



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

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Received 28 March 2013; revised 4 June 2013; accepted for publication 6 June 2013

Conserving the planet's biodiversity is greatly handicapped, in that only a small fraction of it (~14–75%) has been described so far. Integrative taxonomy is making significant inroads in light of this challenge by incorporating multiple data sets across a wide range of disciplines that simultaneously elucidate phylogenetic structure and delimit species-level lineages within a unified species concept. An integrative taxonomic approach to the classification of the gekkonid genus *Hemiphyllodactylus* Bleeker, 1860 reveals that it is far more diverse than posited by a recent taxonomic revision based solely on morphology, and that it is composed of at least 19 species, most of which are montane upland or insular endemics. Three new species (*Hemiphyllodactylus dushanensis* sp. nov., *Hemiphyllodactylus jinpingensis* sp. nov., and *Hemiphyllodactylus longlingensis* sp. nov.) from southern China previously considered to be subspecies of *Hemiphyllodactylus yunnanensis* (Boulenger, 1903) are elevated to full species status, and 10 new species-level lineages ranging from Vietnam, Laos, Thailand, Myanmar, Peninsular Malaysia, the Philippines, and Indonesia are identified. One new species, *Hemiphyllodactylus tehtarik* sp. nov. from Gunung Tebu, Terengganu, Peninsular Malaysia, is described herein, and is differentiated from all other species of *Hemiphyllodactylus* on the basis of morphology, colour pattern, and an 18.1–31.5% sequence divergence from all other congeners. *Hemiphyllodactylus larutensis* (Boulenger, 1900) is removed from the synonymy of *H. harterti* (Werner, 1900). Using an integrative taxonomic approach imbues the revised classification of

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Hemiphyllodactylus with more objectivity, stability, and phylogenetic history, while identifying undescribed species-level lineages in potential need of conservation.

© 2013 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2013, **169**, 849–880.
doi: 10.1111/zoj.12064

ADDITIONAL KEYWORDS: conservation – cryptic species – Gekkonidae – *Hemiphyllodactylus tehtarik* sp. nov. – *Hemiphyllodactylus* – integrative taxonomy – Malaysia – new species.

INTRODUCTION

The most imposing challenge confronting biodiversity conservation and management is that the vast majority of the world's species remain undiscovered. Mora *et al.* (2011) and Costello, May & Sork (2013) collectively estimate that taxonomists have described only 14–75% of the planet's biodiversity, and that the majority of species remain undiscovered in remote areas or exist as unrecognized lineages in understudied species complexes (Funk, Caminer & Ron, 2012). Integrative taxonomy is making significant inroads in addressing these issues. This pluralistic methodology incorporates conceptual issues concerning the origins, limits, and evolution of species across a broad array of data sets (Camargo & Sites, 2013), while simultaneously elucidating the phylogenetic structure of biodiversity and delimiting its central units (species) in the context of a unified lineage-based species concept (*sensu de Queiroz*, 1998, 2007). One of the essential components to integrative taxonomy is coupling the theories and methods of molecular phylogenetics with traditional morphological taxonomy in order to delimit species boundaries, and to add robust, statistical stability to the resulting classifications (Dayrat, 2005). Used in this way, molecular phylogenies not only delineate the occurrence of lineages, but can also outline their ecogeographic distributions (Raxworthy *et al.*, 2007), thus informing investigators where to begin searching for morphological evidence, further supporting these lineages (Sites & Marshall, 2003; Yeates *et al.*, 2011). This approach has been successful for many groups where convergent morphology and cryptic (Siler & Brown, 2010; Funk *et al.*, 2012; Welton *et al.* in press) has made species delimitation and the construction of stable phylogenetic classifications nearly intractable (e.g. Carranza & Arnold, 2006, 2012; Goricki & Trontelj, 2006; Leaché *et al.*, 2009; Bauer *et al.*, 2010, 2013; Siler & Brown, 2010; Linkem, Diesmos & Brown, 2011; Funk *et al.*, 2012; Grismer *et al.*, 2012a; Johnson *et al.*, 2012; Nishikawa *et al.*, 2012; Vasconcelos *et al.*, 2012; Loredó *et al.*, 2013). Because integrative taxonomy incorporates objective, independent molecular data sets that are less prone to researcher bias (Cardoso, Serrano &

Vogler, 2009; Padial *et al.*, 2010; Hey & Pinho, 2012; Camargo & Sites, 2013), it is especially useful for testing the morphological alpha-level taxonomies of groups in which species of relatively similar appearance have resulted in years of competing taxonomic interpretations, synonymies (Bickford *et al.*, 2007; Wiens & Penkrot, 2002), and unrecognized species. Thus, classifications developed by this iterative approach (see Yeates *et al.*, 2011) are likely to be more stable (Dayrat, 2005; de Queiroz, 2007) and inheritantly infused with the group's evolutionary history, and provide a more realistic foundation for broader evolutionary studies.

The gekkonid genus *Hemiphyllodactylus* Bleeker, 1860 has had a long and tangled taxonomic history (for a discussion, see Zug, 2010). It currently comprises eight species (Zug, 2010) that collectively extend from the Mascarene Islands in the western Indian Ocean, eastwards through southern Asia and Indochina. From here the genus ranges southwards through the Philippines and Sundaland, through the Indo-Australian Archipelago, and continues into much of Polynesia as far eastwards as Hawaii. All *Hemiphyllodactylus* are small (snout–vent length, SVL < 63 mm), nocturnal, scansorial, similar in appearance, nondescript, forest-dwelling species that do not constitute a particularly noticeable component of the lizard fauna to which they belong. Many species generally occur as geographically restricted upland or insular populations throughout mainland Asia, or are restricted to islands in western Indonesia and the Philippines. As such, most species are not known from large series of specimens, the known distribution limits of other species remain incomplete, the descriptions of some species are missing key diagnostic features that define other members of the genus, and no attempts have been made to incorporate phylogenetic data into their classification. We propose here to begin resolving some of these issues through an integrative approach (Padial *et al.*, 2010), by incorporating phylogenetic data derived from the mitochondrial gene NADH dehydrogenase subunit 2 (*ND2*) and its flanking regions with existing morphological data. The iterative use of these independent data sets will provide more robust hypotheses for delimiting species

boundaries and generating a taxonomic foundation upon which we will build, with the acquisition of additional material.

MATERIAL AND METHODS

PHYLOGENETIC ANALYSIS

We obtained a substantial volume of sequence data for *ND2* from a number of specimens on GenBank (Table 1). For others, we sequenced a 1505-bp fragment of mitochondrial *ND2*, including the flanking transfer RNAs (*tRNAmet*, *tRNAtrp*, *tRNAala*, *tRNAasn*, *tRNAcys*, and *tRNA tyr*) from 80 in-group samples and eight out-group taxa, based on Heinicke *et al.* 2011a, b (Table 1). Total genomic DNA was isolated from liver or skeletal muscle specimens stored in 95% ethanol using the Qiagen DNeasy™ tissue kit. *ND2* was amplified using a double-stranded polymerase chain reaction (PCR) under the following conditions: 1.0 µL of genomic DNA, 1.0 µL of light strand primer, 1.0 µL of heavy strand primer, 1.0 µL of dinucleotide pairs, 2.0 µL of 5× buffer, 1.0 µL of MgCl 10× buffer, 0.18 µL of Taq polymerase, and 7.5 µL of H₂O. PCR reactions were executed on an Eppendorf Mastercycler 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 and annealing at 47–52 °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 10% agarose gel electrophoresis. Successful targeted PCR products were vacuum purified using MANU 30 PCR plates (Millipore), 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 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 Brigham Young University DNA Sequencing Center. Primers used for amplification and sequencing are presented in Table 2.

For the phylogenetic analyses, we applied a pluralistic approach using the character-based method of maximum parsimony (MP) and two model-based methods, maximum likelihood (ML) and Bayesian inference (BI). The Akaike information criterion (AIC) as implemented in MODELTEST 3.7 (Posada & Crandall, 1998), was used to calculate the best-fitting model of evolution for each codon position (Table 3). Maximum parsimony (MP) trees with associated bootstrap estimates for nodal support were obtained using PAUP* 4.0 (Swofford, 2002). One thousand bootstrap replicates for each heuristic search were run with ten random additional sequence replicates using tree

bisection and reconnection (TBR) branch swapping. The 1000 bootstrap replicates were summarized as a 50% majority rule consensus tree. An ML analysis with 1000 bootstrap pseudoreplicates was performed using RAxML HPC 7.2.3 (Stamatakis, Hoover & Rougemont, 2008), employing the rapid hill-climbing algorithm (Stamatakis *et al.*, 2008). The Bayesian analysis was carried out in MRBAYES 3.1 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) using default priors. Two simultaneous runs were performed with eight chains per run: seven hot and one cold, following default priors. The analysis was run for 2 000 000 generations and sampled every 1000 generations from the Markov chain Monte Carlo (MCMC). The analysis was halted after the average standard deviation split frequency was below 0.01. The program Are We There Yet? (AWTY; Nylander *et al.*, 2008) was employed to plot the log-likelihood scores against the number of generations to assess convergence and to determine the appropriate number of burn-in trees. We conservatively discarded the first 25% of the trees as burn-in. A consensus tree was then computed from the two parallel runs using TreeAnnotator 1.7.4 (Drummond *et al.*, 2012). Nodes with posterior probabilities above 0.95 were considered significantly supported (Wilcox *et al.*, 2002).

