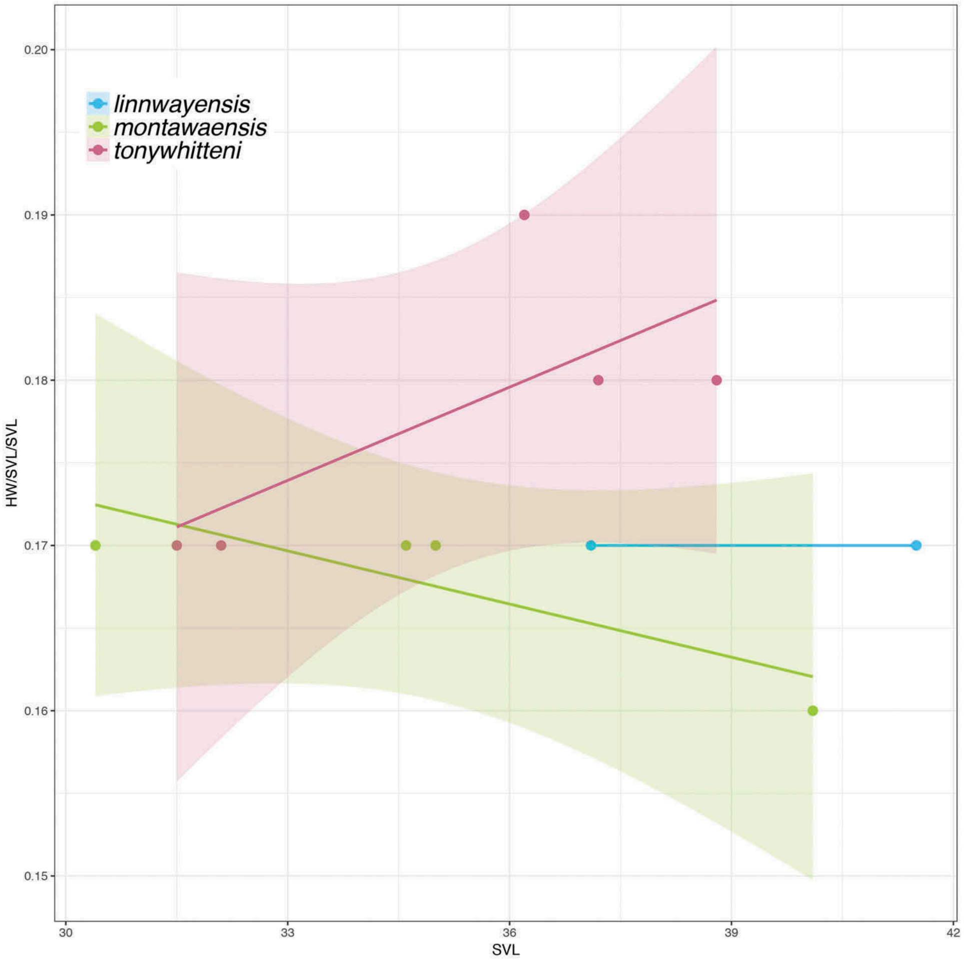

Figure 8. Comparative growth trajectories of head width between *Hemiphyllodactylus montawaensis* sp. nov., *H. tonywhitteni* sp. nov. and *H. linnwayensis* sp. nov. Shaded areas represent the 95% confidence intervals.

Paratypes

Adult male (LSUHC 13011) and adult females (LSUHC 13012–13) bear the same data as the holotype.

Figure 9. (a) Adult female paratype (LSUHC 13012) of *Hemiphyllodactylus montawaensis* sp. nov. from the type locality of Montawa Cave 3.7 km south-west of Taunggyi, Taunggyi District, Shan State, Myanmar. (b) Adult male holotype (LSUHC 13010) from the type locality.

Diagnosis

Hemiphyllodactylus montawaensis sp. nov. can be separated from all other species of *Hemiphyllodactylus* by possessing the unique combination of having a maximum SVL of 40.1 mm; 4–7 chin scales; enlarged postmentals; 4–6 circumnasal scales; 1–4 scales between supranasals (=postrostrals); 8–10 supralabials; eight or nine infralabials; 13 or 14 longitudinally arranged dorsal scales at mid-body contained within one eye diameter and seven or eight ventral scales; varied digital formulae (Table 3); three or four subdigital lamellae on the first finger and toes; 19–21 pore-bearing femoroprecloacal scales; no plate-like subcaudal scales; dark, postorbital stripe not extending onto trunk; no pairs of paravertebral light spots on trunk; dorsal body pattern not unicolour; postsacral marking generally not bearing light-

Figure 10. Type series of *Hemiphyllodactylus montawaensis* sp. nov. from the type locality of Montawa Cave 3.7 km south-west of Taunggyi, Taunggyi District, Shan State, Myanmar.

coloured, anteriorly projecting arms; and caecum and gonads unpigmented. These characters are scored across all species of *Hemiphyllodactylus* from clades 4 and 5 (Table 3).

Description of holotype

Adult male; head triangular in dorsal profile, depressed, distinct from neck; lores and interorbital regions flat; rostrum moderate in length (NarEye/HeadL 0.32); prefrontal region flat to weakly concave; canthus rostralis smoothly rounded, barely discernible; snout moderate, rounded in dorsal profile; eye large; ear opening round, small; eye to ear distance greater than diameter of eye; rostral wider than high, partially divided dorsally, bordered posteriorly by small supranasals; one internasal (=postnasal); external nares bordered anteriorly by rostral, dorsally by supranasal, posteriorly by four postnasals, ventrally by first supralabial (=circumnasals); 8 (R,L) rectangular supralabials tapering to below posterior margin of orbit; 8 (R,L) subrectangular infralabials tapering to below posterior margin of orbit; 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 and posteriorly by two large postmentals; each postmental bordered laterally by a single large, sublabial; seven chin scales; gular scales small, subimbricate, grading posteriorly into slightly larger, subimbricate, throat and pectoral scales which grade into slightly larger, subimbricate ventrals.

Body somewhat elongate (Trunk/SVL 0.51), 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, seven scales contained within one eye diameter; precloacal scales slightly larger than abdominal scales; pore-bearing precloacal scales continuous with pore-bearing femoral scales, totalling 21; 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, larger on right than on left; distal, subdigital lamellae of digits II–V undivided, angular and U-shaped; lamellae proximal to these transversely expanded; lamellar formula of digits II–V 3-4-4-3 (R,L); four transversely expanded lamellae on digit I; claws on digits II–V well developed, sheathed; 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 by 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; 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, sheathed; distal portions of digits strongly curved, terminal joint free, arising from central portion of lamellar pad; dorsal caudal scales small, square, subimbricate; tail original, subcaudals larger, flat, imbricate; ventrolateral caudal scales forming a weak fringe; and tail oval in cross-section. Morphometric data are presented in Table 8.

Coloration before preservation (Figure 9)

Top of head, body, limbs, and tail grey overlain with a darker, broken reticulate pattern transforming to poorly defined bands on the posterior one-half of the tail and smaller irregularly shaped markings on the lower flanks; spotting or striping on trunk absent; distinctive, dark, preorbital stripe; dark, postorbital stripe irregular, bifurcated, and broken on the right side; limbs bearing irregularly shaped, dark markings; ventral surfaces light-coloured with minute dark spots in each scale; spotting more dense beneath hind limbs and tail.

Variation (Figures 9 and 10)

The colour patterns of the paratypes generally match that of the holotype. Light dorsal spotting is more prevalent in LSUHC 13011 and 13013 and the light-coloured postsacral mark is more vivid in the latter. The adult female LSUHC 13012 has a yellow ground colour and an orangish subcaudal region. The intensity of coloration and contrast in colour pattern changes with mood and activity. Differences in scales counts are presented in Table 8.

Distribution

Hemiphyllodactylus montawaensis sp. nov. is known only from the type locality of Montawa Cave, Taunggyi District, Shan State, Myanmar (Figure 1).