MORPHOLOGICAL ANALYSIS

For the descriptive work, colour notes were taken using digital images of specimens prior to preservation. For the purpose of comparison, the terminology and methodology involving the evaluation of mensural and meristic characters generally follows Zug (2010). Mensural data were obtained 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: 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 hindlimb 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

Table 1. A list of specimens used for phylogenetic analyses in this study

Voucher number	Species	Locality	GenBank accession numbers
			ND2
FK 7709	<i>Cyrtodactylus loriae</i>	Milne Bay, Bunis, Papua New Guinea	EU268350
TG 00723	<i>Gehyra fehlmanni</i>	Imported from Malaysia	JN393948
ABTC 13940	<i>Gehyra insulensis</i>	Krakatau, Indonesia	GQ257784
LSUHC 7379	<i>Gehyra mutilata</i>	Pursat Province, Phnom Aural, Cambodia	JN393914
MVZ 215314	<i>Gekko gekko</i>	Phuket Island, Thailand	AF114249
ZRC 24847	<i>Lepidodactylus lugubris</i>	Singapore	JN393944
ACD 1226	<i>Lepidodactylus</i> sp.	unknown	
DWB (no number)	<i>Perochirus ateles</i>	Pohnpei, Dehpelhi Island, Micronesia	JN393946
AMB (no number)	<i>Hemiphyllodactylus aurantiacus</i>	Tamil Nadu, Yercaud, India	JN393933
n/a	<i>Hemiphyllodactylus dushanensis</i>	Guizhou, China	FJ971017
n/a	<i>Hemiphyllodactylus dushanensis</i>	Guizhou, China	FJ971016
USNM 563671	<i>Hemiphyllodactylus ganoklonis</i>	Ngercheu, Palau	–
LSUHC 10383	<i>Hemiphyllodactylus harterti</i>	Bukit Larut, Malaysia	–
LSUHC 10384	<i>Hemiphyllodactylus harterti</i>	Bukit Larut, Malaysia	–
KU 314962	<i>Hemiphyllodactylus insularis</i>	Mindanao, Philippines	–
n/a	<i>Hemiphyllodactylus jinpingensis</i>	Yunnan, China	FJ971045
n/a	<i>Hemiphyllodactylus jinpingensis</i>	Yunnan, China	FJ971048
n/a	<i>Hemiphyllodactylus jinpingensis</i>	Yunnan, China	FJ971046
n/a	<i>Hemiphyllodactylus jinpingensis</i>	Yunnan, China	FJ971047
LSUHC 11295	<i>Hemiphyllodactylus larutensis</i>	Bukit Larut, Malaysia	–
n/a	<i>Hemiphyllodactylus longlingensis</i>	Yunnan, China	FJ971042
n/a	<i>Hemiphyllodactylus longlingensis</i>	Yunnan, China	FJ971038
n/a	<i>Hemiphyllodactylus longlingensis</i>	Yunnan, China	FJ971041
n/a	<i>Hemiphyllodactylus longlingensis inserta sedis</i>	Yunnan, China	FJ971049
n/a	<i>Hemiphyllodactylus longlingensis</i>	Yunnan, China	FJ971040
LSUHC 10693	<i>Hemiphyllodactylus</i> sp. nov. 1	Genting Highlands, Malaysia	–
LSUHC 10700	<i>Hemiphyllodactylus</i> sp. nov. 1	Genting Highlands, Malaysia	–
LSUHC 10699	<i>Hemiphyllodactylus</i> sp. nov. 1	Genting Highlands, Malaysia	–
LSUHC 10694	<i>Hemiphyllodactylus</i> sp. nov. 1	Genting Highlands, Malaysia	–
LSUHC 6487	<i>Hemiphyllodactylus</i> sp. nov. 1	Fraser's Hill, Malaysia	–
LSUHC 6488	<i>Hemiphyllodactylus</i> sp. nov. 1	Fraser's Hill, Malaysia	–
LSUHC 6489	<i>Hemiphyllodactylus</i> sp. nov. 1	Fraser's Hill, Malaysia	–
LSUHC 6477	<i>Hemiphyllodactylus</i> sp. nov. 1	Fraser's Hill, Malaysia	–
LSUHC 8055	<i>Hemiphyllodactylus</i> sp. nov. 1	Fraser's Hill, Malaysia	–
LSUHC 8056	<i>Hemiphyllodactylus</i> sp. nov. 1	Fraser's Hill, Malaysia	–
LSUHC 8080	<i>Hemiphyllodactylus</i> sp. nov. 1	Fraser's Hill, Malaysia	–
LSUHC 8092	<i>Hemiphyllodactylus</i> sp. nov. 1	Fraser's Hill, Malaysia	–
ACD	<i>Hemiphyllodactylus</i> sp. nov. 1	Fraser's Hill, Malaysia	–
LSUHC 5707	<i>Hemiphyllodactylus</i> sp. nov. 2	Pulau Sibul, Malaysia	–
MVZ 239346	<i>Hemiphyllodactylus</i> sp. nov. 3	Pulau Enggano, Sumatra, Indonesia	–
KU 331843	<i>Hemiphyllodactylus</i> sp. nov. 4	Cebu Island, Philippines	–
RMB 4262	<i>Hemiphyllodactylus</i> sp. nov. 5	Palau Island, Philippines	–
KU 314090	<i>Hemiphyllodactylus</i> sp. nov. 6	Mindanao, Philippines	–
KU 314091	<i>Hemiphyllodactylus</i> sp. nov. 6	Mindanao, Philippines	–
LSUHC 9503	<i>Hemiphyllodactylus</i> sp. nov. 7	Chang Mai, Thailand	–
LSUHC 9504	<i>Hemiphyllodactylus</i> sp. nov. 7	Chang Mai, Thailand	–
USNM-FS 36836	<i>Hemiphyllodactylus</i> sp. nov. 8	Mandalay, Pyin Oo Lwin, Myanmar	JN393949
FMNH 258695	<i>Hemiphyllodactylus</i> sp. nov. 9	Champasak, Pakxong, Laos	JN393935
ITB 2450	<i>Hemiphyllodactylus</i> sp. nov. 10	Ba Na-Nui Chua, Vietnam	–

Table 1. Continued

Voucher number	Species	Locality	GenBank accession numbers
			ND2
LSUHC 10904	<i>Hemiphyllodactylus tehtarik</i> sp. nov.	Gunung Tebu, Malaysia	–
LSUHC 10717	<i>Hemiphyllodactylus titiwangsaensis</i>	Cameron Highlands, Malaysia	–
LSUHC 10713	<i>Hemiphyllodactylus titiwangsaensis</i>	Cameron Highlands, Malaysia	–
LSUHC 10714	<i>Hemiphyllodactylus titiwangsaensis</i>	Cameron Highlands, Malaysia	–
LSUHC 10722	<i>Hemiphyllodactylus titiwangsaensis</i>	Cameron Highlands, Malaysia	–
LSUHC 10723	<i>Hemiphyllodactylus titiwangsaensis</i>	Cameron Highlands, Malaysia	–
LSUHC 10718	<i>Hemiphyllodactylus titiwangsaensis</i>	Cameron Highlands, Malaysia	–
LSUHC 7208	<i>Hemiphyllodactylus titiwangsaensis</i>	Cameron Highlands, Malaysia	JN393934
LSUHC 10721	<i>Hemiphyllodactylus titiwangsaensis</i>	Cameron Highlands, Malaysia	–
LSUHC 10716	<i>Hemiphyllodactylus titiwangsaensis</i>	Cameron Highlands, Malaysia	–
LSUHC 10720	<i>Hemiphyllodactylus titiwangsaensis</i>	Cameron Highlands, Malaysia	–
LSUHC 10715	<i>Hemiphyllodactylus titiwangsaensis</i>	Cameron Highlands, Malaysia	–
ABTC 49760	<i>Hemiphyllodactylus typus</i>	Papua New Guinea	GQ257744
ABTC 32736	<i>Hemiphyllodactylus typus</i>	Fiji Suva	GQ257745
LSUHC 10340	<i>Hemiphyllodactylus typus</i>	Pulau Pinang, Malaysia	–
LSUHC 8751	<i>Hemiphyllodactylus typus</i>	Tasik Chini, Malaysia	–
MVZ 226500	<i>Hemiphyllodactylus typus</i>	Vinh Phu, Vietnam	–
n/a	<i>Hemiphyllodactylus yunnanensis</i>	Yunnan, China	FJ971044
n/a	<i>Hemiphyllodactylus yunnanensis</i>	Yunnan, China	FJ971039
n/a	<i>Hemiphyllodactylus yunnanensis</i>	Yunnan, China	FJ971036
n/a	<i>Hemiphyllodactylus yunnanensis</i>	Yunnan, China	FJ971032
n/a	<i>Hemiphyllodactylus yunnanensis</i>	Yunnan, China	FJ971027
n/a	<i>Hemiphyllodactylus yunnanensis</i>	Yunnan, China	FJ971031
n/a	<i>Hemiphyllodactylus yunnanensis</i>	Yunnan, China	FJ971030
n/a	<i>Hemiphyllodactylus yunnanensis</i>	Yunnan, China	FJ971043
n/a	<i>Hemiphyllodactylus yunnanensis</i>	Yunnan, China	FJ971035
n/a	<i>Hemiphyllodactylus yunnanensis</i>	Yunnan, China	FJ971022
n/a	<i>Hemiphyllodactylus yunnanensis</i>	Yunnan, China	FJ971020
n/a	<i>Hemiphyllodactylus yunnanensis</i>	Yunnan, China	FJ971019
n/a	<i>Hemiphyllodactylus yunnanensis</i>	Yunnan, China	FJ971018
n/a	<i>Hemiphyllodactylus yunnanensis</i>	Yunnan, China	FJ971028
n/a	<i>Hemiphyllodactylus yunnanensis</i>	Yunnan, China	FJ971026
n/a	<i>Hemiphyllodactylus yunnanensis</i>	Yunnan, China	FJ971023
n/a	<i>Hemiphyllodactylus yunnanensis</i>	Yunnan, China	FJ971029
n/a	<i>Hemiphyllodactylus yunnanensis</i>	Yunnan, China	FJ971025
n/a	<i>Hemiphyllodactylus yunnanensis</i>	Yunnan, China	FJ971024
n/a	<i>Hemiphyllodactylus yunnanensis</i>	Yunnan, China	FJ971021
n/a	<i>Hemiphyllodactylus yunnanensis</i>	Yunnan, China	FJ971034
n/a	<i>Hemiphyllodactylus yunnanensis</i>	Yunnan, China	FJ971037
n/a	<i>Hemiphyllodactylus yunnanensis</i>	Yunnan, China	FJ971033

Abbreviated identification numbers 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; FMNH, Field Museum of Natural History; KU, Kansas University Museum of Natural History; LSUHC, La Sierra University Herpetological Collection; MVZ, Museum of Vertebrate Zoology (Berkeley); RMB, Rafe M. Brown field series; TG, Tony Gamble; USNM, United States National Museum; USNM-FS, United States National Museum, Field Series.