Natural history

Montawa Cave is situated at 1171 m in elevation along a steep, fast-flowing stream and lies approximately two-thirds the way up a precipitous 130 km north to south tending karstic ridge edging the eastern margin of a flat basin containing Inle and Nam Belu Lakes. The cave is associated with a small monastery and the mouth is approximately 30 m above the monastery level. Steep, vertical karst walls frame the mouth of the cave and extend into the forest in both directions (Figure 11). The limestone at this locality

Table 8. Type series of *Hemiphyllodactylus montawaensis* sp. nov. / = data unavailable.

Sex	LSUHC 13010 holotype m	LSUHC 13011 paratype m	LSUHC 13012 paratype f	LSUHC 13013 paratype f
Chin scales	7	7	4	7
Postmentals distinctly enlarged	yes	yes	yes	yes
Circumnasal scales	6	5	4	5
Scales between supranasals	4	1	2	1
Supralabial scales	8	8	8	10
Infralabial scales	8	8	8	9
Dorsal scales	13	14	13	13
Ventral scales	7	8	7	7
Lamellar formula on hand	3-4-4-3	3-3-3-3	3-3-3-3	3-3-3-3
Lamellar formula on foot	3-4-4-4	3-5-5-5	4-4-4-4	3-4-4-4
Subdigital lamellae on first finger	4	4	4	3
Subdigital lamellae on first toe	3	3	3	4
Precloacal and femoral pore series continuous	yes	yes	/	/
Femoroprecloacal pores	21	19	/	/
Cloacal spurs on each side	1	1	1	1
Subcaudals enlarged, plate-like	no	no	no	no
Dark postorbital stripe	yes	yes	yes	yes
Adult females yellow	/	/	yes	/
Pairs of paravertebral light spots on trunk	no	no	no	no
Dark dorsolateral stripe on trunk	no	no	no	no
Dorsal pattern unicolour	no	no	no	no
Dark dorsal transverse blotches/bands	no	no	no	no
Dark reticulate pattern on dorsum	yes	yes	yes	yes
Postsacral marking bearing light-coloured anteriorly projecting arms	no	no	yes	no
Caecum pigmented	no	no	no	no
Gonads pigmented	no	no	no	no
SVL	35	34.6	40.1	30.4
Trunk	18	16.7	20.9	15.6
HeadL	8.2	8.3	9.5	7.8
HeadW	6	5.9	6.5	5.3
SnEye	3.6	3.4	4.1	3.4
NarEye	2.6	2.8	3.1	2.3
EyeD	2	1.9	2.1	1.7
SnW	1.2	1.2	1.2	1.1
Trunk/SVL	0.51	0.48	0.52	0.51
HeadL/SVL	0.23	0.24	0.24	0.26
HeadW/SVL	0.17	0.17	0.16	0.17
SnEye/HeadL	0.44	0.41	0.43	0.44
NarEye/HeadL	0.32	0.34	0.33	0.29
EyeD/HeadL	0.24	0.23	0.22	0.22

was not as weathered and porous as that of the Phapant Cave region but was more sedimentary in composition. We believe *H. montawaensis* sp. nov. is a karst-adapted species. All lizards were found at night between 1900 and 2300 hours 1–3 m above the ground on the flat, uneroded limestone faces outside the cave in open areas generally devoid of vegetation. No *Hemiphyllodactylus* were seen on the surrounding man-made structures of the monastery, within the cave, or on vegetation. Adult female LSUHC 13012 contained two eggs.

Etymology

This specific epithet '*montawaensis*' refers to the type locality of Montawa cave.

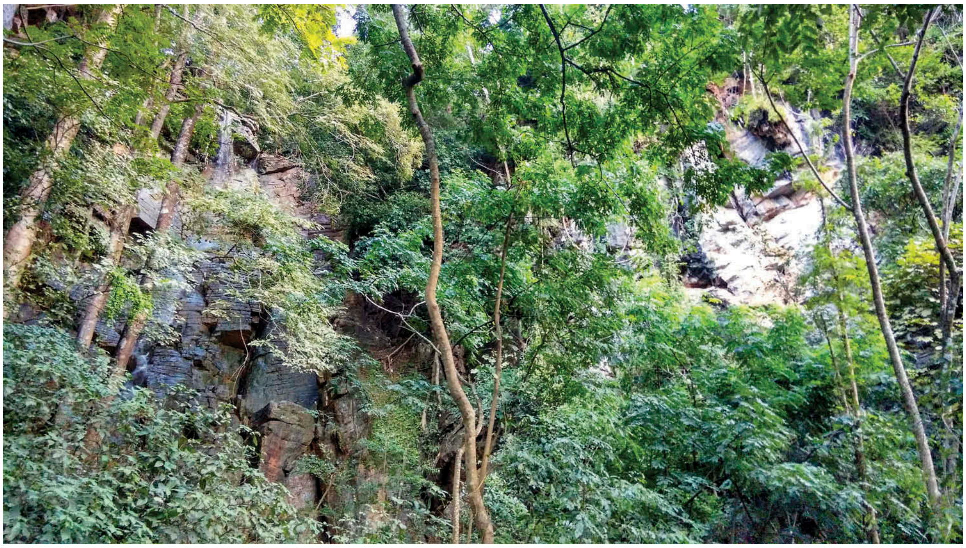

Figure 11. Forested karstic ridge of the type locality of *Hemiphyllodactylus montawaensis* sp. nov.

Comparisons

The molecular analyses indicate that *Hemiphyllodactylus montawaensis* sp. nov. is embedded within clade 4 of the *typus* group and is the sister species of *H. tonywhitteni* sp. nov. *Hemiphyllodactylus montawaensis* sp. nov. can be distinguished from all other species in clade 3 by having 4–7 as opposed to 7–12 chin scales, collectively; it differs further from all species of these two clades by having a dark, reticulate, dorsal pattern. It differs further from *H. tonywhitteni* sp. nov. in having relatively narrower head (0.16–0.17 versus 0.17–0.19) throughout its growth trajectory (Figure 8) and a statistically significantly narrower head ($p < 0.024$, $n = 6$) as an adult. Uncorrected pair-wise sequence divergence between *H. montawaensis* sp. nov. and all other species of clades 3 and 4 ranges from 6.4–19.3% (Table 7). See comparison section for *H. tonywhitteni* sp. nov. for a discussion of the PCA and DAPC results and for comparisons to *H. tonywhitteni* sp. nov.

Hemiphyllodactylus linnwayensis sp. nov.
Linn-Way dwarf gecko
(Figure 12)

Holotype

Adult female (LSUHC 12987) collected on 14 October 2016 at 1800 hours by L. Lee Grismer, Evan S. H. Quah, Perry L. Wood, Jr., Matthew L. Murdoch, Thaw Zin, Myint Kyaw Thura, Htet Kyaw, and Marta S. Grismer from Linn-Way Village, 64.7 km north of Kalaw, Taunggyi District, Shan State, Myanmar (21°13.356N, 96°32.780E; 1306 m).

Paratype

Adult female (LSUHC 12969) collected on 13 October 2016 by Myint Kyaw Thura from the same locality as the holotype.

Figure 12. (a) Adult female holotype (LSUHC 12987) of *Hemiphyllodactylus linnwayensis* sp. nov. from the type locality of Linn-Way Village, 64.7 km north of Kalaw, Taunggyi District, Shan State, Myanmar. (b) Adult female paratype (LSUHC 12869) from the type locality.

Diagnosis

Hemiphyllodactylus linnwayensis sp. nov. can be separated from all other species of *Hemiphyllodactylus* by possessing the unique combination of having a maximum SVL of 41.5 mm; 4–6 chin scales; enlarged postmentals; five circumnasal scales; two scales between supranasals (=postrostrals); nine or 10 supralabials; eight infralabials; 13 or 14 longitudinally arranged dorsal scales at midbody contained within one eye diameter and eight ventral scales; varied digital formulae (Table 3); three or four subdigital lamellae on the first finger; four or five subdigital lamellae on the first toe; no plate-like subcaudal scales; adult females not yellow; dark postorbital stripe not extending onto trunk; pairs of light-coloured paravertebral spots on trunk; dorsal body pattern not unicolour; postsacral marking not bearing light-coloured anteriorly projecting arms; and caecum and gonads unpigmented. These characters are scored across all species of *Hemiphyllodactylus* from clades 3 and 4 (Table 3).