rostrum. Meristic character states, evaluated on the holotype and comparative material (see Appendix; Zug, 2010), included: 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

Table 2. A list of primers used for PCR amplification and sequencing (for specific amplification conditions, see Material and methods)

Primer name	Primer citation		Sequence
L4437b	(Macey & Schulte 1999)	External	5'-AAGCAGTTGGGCCCATACC-3'
CyrtintF1	(Siler <i>et al.</i> 2010)	Internal	5'-TAGCCYTCTCYTCYATYGCCC-3'
CyrtintR1	(Siler <i>et al.</i> 2010)	Internal	5'-ATTGTKAGDGTGRCYAGGSTKGG-3'
H5934	(Macey & Schulte 1999)	External	5'-AGRGTGCCAATGTCTTTGTGRTT-3'

Table 3. Models of molecular evolution used for maximum-likelihood and Bayesian analyses

Gene	Model selected	Model applied for ML	Models applied for BI
<i>ND2</i>			
1st pos	TVM+I + Γ	GTR+I + Γ	GTR+I + Γ
2nd pos	GTR+I + Γ	GTR+I + Γ	GTR+I + Γ
3rd pos	GTR+ Γ	GTR+I + Γ	GTR+ Γ
tRNAs	HKY+ Γ	GTR+I + Γ	HKY+ Γ

Models were estimated by the Akaike's information criterion (AIC) employed in MODELTEST 3.7 (Posada & Crandall, 1998). Selected models were applied when applicable for maximum likelihood (ML) and Bayesian inference (BI), and the next complex model was used when the selected model could not be employed.

the rostral and mental scales, respectively; the number of longitudinal ventral scales at midbody contained within one eye diameter; the number of longitudinal dorsal scales at midbody 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 on the digital pads on digits 2–5 of the hands and feet; the total number of preloacal and femoral pores (i.e. the contiguous or discontinuous rows of femoral and preloacal scales bearing pores); and the number of cloacal spurs. Colour pattern characters evaluated were the presence or absence of dark pigmentation in the gonadal tracts and caecum; presence or absence of a dark postorbital stripe extending to at least the neck; and the presence or absence of a linear series of white postorbital spots above the dark postorbital stripe. Some of the information on character states and their distribution in other species was obtained from Zug (2010). LSUHC refers to the La Sierra University Herpetological Collection, La Sierra University, Riverside, California, USA; and LSUDPC refers to the La Sierra University Digital Photo Collection. Other acronyms follow Sabaj-Pérez (2010).

DESIGNATION OF SPECIES-LEVEL LINEAGES

Named and unnamed lineages neither imbedded in the phylogenetic structure of named species nor found to be phylogenetically imbedded within a differently named species were initially considered as candidates for species recognition. If these lineages could be morphologically diagnosed we considered them confirmed candidate species (CCSs) using a modified convention proposed by Vieites *et al.* (2009). If morphological data were unavailable or sample sizes were too small for a complete morphological analysis, these lineages were considered unconfirmed candidate species (UCSs). In lineages for which we were unable to assess morphological diagnosability because specimens were unavailable, we used a rough uncorrected mitochondrial *ND2* sequence divergence value of 5% to flag UCSs. We chose this sequence divergence value based on our finding that morphologically distinct *Hemiphyllodactylus* species differ by as little as 5.8% for *ND2*, and because similar thresholds using this gene have been identified for a diversity of gekkonid taxa (Bauer *et al.*, 2010, 2011, 2013; Heinicke *et al.*, 2011a, b; Grismer *et al.*, 2012a, b, 2013; Johnson *et al.*, 2012). We note that we are simply using this threshold to encourage future corroborative analyses as specimens become available for study.

RESULTS

The molecular phylogeny for *Hemiphyllodactylus* (Fig. 1) brings into sharp focus a myriad of taxonomic and biogeographical issues and hypotheses concerning nearly all of its currently recognized species (Zug, 2010), which can now be evaluated further within the context of an integrated approach. The phylogeny indicates that *Hemiphyllodactylus* is composed of two major, deeply divergent, and strongly supported monophyletic groups, designated here as the *harterti* group and the *typus* group. The *harterti* group is composed solely of the upland endemic species from Peninsular Malaysia *Hemiphyllodactylus harterti* (Werner, 1900), *Hemiphyllodactylus larutensis* (Boulenger, 1900), *Hemiphyllodactylus titiwangsaensis* Zug, 2010 (including *Hemiphyllodactylus* sp. nov. 1,

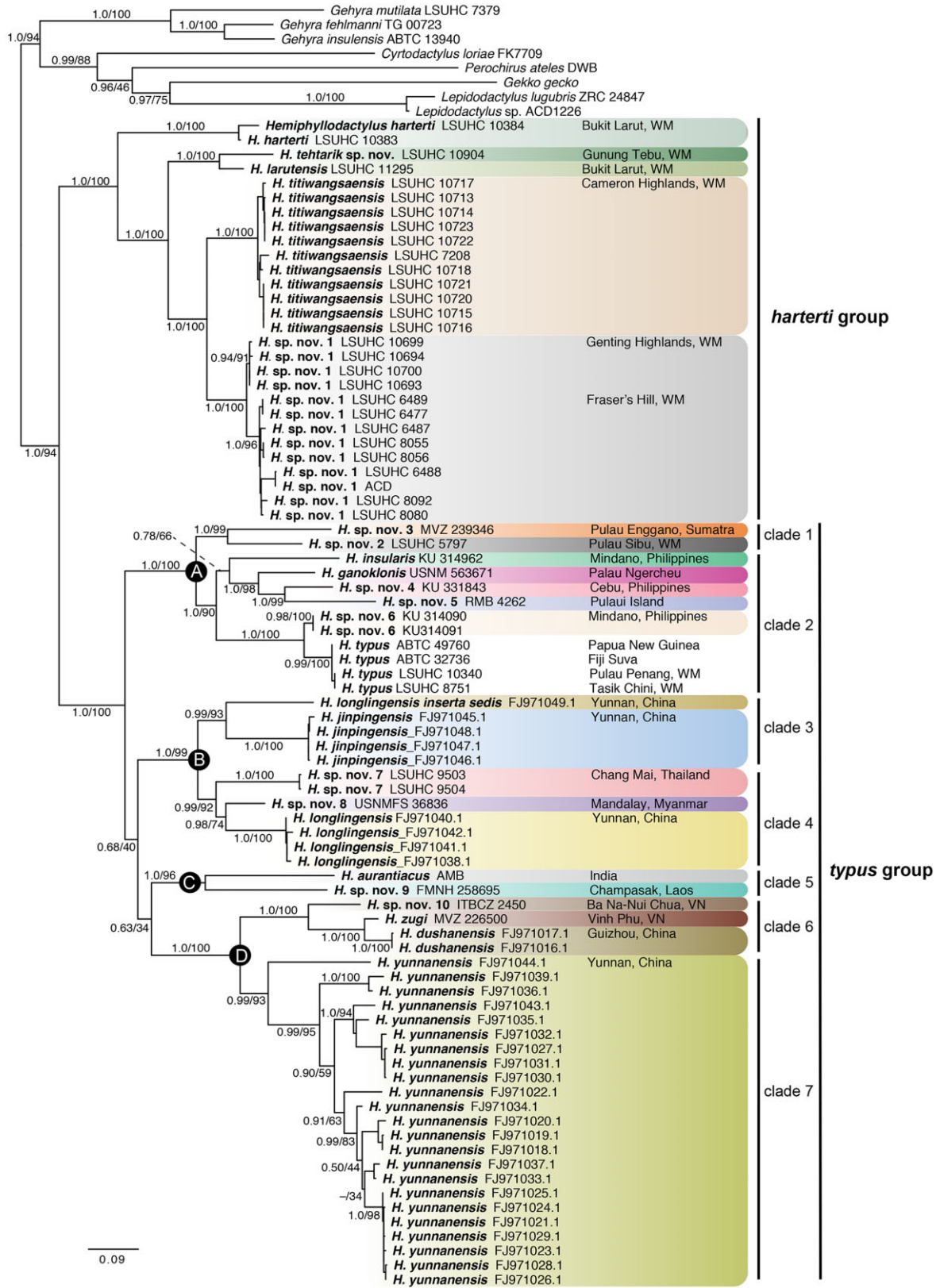


Figure 1. Maximum-likelihood phylogram ($-\ln L$ 22097.690183) of the genus *Hemiphyllodactylus* Bleeker, 1860 with Bayesian posterior probabilities and maximum-likelihood bootstrap values, respectively.

see below), and a new species (*Hemiphyllodactylus tehtarik* sp. nov., described below) from Gunung Tebu in the Banjaran Timur (eastern mountain range). Phylogenetic substructuring within the *harterti* group is well supported, with *H. harterti* being sister to the remaining lineages and *H. larutensis* and *H. tehtarik* sp. nov. being sister species and composing the sister lineage to *H. titiwangsaensis* (Fig. 1).

All other lineages compose the *typus* group (Fig. 1). Although resolution among the four strongly supported basal lineages (A–D) of this group is poor, well-supported substructuring within each lineage delineates seven clades from distinct biogeographic regions. Sister clades 1 and 2 compose basal lineage A, which contains mostly insular species from the Indo-Australian Archipelago, the Philippines, and the South Pacific (Fig. 2). All members of lineage A have the distinctive slender, elongate body morphology, with relatively short limbs of *Hemiphyllodactylus typus* Bleeker, 1860, as opposed to the more robust body stature of *Hemiphyllodactylus margarethae* Brongersma, 1931 (Fig. 3). Clade 1 is composed of an insular population from Pulau Sibul, Peninsular Malaysia, and another from Pulau Enggano, Indonesia, that are currently recognized as *H. typus* (Wood *et al.*, 2004; Grismer *et al.*, 2006; Zug, 2010; Grismer, 2011a, b). Clade 2 is composed of Philippine and Palau Ngercheu island populations of the endemic species *Hemiphyllodactylus insularis* Taylor, 1918, *H. ganoklonis* Zug, 2010, and the wide-ranging unisexual species *H. typus* (including *Hemiphyllodactylus* sp. nov. 4 and 6, see below) as well as a new species from Pulaui Island (*Hemiphyllodactylus* sp. nov. 5).