Description of holotype

Adult female; head triangular in dorsal profile, depressed, distinct from neck; lores and interorbital regions flat; rostrum moderate in length (NarEye/HeadL 0.31); prefrontal region flat to weakly concave; canthus rostralis smoothly rounded, barely discernible; snout moderate, rounded in dorsal profile; eye large; ear opening round, small; eye to ear distance greater than diameter of eye; rostral wider than high, bordered posteriorly by supranasals; two internasals (=postnasal); 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 orbit; 8 (R,L) subrectangular infralabials tapering to below posterior margin of orbit; scales of rostrum, lores, top of head, and occiput small, granular, those of rostrum largest and slightly raised; dorsal superciliaries flat, mostly square, subimbricate, similar in size throughout; mental triangular, bordered laterally by first infralabials and posteriorly by two large postmentals; each postmental bordered laterally by a single large, sublabial; four chin scales; gular scales small, subimbricate, grading posteriorly into slightly larger, subimbricate, throat and pectoral scales which grade into slightly larger, subimbricate ventrals.

Body somewhat elongate (Trunk/SVL 0.49), 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 scales contained within one eye diameter; precloacal scales slightly larger than abdominal scales; pore-bearing precloacal scales continuous with pore-bearing femoral scales, pores small, poorly developed; 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; 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, partially sheathed; 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 by 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; lamellar formula of digits II–V 4-5-4-4 (R,L); five transversely expanded lamellae on digit I; claws on digits II–V well developed, partially sheathed; distal portions of digits strongly curved, terminal joint free, arising from central portion of lamellar pad; dorsal caudal scales small, square, subimbricate;; tail original, subcaudals larger than dorsals, flat, imbricate; ventrolateral caudal scales forming a weak fringe; and tail oval in cross-section. Morphometric data are presented in Table 9.

Coloration before preservation (Figure 12)

Ground colour of top of head and vertebral and paravertebral region of trunk grey; side of head, flanks, limbs, and tail light-grey to beige; thin, dark, preorbital stripe; thicker, dark postorbital stripe extending to shoulder region; thin, dark stripe on each side of nape; area between nape and postorbital stripes light-coloured; trunk overlain with small, square to rectangularly shaped, dark, paravertebral markings highlighted

Table 9. Type series of *Hemiphyllodactylus linnwayensis* sp. nov. / = data unavailable.

Sex	LSUHC 12969 paratype f	LSUHC 12987 holotype f
Chin scales	6	4
Postmentals distinctly enlarged	yes	yes
Circumnasal scales	5	5
Scales between supranasals	2	2
Supralabial scales	9	10
Infralabial scales	8	8
Dorsal scales	14	13
Ventral scales	8	8
Lamellar formula on hand	4-4-4-4	4-4-4-4
Lamellar formula on foot	4-5-5-4	4-5-4-4
Subdigital lamellae on first finger	3	4
Subdigital lamellae on first toe	4	5
Precloacal and femoral pore series separate	/	/
Precloacal and femoral pores	/	/
Cloacal spurs on each side	1	1
Subcaudals enlarged, plate-like	/	no
Dark postorbital stripe	yes	yes
Adult females yellow	no	no
Pairs of light-coloured paravertebral spots on trunk	yes	yes
Dark dorsolateral stripe on trunk	no	no
Dorsal pattern unicolour	no	no
Dark dorsal transverse blotches/bands	no	no
Dark reticulate pattern on dorsum	no	no
Postsacral marking bearing light-coloured anteriorly projecting arms	no	no
Caecum pigmented	no	no
Gonads pigmented	no	no
SVL	37.1	41.5
Trunk	17.7	20.4
HeadL	9.3	9.6
HeadW	6.3	7.1
SnEye	3.7	4
NarEye	2.8	3
EyeD	2	2.4
SnW	1.3	1.3
Trunk/SVL	0.48	0.49
HeadL/SVL	0.25	0.23
HeadW/SVL	0.17	0.17
SnEye/HeadL	0.40	0.42
NarEye/HeadL	0.30	0.31
EyeD/HeadL	0.22	0.25
SnW/HeadL	0.14	0.14

posteriorly by small, diffuse, light-coloured blotches; dark, square, postsacral, marking lacking well-defined, light-coloured, anteriorly projecting arms; nine dark, irregularly shaped, caudal markings forming a weak banding pattern; ventral region of head, body, and limbs generally lighter medially and darker laterally due to increased stippling; and mid-ventral, subcaudal region dull-orange, lateral regions dark.

Variation (Figure 12)

The colour pattern of the paratype closely matches that of the holotype. The overall ground colour is generally lighter and the dark, paravertebral markings on the dorsum are more paired than broken. The intensity of coloration and contrast in the pattern changes with mood and activity. Differences in scales counts are presented in Table 9.

Distribution

Hemiphyllodactylus linnwayensis sp. nov. is known only from the type locality of Linn-Way Village, Taunggyi District, Shan State, Myanmar (Figure 1).

Natural history

Linn-Way village is a small, spread-out, somewhat isolated village on the western fringes of the Shan Plateau surrounded by secondary, upland forest (Figure 13). Four *Hemiphyllodactylus linnwayensis* sp. nov. were seen in this region but only two were collected. The paratype (LSUHC 12969) was found beneath a small log on the grounds of a monastery at 0100 hours and the holotype (LSUHC 12987) was collected from an interior wall of a small house in the village at 2200 hours while we were being served dinner. Another specimen was observed on the same wall the following night but escaped collection. Another specimen that we presume was the same species was observed on a small wooden structure in the middle of a fallow field 3.4 km south of Linn-Way Village outside Yae Whin Cave that also escaped collection. No specimens were seen on karst microhabitats in the region that we extensively explored.

Etymology

This specific epithet '*linnwayensis*' refers to the type locality of Linn-Way Village.

Comparisons

The molecular analyses indicate that *Hemiphyllodactylus linnwayensis* sp. nov. is embedded within clade 4 of the *typus* group and is the sister lineage to the sister species *H. tonywhitteni* sp. nov. and *H. montawaensis* sp. nov. *Hemiphyllodactylus*

Figure 13. Forested village habitat of *Hemiphyllodactylus linnwayensis* sp. nov.

linnwayensis sp. nov. can be separated from all species of clades 3 and 4 except *H. montawaensis* sp. nov. by having fewer chin scales (4–6 as opposed to 5–12, collectively). It differs further from *H. jinpingensis, H. chiangmaiensis, H. changningensis*, and *H. longlingensis* in lacking as opposed to having dark, dorsolateral stripes on the trunk and dark, dorsal, transverse blotches. It differs from *H. tonywhitteni* sp. nov. in lacking well-defined, light-coloured, anteriorly projecting arms of the postsacral marking. It differs from *H. montawaensis* sp. nov. in that adult females are grey as opposed to yellow and having pairs of light-coloured, paravertebral spots on the trunk. See comparison section for *H. tonywhitteni* sp. nov. for a discussion of the PCA and DAPC results.

Remarks

The molecular phylogeny of Grismer et al. (2013) identified a specimen from Pyin Oo Lwin, Mandalay Region in the western Shan Hills as an undescribed new species they referred to as *Hemiphyllodactylus* sp. nov. 8. The molecular phylogeny herein (Figure 2) recovers this specimen as the sister lineage to *H. linnwayensis* sp. nov. from Linn-Way Village in Shan State, 90 km to the south. The uncorrected pair-wise sequence divergence (p-distance) between these two species is 4.6%, less than the 5% Grismer et al. (2013) used to flag potential unconfirmed candidate species they were unable to examine. In sharp contrast, we note that the p-distance between the sister species *H. montawaensis* sp. nov. and *H. tonywhitteni* sp. nov. is 6.4% and they are separated by only 25 km (Figures 1 and 14). Additionally, we propose that latter are karst-adapted species that cannot range continuously throughout forested habitats whereas *H. linnwayensis* sp. nov. is a forest-adapted species and may even be in a human commensal relationship, given that they can be found on man-made structures and within homes. The collection data of the Pyin Oo Lwin specimen are similar to *H. linnwayensis* sp. nov. in that it was found in a secondary growth forest in a botanical garden on a wooden viewing platform (2017 email from GR Zug to LLG). Based on the above, we hypothesize the potential for gene exchange between these two populations is likely, and thus conservatively consider *Hemiphyllodactylus* sp. nov. 8. as *H.* cf. *linnwayensis* sp. nov. until specimens become available for examination.