Sister clades 3 and 4 compose basal lineage B (Fig. 1) and contain upland species that range across southern Indochina from north–central Myanmar and northern Thailand to southern China (Fig. 2). Clade 3 is composed of populations from southern China, referred to as the subspecies *Hemiphyllodactylus yunnanensis jinpingensis* Zhou, Liu & Yang, 1981, with one outlying member of *Hemiphyllodactylus yunnanensis longlingensis* Zhou & Liu, 1981 (Zhou, Lui & Yang, 1981). Clade 4 contains a basal lineage from Chang Mai, Thailand (*Hemiphyllodactylus* sp. nov. 7) currently considered *Hemiphyllodactylus yunnanensis* (Boulenger, 1903) (Zug, 2010). Its sister lineage contains a specimen from Pyin-Oo-Lwin, Mandalay Division, Myanmar, (*Hemiphyllodactylus* sp. nov. 8), also currently recognized as *H. yunnanensis* (Zug, 2010) and *H. y. longlingensis* from southern China (Zhou *et al.*, 1981).

Clade 5 represents basal lineage C, and is composed of *Hemiphyllodactylus aurantiacus* (Beddome, 1870) from southern India and Sri Lanka and a distantly related (20.0% uncorrected sequence diver-

gence) population from Champasak, southern Laos, currently referred to as '*H. yunnanensis*' (Zug, 2010).

Sister clades 6 and 7 compose basal lineage D, which contains upland species from northern Vietnam and southern China (Fig. 2). Clade 6 is composed of a basal lineage (*Hemiphyllodactylus* sp. nov. 10) from Ba Na-Nui Chua Nature Reserve, Da Nang City, Central Vietnam ('*H. yunnanensis*' Zug, 2010), together with sister lineages *H. zugi* Nguyen, Lehmann, Le, Duong, Bonokowski and Ziegler 2013 from Vinh Phuc Province in northern Vietnam and *Hemiphyllodactylus yunnanensis dushanensis* Zhou & Liu, 1981 from southern China (Zhou *et al.*, 1981). Clade 7 is restricted to southern China and is composed of *H. y. yunnanensis* (Zhou *et al.*, 1981).

SYSTEMATICS AND TAXONOMY

The Harterti group

Currently, there are three species of *Hemiphyllodactylus* recognized from Peninsular Malaysia (Grismer, 2011a): the widely distributed unisexual *H. typus* and the bisexual, upland species *Hemiphyllodactylus harterti* (Werner, 1900) from the Banjaran Bintang, and *Hemiphyllodactylus titiwangsaensis* Zug, 2010, from the Banjaran Titiwangsa. The latter two species are endemic to their respective mountain ranges, and make up the *harterti* group (Fig. 4). We report on a gravid gekkonid collected during an expedition to Gunung Tebu in the Banjaran Timur found at 600 m a.s.l. We assign this specimen to the genus *Hemiphyllodactylus* for having undivided, U-shaped, terminal lamellar pads on digits 2–5 of the hands and feet, free terminal phalanges that are not united with the lamellar pad, a clawless, vestigial first digit on the hands and feet, lidless eyes with vertical pupils, and for lacking a ventrolateral fringe or fold of skin extending between the axilla and the groin. However, this specimen is not referable to any known species of *Hemiphyllodactylus* in that it has a rust–orange, unicoloured dorsal body pattern, no white postorbital spots, and a lamellar foot formula of 3-4-5-4: characters not known from any other *Hemiphyllodactylus*. Additionally, it bears a unique combination of other morphological and colour pattern characters that separate it from all other known congeners. We consider this specimen to be a member of the *harterti* group given that it is the sister lineage of *H. larutensis* (see below), and describe it herein as a new species.

Hemiphyllodactylus tehtarik sp. nov.

Tebu Mountain Slender-toed Gecko

Holotype: Adult female (ZRC LSUHC 10904) collected on 2 September 2010 by Mohd Abdul Muin and Shahrul Anuar and at 2200 h from Gunung Tebu,

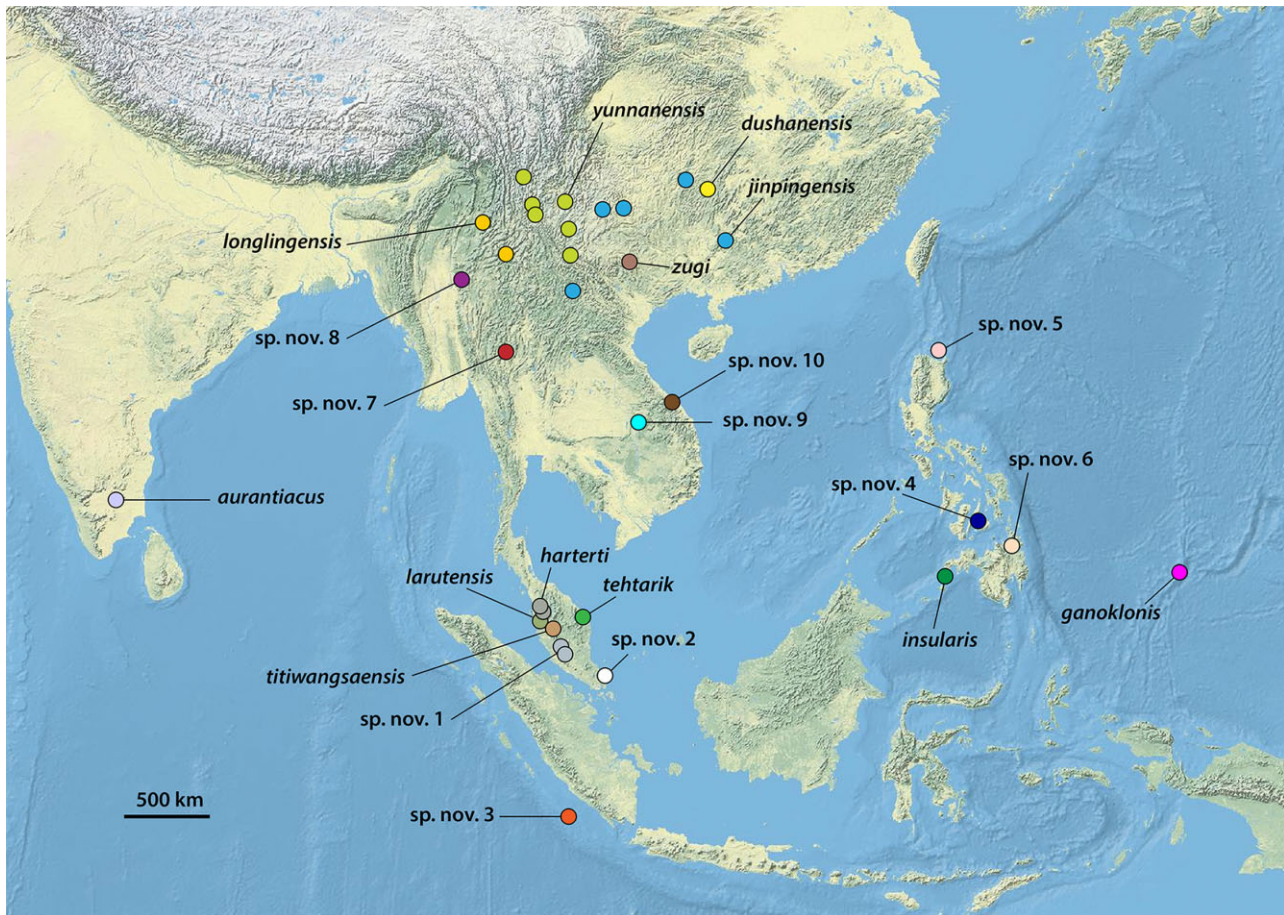


Figure 2. Distribution of the species of *Hemiphyllodactylus* examined (see the Appendix for a list of the *Hemiphyllodactylus typus* examined). *Hemiphyllodactylus aurantiacus* from Yercaud, Salem District (Shevaroyan Hill Range), Tamil Nadu, India; *Hemiphyllodactylus ganoklonis* from Palau Ngercheu; *Hemiphyllodactylus harterti* and *Hemiphyllodactylus larutensis* from Bukit Larut, Perak, Malaysia; *Hemiphyllodactylus insularis* from the Municipality of Pasonaca, Zamboanga City, Zamboanga City Province, Philippines; *Hemiphyllodactylus tehtarik* from Gunung Tebu, Terengganu, Malaysia; *Hemiphyllodactylus titiwangsaensis* from the Cameron Highlands, Pahang, Malaysia; *Hemiphyllodactylus* sp. nov. 1 from Fraser's Hill and the Genting Highlands, Pahang; *Hemiphyllodactylus* sp. nov. 2 from Pulau Sibul, Johor, Malaysia; *Hemiphyllodactylus* sp. nov. 3 from Pulau Enggano, Bengkulu Province, Sumatra, Indonesia; *Hemiphyllodactylus* sp. nov. 4 from Mount Lantoy, Municipality of Argao, Cebu Province, Cebu, Philippines; *Hemiphyllodactylus* sp. nov. 5 from Pulaui Island, Barangay Palau, Municipality of Santa Ana, Cagayan Province, Philippines; *Hemiphyllodactylus* sp. nov. 6 from Barangay Kaim, Municipality of San Francisco, Agusan del Sur Province, Mindanao, Philippines; *Hemiphyllodactylus* sp. nov. 7 from Chiang Mai, Chiang Mai Province, Thailand; *Hemiphyllodactylus* sp. nov. 8 from Pyin-Oo-Lwin, Mandalay Division, Myanmar; *Hemiphyllodactylus* sp. nov. 9 from Pakxong District, Champasak Province, Laos; *Hemiphyllodactylus zugi* from Vinh Phu, Vietnam; and *Hemiphyllodactylus* sp. nov. 10 from Ba Na-Nui Chua Nature Reserve, Da Nang Province, Vietnam. Localities of *Hemiphyllodactylus dushanensis* (closed yellow circles), *Hemiphyllodactylus jinpingensis* (closed blue circles), *Hemiphyllodactylus longlingensis* (closed orange circles), and *Hemiphyllodactylus yunnanensis* (closed green circles) follow Zhou *et al.* (1981), except for the southern specimen of *H. dushanensis* from Vinh Phuc, Vinh Phuc Province, Vietnam reported here.

Terengganu, Malaysia (05°36.11' N, 102°36.19' E; 600 m a.s.l.).

Diagnosis: *Hemiphyllodactylus tehtarik* sp. nov. can be separated from all other species of *Hemiphyllodactylus* by the unicolour rust–orange

dorsal pattern, absence of white postorbital spots, and a lamellar foot formula of 3-4-5-4. It is further separated from all other congeners by: the unique combination of a maximum SVL of 40.4 mm in females (males unknown); eight chin scales, extending transversely from unions of second and third infralabials,



Figure 3. A, *Hemiphyllodactylus typus* (LSUDPC 7023) from Kepong, Selangor, Peninsular Malaysia (photo by L. Grismer). B, *Hemiphyllodactylus margarethae* (LSUDPC 7022) from Gunung Marapi, West Sumatra, Indonesia (photo by G. Vogel).

and the posterior margin of mental; enlarged postmental scales; five circumnasal scales; three scales between supranasals (= postrostrals); 11 supralabials; 10 infralabials; 18 longitudinally arranged dorsal scales at midbody contained within one eye diameter; 12 longitudinally arranged ventral scales at midbody, contained within one eye diameter; lamellar formula on hand 3-3-3-3; no precloacal or femoral pores in females (males unknown); postsacral mark orange and bearing anteriorly projecting arms;

and ceacum and oviducts unpigmented. These characters and potentially diagnostic morphometric characters are scored across all species in Table 4.

Description of holotype: Adult female; head triangular in dorsal profile depressed, distinct from neck; lores and interorbital regions flat; rostrum relatively long ($NarEye/HeadL = 0.40$); prefrontal region flat to weakly concave; canthus rostralis smoothly rounded, barely discernible; snout moderate, rounded in dorsal

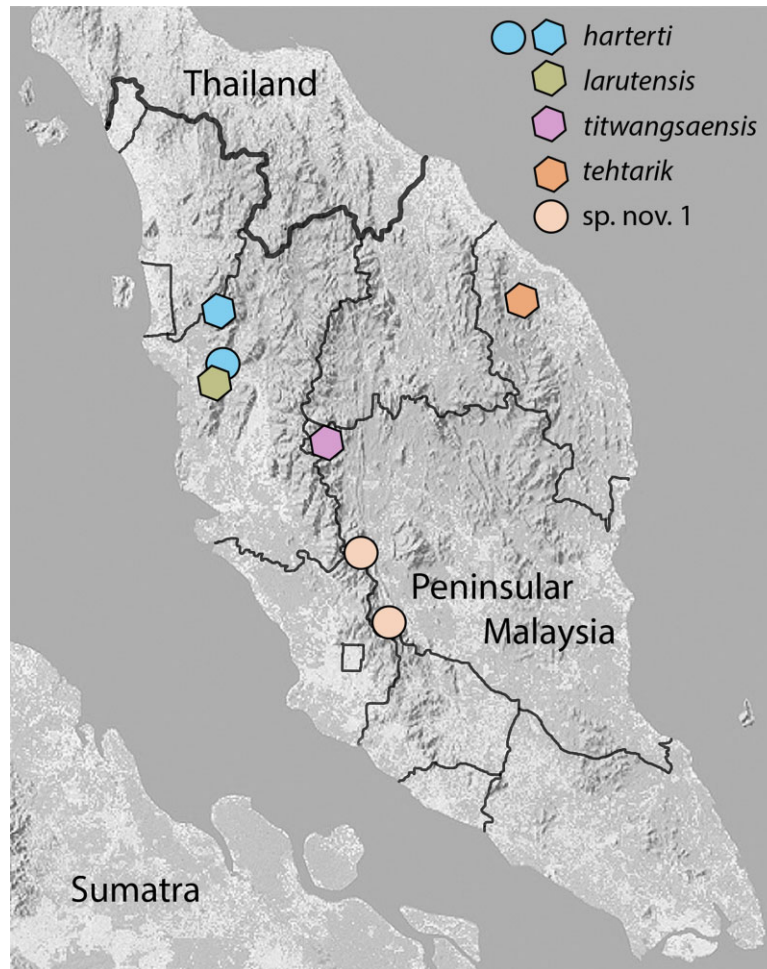


Figure 4. Distribution of the species of the *harterti* group. Polygons represent type localities.

profile; eye large; ear opening oval, small; eye to ear distance greater than diameter of eye; rostral wider than high, partially divided dorsally, bordered posteriorly by large supranasals; three internasals (= postnasals); external nares bordered anteriorly by rostral, dorsally by supranasal, posteriorly by two postnasals, ventrally by first supralabial (= circumnasals 5R,L); 11 (R,L) square supralabials tapering to below posterior margin of orbit; 10 (R,L) square infralabials tapering to below posterior margin of orbit; scales of rostrum, lores, top of head, and occiput small, granular, those of rostrum largest; dorsal superciliaries flat, rectangular, imbricate; mental triangular, bordered laterally by first infralabials and posteriorly by two large postmentals; each postmental bordered laterally by a single sublabial; four enlarged sublabials extending posteriorly to third infralabial; row of eight scales extending transversely from juncture of second and third infralabials, and contacting mental; gular scales triangular, small, granular, grading posteriorly into

slightly larger, subimbricate, throat and pectoral scales, which grade into slightly larger, subimbricate ventrals.

Body somewhat elongate, dorsoventrally compressed; ventrolateral folds absent; dorsal scales small, granular, 18 scales contained within one eye diameter; ventral scales, flat, subimbricate, much larger than dorsal scales, 12 scales contained within one eye diameter; no enlarged, precloacal scales; row of enlarged, poreless femoral scales extend continuously from midway between the knee and hindlimb insertion of one leg to the other; forelimbs short, robust in stature, covered with granular scales dorsally, and with slightly larger, flat, subimbricate scales 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 3-3-3-3 (R,L); five transversely expanded lamellae on digit I; claws on digits II–V well

Table 4. Diagnostic characters (bold) separating the species of *Hemiphyllodactylus* fide Zug (2010)

	<i>aurantiacus</i>	<i>ganoklonis</i>	<i>harterti</i>	<i>larutensis</i>	<i>insularis</i>	<i>margarethae</i>	<i>titiuangsensis</i>	<i>typus</i> [†]	<i>yunnanensis</i> *	<i>tehtarik</i> sp. nov.
Max SVL	37.9	34.2	42.1	52.2	37.3	46.9	62.1	46.1	49.3	40.4
Chin scales	10–14	9–12			8–14	6–11	8,9	9–14	6–11	8
Postmentals distinctly enlarged (1) or not (0)	0	0	1	1	0	1	1	1	1	1
Circumnasal scales	2–4	2–4	3–5	3–5	1–4	2,3	3	1–5	2–4	5
Scales between supranasals	3–6	3–5	2,3	3	2–4	2–4	1–3	1–5	2–5	3
Supralabial scales	10–13	8–11	10–11	9,10	9–13	10–13	9–11	9–14	8–13	11
Infralabial scales	8–12	8–10	10–11	7–10	9–11	9–12	8–10	7–13	8–12	10
Dorsal scales	11–17	11–18	14–19	13–20	13–18	11–17	14–19	12–19	9–18	18
Ventral scales	8–12	9–12	10–14	7–13	8–14	6–12	7–9	8–14	6–12	12
Lamellar formula on hand	2222	3443	3333	see table 5	3333	4444	3444	3444	3333	3333
Lamellar formula on foot	2232/2233	3444	3343	see table 5	34444	4555	4555	4454	3444	3454
Subdigital lamellae on first finger	3,4	3–5	3	3,4	2–5	4–8	4–6	4,5	4–6	5
Subdigital lamellae on first toes	4,5	3–5	4	3–5	3–6	4–7	5–8	5,6	4–7	5
Preclacal and femoral pore series separate (1) or continuous (0)	1/r	1/n	0	0	1/n	1/o	0/n	1/o	0/r	none
Preclacal and femoral pores	16–25	16–28	42–45	27–36	17–38	0–29	17–39	0–26	11–25	0
Cloaca spurs	1–3	1–4	1	2,3	0–3	1,2	1–4	1–5	0–2	3
Subcaudals enlarged, plate-like (1) or not (0)	0	0	0	0	0	0	0	0	0	/
Dark postorbital stripe present (1) or absent (0)	1	1	1	1	1	1	1	1	1	1
Light postocular or trunk spots (1) or absent (0)	1	1	1	1	1	/	1	1	1	0
Dark dorsolateral stripe on trunk (1) or not (0)	0	0	0	0	0	/	0	0	0	0
Dorsal pattern unicolor (1) or not (0)	0	0	0	1	0	/	0	0	0	1
Dark dorsal transverse blotches (1) or not (0)	1	0	0	0	0	0	0	0	0	0
Longitudinal series of white (1) or yellow or red (0) dorsal spots	1	0	0	0	0	0	0	1	0	0
Postsacral mark brown or orange (2), outer edge yellow or red (1), outer edge red (0)	2	1	0	1	0	0	0	2	0	2
Postsacral mark lacking anterior arms (1) or arms present (0)	1	0	1	0	0	?	1	0	1	0
Caecum pigmented (1) or not (0)	1	1	0	0	0	0	0	1	0	0
Gonads pigmented (1) or not (0)	1	1	/	0	/	0,1	0	1	0	0
Trunk/SVL	0.44–0.51	0.49–0.57	0.48–0.53	0.46–0.51	0.45–0.58	0.40–0.54	0.42–0.50	0.40–0.65	0.40–0.55	0.55
HeadL/SVL	0.21–0.26	0.20–0.23	0.22–0.24	0.21–0.24	0.21–0.24	0.21–0.26	0.23–0.27	0.18–0.24	0.21–0.26	0.2
HeadW/SVL	0.14–0.19	0.12–0.15	0.15–0.18	0.15–0.17	0.12–0.18	0.15–0.19	0.16–0.19	0.10–0.16	0.14–0.22	0.16
HeadW/HeadL	0.57–0.79	0.53–0.65	0.65–0.85	0.63–0.73	0.54–0.82	0.66–0.79	0.64–0.73	0.51–0.77	0.59–0.83	0.8
SnEye/HeadL	0.34–0.42	0.36–0.45	0.41–0.48	0.39–0.51	0.26–0.44	0.39–0.46	0.37–0.43	0.34–0.48	0.34–0.46	0.47
NarEye/HeadL	0.27–0.33	0.28–0.34	0.28–0.33	0.27–0.36	0.27–0.42	0.29–0.35	0.26–0.32	0.24–0.40	0.26–0.35	0.4
EyeD/HeadL	0.22–0.28	0.23–0.28	0.27–0.30	0.22–0.28	0.23–0.32	0.16–0.25	0.21–0.30	0.20–0.32	0.22–0.29	0.28
SnW/HeadL	0.14–0.20	0.13–0.19	0.15–0.12	0.11–0.15	0.14–0.21	0.15–0.19	0.14–0.21	0.11–0.21	0.11–0.22	0.16
EyeD/NarEye	0.69–0.96	0.73–0.95	0.83–1.00	0.66–0.90	0.74–0.95	0.47–0.81	0.68–0.94	0.61–1.06	0.63–1.00	0.72
SnW/HeadW	0.21–0.30	0.23–0.32	0.20–0.32	0.18–0.21	0.20–0.37	0.22–0.28	0.21–0.31	0.16–0.34	0.15–0.36	0.2

For morphological abbreviations, see Material and methods.