Discussion

The discovery of three new species of *Hemiphyllodactylus* from montane regions in eastern Myanmar is more expected than it is remarkable. Species of this genus are notable for their upland, circumscribed distributions (Grismer et al. 2013; Grismer, Riyanto, et al. 2014; Grismer, Wood, et al. 2014; Grismer et al. 2015; Nguyen et al. 2013, 2014; Tri et al. 2014; Guo et al. 2015; Cobos et al. 2016; Yan et al. 2016) and the discovery of these species simply extends the distribution of a monophyletic group composed of clades 3 and 4 to the west through a contiguous series of parallel mountain ranges originating in western China and northern Thailand. More importantly, however, is the discovery of two more karst forest-adapted geckos. This continues to underscore the growing realization that karst habitats harbour an untold amount of herpetological diversity in South-East Asia (see Grismer, Wood, Anuar, et al. 2016; Grismer, Wood, Aowphol, et al. 2016; Grismer et al. 2017 and references therein). These distinctive, insular micro-ecosystems provide unique combinations of

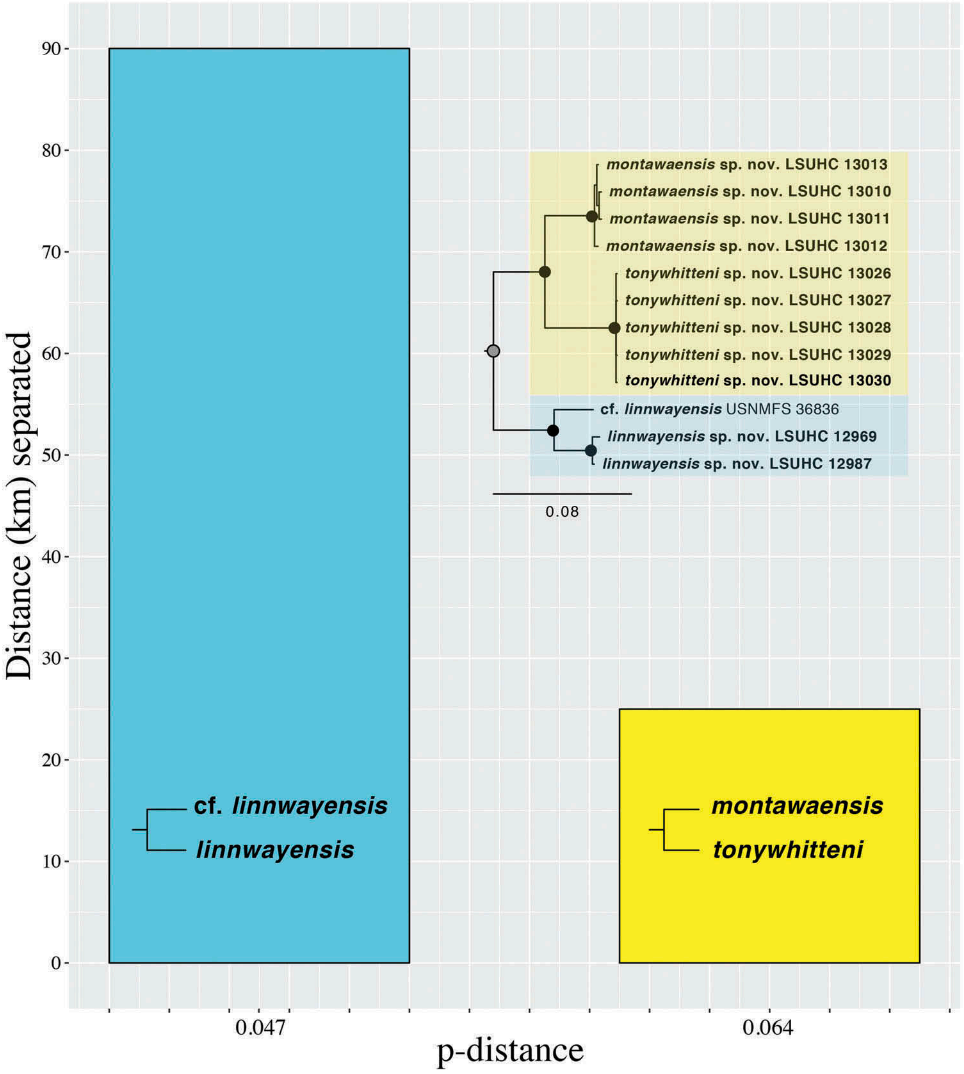

Figure 14. Bar graph comparing the relationship of distance (km) of separation and uncorrected pairwise sequence divergence (p-distance) within and between the pairs of sister lineages *Hemiphyllodactylus tonywhitteni*–*H. montawaensis* and *H. linnwayensis*–*H.* cf. *linnwayensis*.

ecological features – vertical to inverted rocky substrates, climatic stability, low illumination, relaxed predation, reduced prey base – not found in the surrounding forested areas that can promote and drive ecological speciation (Schluter 2001; Rundle and Nosil 2005; Nosil 2012; Grismer et al. 2017). Thus, the potential for the discovery of new species in these understudied ecosystems cannot be overstated. Grismer et al. (2017) described 12 new species of bent-toed geckos (*Cyrtodactylus*) from eastern and southern Myanmar from one of the same localities reported here (Linn-Way region) for the new *Hemiphyllodactylus*. We are also in the process of describing two new species of karst forest-adapted house geckos (*Hemidactylus*) from the Shan Hills. The need for additional field research in the karst regions in

South-East Asia in general and the Shan Plateau in particular needs to be emphasized.

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Disclosure statement

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Appendix. Specimens examined

The following specimens were examined. Museum acronyms follow Frost (2016).

Hemiphyllodactylus banaensis. – Ba Na summit of Ba Na–Nui Chua Nature Reserve, HoaVang District, Da Nang City, Vietnam, ITBCZ 2450, 2461–2468.

Hemiphyllodactylus bintik. – Gunung Tebu, Terengganu, Peninsular Malaysia, LSUHC 11216.

Hemiphyllodactylus chiangmaiensis. – Thailand: Chiang Mai Province, Chiang Mai NSMNH 15192–200.

Hemiphyllodactylus cicak. – Penang Hill, Pulau Pinang, Peninsular Malaysia, LSUHC 11762–65.

Hemiphyllodactylus engganoensis. – Indonesia, Sumatra, Bengkulu Province, Pulau Enggano MVZ 236345–46.

Hemiphyllodactylus ganoklonis. – Palau: Palau Ngercheu KU 314962.5797. *Hemiphyllodactylus harterti*. – Malaysia: Perak, Bukit Larut LSUHC 10383–84. *Hemiphyllodactylus insularis*. – Philippines: Zamboanga City Province, Municipality of Pasonanca, Zamboanga City KU 314962.

Hemiphyllodactylus sp. nov. 2. – Malaysia, Johor, Pulau Sibu LSUHC 5797.

Hemiphyllodactylus sp. nov. 4. – Philippines: Cebu Province, Municipality of Argao, Mount Lantoy KU 331843.

Hemiphyllodactylus sp. nov. 6. – Philippines: Agusan del Sur Province, Municipality of San Francisco, Barangay Kaim KU 314090–91.

Hemiphyllodactylus sp. nov. 9. – Laos: Champasak Province, Pakxong District FMNH 258696.

Hemiphyllodactylus titiwangsaensis. – Malaysia: Pahang, Cameron Highlands LSUHC 7208–14; 9076, 9161–61, 9815, 10254, 10273, 10385, 10713–23.

Hemiphyllodactylus typus. – Malaysia: Pahang, Tasik Chini LSUHC 8664, 8751; Penang, Pulau Pinang, Air Terjun Titi Kerawang LSUHC 10342.

Hemiphyllodactylus cf. *yunnanensis*. – Cambodia; Pursat Province, Phnom Samkos LSUHC 8242.

Hemiphyllodactylus cf. *titiwangsaensis*. – Malaysia: Pahang, Fraser's Hill LSUHC 6477, 6487–89, 8055–57, 8080, 8092; Genting Highlands LSUHC 10693–94, 10699–700