Values set in bold are diagnostic from *Hemiphyllodactylus tehtarik* sp. nov.

*Zug's (2010) concept of *Hemiphyllodactylus yunnanensis*, including the subspecies *H. y. jingpingensis*, *H. y. longlingensis*, *H. y. yunnanensis*, the Mandalay, Myanmar, population, the Cjiang Mai, Thailand, population, and the Vietnam populations.

†Zug's (2010) concept of *Hemiphyllodactylus typus*, which includes the Pulau Sibiu, Malaysia and Pulau, Enggano, and Indonesia populations.

developed, unsheathed; distal portions of digits strongly curved, terminal joint free, arising from central portion of lamellar pad; hindlimbs short, more robust than forelimbs, covered with slightly pointed, 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 3-4-5-4 (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; tail relatively short, regenerated, approximately 0.8 times SVL, round in cross section; all caudal scales flat, imbricate, not forming distinct caudal segments. Morphometric data are presented in Table 4.

Coloration in life (Fig. 5): Top of head unicolour dull orange, transitioning into a slightly darker rust–orange coloration on body; longitudinal series of small, dark, faint, diffuse, postorbital spots; faint, dark, diffuse preorbital stripe; a slightly more prominent postorbital stripe extends to anterior margin of forearm, becoming more faint and diffuse, and wider, as it continues along ventrolateral margin of body to groin, and into postsacral region; light postsacral marking orange, bearing anteriorly projecting arms and dark medial spot; dorsal surface of limbs same colour as body; tail regenerated immediately posterior to postsacral marking, and unicolour dark brown dorsally and ventrally; distinct transition between dull or rust–orange dorsal coloration of head, body, and limbs, and immaculate, cream-coloured venter.

Distribution: *Hemiphyllodactylus tehtarik* sp. nov. is known only from the type locality on Gunung Tebu, Terengganu, Peninsular Malaysia (Fig. 4), but is expected to range more widely throughout this portion of the Banjaran Timur.

Natural history: The holotype was seen at night on the leaf of a palm tree (*Licuala* sp.), approximately 1 m above the ground, along the edge of a small stream coursing through large granite boulders. During a first attempt to capture it, the lizard dropped to the ground and escaped, but was captured later that night on a different leaf of the same tree. The holotype is an adult female carrying two eggs, indicating that the reproductive season of this species extends at least through August. From only a single female, it cannot be determined if *H. tehtarik* sp. nov. is unisexual or bisexual.

Etymology: This species is named after a traditional Malaysian tea, *Teh Tarik*, which bears the rich orangish coloration of the holotype.

Comparisons: The taxonomy of Zug (2010) is used in the comparisons below. *Hemiphyllodactylus tehtarik* sp. nov. differs from all other species of *Hemiphyllodactylus* in: a lamellar foot formula of 3-4-5-4; no white postorbital or body spots; and a unicolour dorsal body pattern. It differs further from *Hemiphyllodactylus ganoklonis* Zug, 2010 in having a maximum known SVL of 40.4 mm versus 34.2 mm, and from *Hemiphyllodactylus margarethae* Brongersma, 1931, *H. titiwangsaensis*, *H. typus*, and *H. yunnanensis* by having a maximum SVL less than 46.1–49.3 mm. It differs from *H. aurantiacus*, *H. ganoklonis*, and *H. insularis* in having enlarged as opposed to small postmentals. *Hemiphyllodactylus tehtarik* sp. nov. has five circumnasal scales that separate it from *H. aurantiacus*, *H. ganoklonis*, and *H. yunnanensis* having two to four, *H. insularis* having one to four, *H. margarethae* having two or three, and *H. titiwangsaensis* having three. It is further separated from *H. aurantiacus* and *H. margarethae* in having 18, as opposed to 11–17, dorsal scales, and from *H. titiwangsaensis* in having 12, as opposed to between seven and nine, ventral scales. *Hemiphyllodactylus tehtarik* sp. nov. has a lamellar hand formula of 3-3-3-3, which separates it from *H. aurantiacus* having 2-2-2-2, *H. ganoklonis* having 3-4-4-3, *H. margarethae* having 4-4-4-4, and *H. titiwangsaensis* and *H. typus* having 3-4-4-4. From *H. harterti*, *H. tehtarik* sp. nov. differs in having five transversely expanded subdigital lamellae beneath digits I on the hands and feet, as opposed to having three on digit I of the hand and four on digit I of the foot. It can be separated further from *H. harterti* in having three cloacal spurs as opposed to one, and from *H. yunnanensis*, which has between zero and two cloacal spurs. *Hemiphyllodactylus tehtarik* sp. nov. has an orangish postsacral marking, which separates it from all other species except *H. aurantiacus* and most *H. typus*. The postsacral markings in *H. tehtarik* sp. nov. bear anteriorly projecting arms that differentiate it from *H. aurantiacus*, *H. harterti*, *H. titiwangsaensis*, and *H. yunnanensis*. The caecum and gonadal tracts of *H. tehtarik* sp. nov. are unpigmented, further differentiating them from *H. aurantiacus*, *H. ganoklonis*, some *H. margarethae*, and *H. typus*. A number of morphometric ratios of other species of *Hemiphyllodactylus* differ discretely from the corresponding ratio in *H. tehtarik* sp. nov.; however, having a sample size of one does not allow for observing the range of ratios that must exist, and therefore they are not considered definitive at this point, but they are illustrated in Table 4.



Figure 5. A, holotype of *Hemiphyllodactylus tehtarik* sp. nov. (LSUHC 10904) from Gunung Tebu, Terengganu, Malaysia; photo by L. Grismer. B, adult female *Hemiphyllodactylus larutensis* (LSUHC 11294) from Bukit Larut, Perak, Malaysia; photo by L. Grismer. C, adult male holotype of *Hemiphyllodactylus larutensis* (holotype BM 1901.3.20.2) from Bukit Larut, Perak, Malaysia; photo by G. Zug. D, adult male *Hemiphyllodactylus larutensis* (LSUHC 11298) from Bukit Larut, Perak, Malaysia; photo by L. Grismer. E, adult male *Hemiphyllodactylus harterti* (LSUHC 10383) from Bukit Larut, Perak, Malaysia; photo by L. Grismer. F, adult female *Hemiphyllodactylus harterti* (holotype ZMB 1360) from Gunung Hijau, Perak, Peninsular Malaysia; photo by M.-O. Rödel.

Phylogenetic relationships: *Hemiphyllodactylus tehtarik* sp. nov. is part of an upland clade of species endemic to the mountain systems of Peninsular Malaysia (Fig. 4). The basal member of this clade,

H. harterti, occurs in the westernmost range, the Banjaran Bintang, whereas *H. tehtarik* is known only from an outlying section of the eastern ranges (referred to collectively as the Banjaran Timur), but is

the sister species of *H. larutensis* from the Banjaran Bintang.

Remarks and comments: There have been no published herpetofaunal surveys from the extensive mountain systems of north-eastern Peninsular Malaysia (Banjaran Timur), save for Boulenger (1908) and Dring (1979). Thus, the discovery of a new species from a widespread lineage of small, secretive geckos from a remote unexplored upland area in a region in which nearby mountain ranges are rich in lizard diversity (Grismer, 2011a) is not surprising. Nonetheless, it further underscores our lack of knowledge concerning the herpetological composition of the Banjaran Timur in general, and Gunung Tebu in particular. The fact that our expedition was able to collect three new species of lizards, three new species of frogs, and a new species of snake in two nights (see Grismer *et al.*, 2013; E. Quah, unpubl. data) is a clear indication that sampling from this mountain is far from complete. Given the high degree of herpetological endemism and diversity seen in the other two major upland systems of Peninsular Malaysia, the Banjaran Bintang and Banjaran Titiwangsa (see Grismer & Pan, 2008; Grismer *et al.*, 2010b; Grismer, 2011a and references therein), and what relatively few species are known from the upland areas of the Banjaran Timur (see Boulenger, 1908; Dring, 1979), we can estimate that only a small fraction of this herpetofauna is known. Effective management and conservation strategies can only be accomplished once this herpetofauna is more fully understood.

Some (i.e. Dayrat, 2005) have grave concerns about descriptions of new species based on only a single specimen, and posit that this should ‘never’ be reported because such a description cannot take into account infraspecific variation that could potentially preclude its specific recognition. Although this is a theoretically noble notion, it is counterproductive in reality, and might impede biodiversity studies in general and taxonomy in particular, given that recent estimates show that 19% of all new vertebrate species described between 2000 and 2010 were based on a single specimen (Lim, Balke & Meier, 2012). In the context of the monographic revision of *Hemiphyllodactylus* by Zug (2010) and the molecular data presented here, it is clear the morphology, colour pattern, and genetics of *H. tehtarik* lie well outside that of the known species boundaries of all other *Hemiphyllodactylus*, and would thus require a significant amount of contradictory evidence to provide a robust, scientific reason for *not* describing *H. tehtarik* sp. nov. If future work proves that this name (i.e. hypothesis about the relationships of individuals discovered in the future) is falsified and *H.*

tehtarik is a junior synonym of some other taxon, then it is the very testability of the name that makes it a legitimate hypothesis (Valdecasas, Williams & Wheeler, 2008).

Hemiphyllodactylus harterti

The convoluted taxonomic history of *H. harterti* has accumulated from a sequence of compounding errors including: (1) the imprecise designation of its type locality (Werner, 1900); (2) the fact that two names, *H. harterti* and *Hemiphyllodactylus larutensis* (Boulenger, 1900) were available for different populations from the Banjaran Bintang for well over a century; (3) various authors (i.e. Chan-ard *et al.*, 1999) indiscriminately applying both names to a single population (Cameron Highlands) from an entirely different mountain range (the Banjaran Titiwangsa); (4) erroneous reports (Bauer & Günther, 1991) as to what Boulenger (1912) actually considered the type locality of *H. harterti* (see discussion in Grismer, 2011a: 499); (5) colour descriptions of *H. harterti* based on the wrong species (Zug, 2010: 29); and (6) no recent material of either species being available for morphological and molecular analyses since 1900. We examined two specimens recently collected from Bukit Larut (LSUHC 10383–84) that are consistent with the description of *H. harterti* (Werner, 1900) and with images of the holotype from Gunung Hijau (Fig. 5) and nine specimens recently collected from Bukit Larut (LSUHC 11293–96, 11298–99, 11542, 11591–92) that match the description and images of the holotype of *H. larutensis* (Boulenger, 1900; Fig. 5). These specimens provide the basis for more complete descriptions of both species [commensurate with those descriptions of other species of *Hemiphyllodactylus* following Zug (2010)] as well as a molecular analysis in order to determine their phylogenetic placement within the genus—in particular their relationships to each other and other upland populations from Peninsular Malaysia.

Boulenger (1912) noted that the imprecise type locality designation of ‘Melacca’ by Werner (1900) for *H. harterti* essentially referred to the entire west coast of the Thai-Malay Peninsula and noted that the specimen collected by Ernest J. O. Hartert came from ‘Gunong’ (= Gunung) Inas, a peak in the northern portion of the Banjaran Bintang. Shortly after Werner’s (1900) description, Boulenger (1900) described *H. larutensis* from the Larut Hills (= Bukit Larut)—another upland locality approximately 40 km south of Gunung Inas in the same mountain range—and later indicated (Boulenger, 1912) that these two populations were probably conspecific. Kluge (1991, 2001), by implication, was the first to apply the nomen *H. harterti* to both populations and was followed by Grismer *et al.* (2010b) who listed a complete

synonymy of names. Zug (2010) was the first in over a century to examine the holotype of *H. larutensis* and by comparing it to a series of photographs of the holotype of *H. harterti*, he indicated the two species were conspecific. A morphological (Table 5; Fig. 5 and see below) and molecular analysis of the newly collected material of both species from Bukit Larut confirms that not only are they different species, they are not even each others' closest relatives, in that *H. larutensis* is the sister species of *H. tehtarik*—an upland species across three different mountain ranges 175 km to the east (Figs 1, 4). Additionally, *H. harterti* and *H. larutensis* have a sequence divergence of 20.6% despite being sympatric.

Werner's (1900) short description of the adult female holotype of *Hemiphyllodactylus harterti* (ZMB 1360) does not unequivocally diagnose it from Boulenger's (1900) slightly better description of the adult male holotype of *H. larutensis* (BM 1901.3.20.2). Nonetheless, *H. harterti* can be separated from *H. larutensis* on the basis of a number of characteristics observable on a series of photographs of the holotype ZMB 1360 (LSUHC 8080–86) that were confirmed on specimens LSUHC 10383–84. The body stature of *H. harterti* is more robust than that of *H. larutensis* (Fig. 5B–F) and it has a smaller adult SVL. Adult male (as determined by gonadal inspection) *H. harterti* are 33.2–34.7 mm SVL versus 42.7–43.1 mm in adult male *H. larutensis*. The female holotype of *H. harterti* measures 42 mm SVL versus 44.3–52.2 mm for adult female *H. larutensis*. Male *H. larutensis* have 27–36 femoropreloacal pores and two or three cloacal spurs whereas male *H. harterti* have 44 or 45 femoropreloacal pores and a single cloacal spur. The subcaudal scales of the holotype and recently collected material of *H. harterti* are nearly twice the size as the dorsal caudal scales whereas in *H. larutensis* dorsal and subcaudal scales are the same size. Werner (1900) did not describe the colour pattern of *H. harterti* but mentioned it matched that of *L. lugubris* which Zug (2010) interpreted to mean having dark wavy crossbars. The only colour photograph of a living specimen of *H. harterti* appeared in Grismer, 2011a, which showed it to have a generally spotted dorsum (that is only vaguely visible on the faded holotype) as opposed to the generally unicolour dorsal pattern of *H. larutensis* (Fig. 5). The colour photograph of the unicoloured specimen in Zug (2010: fig. 11c) from Bukit Larut labelled as *H. harterti* is actually *H. larutensis*. Zug (2010: 29) used a colour photograph of a different nearly unicoloured specimen of *H. larutensis* appearing in Chan-ard *et al.* (1999: 130) to form the basis of his colour pattern description of *H. harterti*. Boulenger (1900) noted that the caudal colour pattern of *H. larutensis* was 'yellowish with . . . a vertebral series of small blackish spots widely sepa-

rated from each other'. This pattern is still clearly visible on the holotype and occurs in the newly collected specimens (Fig. 5) whereas the caudal pattern of *H. harterti* consists of randomly arranged spots that are visible on the holotype and the specimens from Bukit Larut (Fig. 5). The base of the sacral marking in *H. larutensis* is bordered by a medial, dark, triangular marking whereas in *H. harterti* the base is bordered by a pair of dark lateral blotches (Fig. 5).

The following redescrptions of *H. harterti* and *H. larutensis* are based on two adult males (LSUHC 10383–84) and one adult female (ZMB 1360) of the former and four adult males (BM 1901.3.20.2; LSUHC 11298, 11591–92) and six adult females (LSUHC 11293–96, 11299, 11542) of the latter. A number of the recently collected specimens from Bukit Larut were photographed shortly after capture (Fig. 5). For comparative purposes, the following redescrptions are generally styled after those of other *Hemiphyllodactylus* (Zug, 2010).

Redescription of *Hemiphyllodactylus harterti* (Werner, 1900)

Head triangular in dorsal profile depressed, distinct from neck; lores and interorbital regions flat; rostrum moderate in length; prefrontal region flat; canthus rostralis smoothly rounded, barely discernible; snout moderate, rounded in dorsal profile; eye large; ear opening oval, small; eye to ear distance greater than diameter of eye; rostral wider than high, partially divided dorsally, bordered posteriorly by large supranasals; two or three internasals (= postnasals); external nares bordered anteriorly by rostral, dorsally by supranasal, posteriorly by two large postnasals, ventrally by first supralabial (= circumnasals 5R,L); ten or 11 square supralabials tapering to below posterior margin of orbit; ten or 11 square infralabials tapering to below posterior margin of orbit; scales of rostrum raised, juxtaposed; scales of lores, top of head, and occiput small, granular, smaller than those of rostrum; dorsal superciliaries flat, rectangular, imbricate; mental triangular, bordered laterally by first infralabials and posteriorly by two large postmentals; each postmental bordered laterally by one or two sublabials; two enlarged sublabials extending posteriorly to second infralabial; row of eight scales extending transversely from juncture of second and third infralabials and contacting mental; gular scales triangular small, granular, grading posteriorly into slightly larger, subimbricate, throat and pectoral scales which grade into slightly larger, subimbricate ventrals.

Body somewhat stout, dorsoventrally compressed; ventrolateral folds absent; dorsal scales small, granular, 14–19 scales contained within one eye diameter; ventral scales, flat, subimbricate much larger than

Table 5. Character states within *Hemiphyllodactylus harterti* from Gunung Hijau (holotype) and *H. laruetensis* from Bukit Larut. / = data unavailable; f = female and m = male. All measurements in mm

	<i>Hemiphyllodactylus laruetensis</i>										<i>Hemiphyllodactylus harterti</i>			
	LSUHC 11294	LSUHC 11298	LSUHC 11591	LSUHC 11592	LSUHC 11296	LSUHC 11299	LSUHC 11295	LSUHC 11293	LSUHC 11542	BM 1901.3.20.2 holotype	LSUHC 10383	LSUHC 10384	ZMB 1360 holotype	
Sex	f	m	m	m	f	f	f	f	f	m	m	m	f	
Chin scales	7	9	7	6	8	8	6	7	8	9	7	8	6	
Postmentals distinctly enlarged (1) or not (0)	1	1	1	1	1	1	1	1	1	1	1	1	1	
Circumnasal scales	5	5	5	5	5	5	5	3	4	2	5	5	/	
Scales between supranasals	3	3	3	3	3	3	3	3	3	3	2	3	/	
Supralabial scales	9	10	9	10	9	9	9	10	10	10	11	10	10	
Infralabial scales	7	10	8	10	8	7	10	8	8	10	10	10	11	
Dorsal scales	13	17	17	19	15	13	18	16	20	15	19	14	/	
Ventral scales	8	9	9	10	8	7	13	9	9	6	14	10	/	
Lamellar formula on hand	3-4-4-3	3-4-4-4	3-4-4-4	2-4-4-4	3-4-4-3	3-4-4-3	3-4-4-3	3-4-4-4	3-4-4-4	3-4-4-4	3-4-4-4	3-4-4-4	/	
Lamellar formula on foot	3-4-4-4	4-5-5-5	3-4-4-4	3-5-5-4	3-4-4-4	4-5-5-5	3-4-4-4-4	4-5-5-5	4-5-5-5	3-4-4-4	3-4-4-4	3-4-4-4	/	
Subdigital lamellae on first finger	3	3	3	3	4	4	4	4	4	3	3	3	/	
Subdigital lamellae on first toe	3	4	3	4	4	4	4	5	5	4	4	4	/	
Precloacal and femoral pore series	/	27	28	27	/	/	/	/	/	36	45	44	/	
Separate (1) or continuous (0)	/	0	0	0	/	/	/	/	/	0	0	0	/	
Cloacal spurs	3	3	2	2	2	3	3	3	3	2	1	1	1	
Subcaudals enlarged, plate-like (1) or not (0)	0	0	0	0	0	0	0	0	0	0	0	0	0	
Dark postorbital stripe present (1) or absent (0)	1	1	1	1	faint	faint	0	faint	faint	1	1	1	/	
Light postocular or trunk spots (1) or absent (0)	1	1	1	1	1	1	1	1	1	1	1	1	/	
Dorsal dorsolateral stripe on trunk (1) or not (0)	0	0	0	0	0	0	0	0	0	0	0	0	/	
Dorsal pattern unicolor (1) or generally spotted (0)	1	1	1	1	1	1	1	1	1	1	0	0	/	
Longitudinal series of white (0) or yellow													/	
Or red (1) dorsal spots or no spots (2)	0	0	0	0	0	0	0	0	0	/	0	0	/	
Outer edge yellow or red (0), outer edge red (1), or yellowish (2)	1	1	1	1	1	1	1	1	1	/	1	1	/	
Postsacral mark lacking anterior arms (1) or arms present (0)	0	0	0	0	0	0	0	0	0	0	0	0	0	
Caecum pigmented (1) or not (0)	0	0	0	0	0	0	0	0	0	0	0	0	/	
Gonads pigmented (1) or not (0)	0	0	0	0	0	0	0	0	0	/	0	0	/	
SVL	52.2	42.7	43.1	42.8	46.5	44.3	44.4	45.1	45.3				42	
Trunk/SVL	0.47	0.48	0.47	0.47	0.51	0.46	0.51	0.49	0.51	/	0.53	0.48	0.53	
HeadL/SVL	0.21	0.25	0.23	0.23	0.25	0.23	0.21	0.24	0.23	/	0.23	0.22	0.24	
HeadW/SVL	0.15	0.16	0.16	0.17	0.15	0.15	0.16	0.15	0.16	/	0.18	0.18	0.15	
HeadW/HeadL	0.71	0.63	0.69	0.72	0.63	0.68	0.73	0.65	0.71	/	0.85	0.8	0.65	
SnEye/HeadL	0.46	0.39	0.45	0.43	0.38	0.43	0.51	0.43	0.42	/	0.48	0.46	0.41	
NarEye/HeadL	0.33	0.29	0.34	0.31	0.27	0.32	0.36	0.33	0.34	/	0.32	0.28	0.33	
EyeD/HeadL	0.26	0.24	0.24	0.28	0.22	0.25	0.28	0.26	0.26	/	0.27	0.28	0.3	
SnW/HeadL	0.12	0.12	0.14	0.14	0.11	0.13	0.15	0.12	0.15	/	0.17	0.15	0.21	
EyeD/NarEye	0.78	0.81	0.71	0.9	0.76	0.78	0.79	0.8	0.66	/	0.83	1	0.91	
SnW/HeadW	0.19	0.19	0.21	0.2	0.18	0.19	0.2	0.19	0.19	/	0.2	0.32	0.32	

For morphological abbreviations, see the Material and methods.

dorsal scales, ten–14 scales contained within one eye diameter; no enlarged, precloacal scales; row of 44 or 45 enlarged, pore-bearing femoral scales extend continuously from midway between the knee and hindlimb insertion of one leg to the other; forelimbs short, robust in stature, covered with flat, subimbricate scales dorsally and ventrally of similar size; 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 3-3-3-3; 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 subimbricate scales dorsally and ventrally of similar size; 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 3-3-4-3; 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 relatively short, not forming distinct caudal segments; original tail (LSUHC 10384, ZMB 1306) round in cross-section, covered with flat imbricate scales, subcaudal scales nearly twice the size of dorsal caudals; regenerated tail (LSUHC 10383) more flat in cross-section covered with flat imbricate scales, and bearing a weak ventrolateral fringe of scales, subcaudal scales slightly larger than dorsal caudals. Morphometric and mensural data are presented in Table 5.

Coloration (Fig. 5): The ground colour of the dorsal surface of the head, body, limbs, and tail is light brown and overlain with semi-regularly arranged longitudinal rows of diffuse, irregularly shaped darker dorsolateral markings; light and dark speckling occurs on the top of the head; there is a faint, irregular dark, preorbital and postorbital stripe bordered dorsally by a faint, beige line or a series of diffuse blotches; light, diffuse, irregularly shaped markings occur on the back and extend from the nape to the base of the tail; a diffuse, barely discernible postsacral marking begins at the base of the tail with paired light coloured blotches edged anteriorly by dark markings and anteriorly projecting arms extend to just beyond the anterior margin of the hind limb insertions; both the regenerated and original tails have a lighter base colour than the dorsum and are

covered with semi-longitudinally arranged diffuse small, dark, irregularly shaped blotches; faint, dark, diffuse markings occur on the limbs much like the body; there are no distinct, large, white to orange spots on the digits; all the ventral surfaces are beige with each scale bearing 0–2 small black stipples.

Redescription of *Hemiphyllodactylus larutensis* (Boulenger, 1900)

Head triangular in dorsal profile depressed, distinct from neck; lores and interorbital regions flat; rostrum moderate in length; prefrontal region flat; canthus rostralis smoothly rounded, barely discernible; snout moderate, rounded in dorsal profile; eye large; ear opening oval, small; eye to ear distance greater than diameter of eye; rostral wider than high, partially divided dorsally, bordered posteriorly by large supranasals; three internasals (= postnasals); external nares bordered anteriorly by rostral, dorsally by supranasal, posteriorly by one or two large postnasals, ventrally by first supralabial (= circumnasals); nine–11 square supralabials tapering to below posterior margin of orbit; seven–ten square infralabials tapering to below posterior margin of orbit; scales of rostrum raised, juxtaposed; scales of lores raised, larger than those of rostrum; scales of top of head and occiput small, granular, smaller than those of rostrum; dorsal superciliaries flat, rectangular, subimbricate; mental triangular, bordered laterally by first infralabials and posteriorly by two large postmentals; each postmental bordered laterally by one or two sublabials; two or three enlarged sublabials extending posteriorly to second infralabial; row of six–nine scales extending transversely from juncture of second and third infralabials and contacting mental; gular scales triangular small, flat, grading posteriorly into slightly larger, subimbricate, throat and pectoral scales which grade into slightly larger, subimbricate ventrals.

Body somewhat elongate, dorsoventrally compressed; ventrolateral folds absent; dorsal scales small, granular, 13–20 scales contained within one eye diameter; ventral scales, flat, subimbricate much larger than dorsal scales, six–13 scales contained within one eye diameter; no enlarged, precloacal scales; row of 27–36 enlarged, pore-bearing femoral scales extend continuously from midway between the knee and hind limb insertion of one leg to the other; forelimbs short, robust in stature, covered with flat, subimbricate scales dorsally and ventrally of similar size; 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 2-4-4-3, 3-3-3-3, 3-4-4-3, or 3-4-4-4; 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; hindlimbs short, more robust than forelimbs, covered with flat subimbricate scales dorsally and ventrally of similar size; 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 3-3-4-3, 3-4-4-4, 3-5-5-4, or 4-5-5-5; 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 relatively short, not forming distinct caudal segments; original and regenerated tail round in cross-section, covered with flat imbricate scales, subcaudal scales same size as dorsal caudals. Morphometric and mensural data are presented in Table 5.

Coloration (Fig. 5): The ground colour of the dorsal surface of the head, body, limbs, and tail is dark brown to tan and generally unicolour except for very faint, diffuse, irregularly shaped darker dorsolateral markings; faint, diffuse dark, preorbital and postorbital stripe; a series of small postocular dots extend onto neck; postsacral marking begins at the base of the tail with a medial triangular dark marking; orangish coloured anteriorly projecting arms extend to just beyond the anterior margin of the hind limb insertions; both the regenerated and original tails are orangish in colour bearing a series of dark, widely spaced vertebral spots, spots sometimes form a faint vertebral line; limbs immaculate; there are no distinct, large, white to orange spots on the digits; and all the ventral surfaces are beige with each scale bearing zero–four small black stipples.

Hemiphyllodactylus titiwangsaensis

Hemiphyllodactylus titiwangsaensis is known from three populations within the Banjaran Titiwangsa of Peninsular Malaysia: a northern population from the Cameron Highlands, Pahang, and two southern populations, one from Fraser's Hill, and another from Genting Highlands, Pahang (Fig. 6). Zug's (2010) description of *H. titiwangsaensis* included only specimens from the Cameron Highlands, although he mentioned the occurrence of this species at Fraser's Hill, but did not note its presence from the Genting Highlands (Smedley, 1932). Grismer (2011a) alluded to the differences between the northern and the two southern populations, which is well-supported in the molecular analysis (Fig. 1). This cladogenic split along the Banjaran Titiwangsa is also seen

in the sister species *Cyrtodactylus trilatofasciatus* Grismer *et al.*, 2012a and *Cyrtodactylus australotitiwangsaensis* Grismer *et al.*, 2012a, and is a common pattern beginning to emerge in a number of other taxa (L. L. Grismer, P. L. Wood, E. S. H. Quah, S. Anuar, M. A. Muin & A. Norhayati, unpubl. data). The two lineages of *Hemiphyllodactylus* are separated by approximately 85 km and have a sequence divergence of 12.4–12.8%, strongly suggesting that gene flow between them does not exist. The sequence divergence within the southern clade between the sister lineages from Fraser's Hill and the Genting Highlands is 3.5%, and occurs over a distance of approximately 35 km (Fig. 5). Based on the sequence divergence and discrete morphological differentiation (L. Grismer, unpubl. data), we restrict the distribution of *H. titiwangsaensis* to the Cameron Highlands and, at this juncture, consider the populations from Fraser's Hill and the Genting Highlands as the CCS *H. sp. nov.* 1, which is currently being described.

The typus group

Zug (2010) speculated that *Hemiphyllodactylus* was composed of two 'subclades' (for which no explicit data of monophyly for either were presented), based on generally non-discrete overlapping morphological characters. He proposed the *typus* species group to contain *Hemiphyllodactylus auarntiacus* (Beddome, 1870), *H. ganoklonis*, *H. insularis*, *H. typus*, and populations in Borneo, and the *yunnanensis* species group to contain at least *H. harterti*, *H. margarethae*, and *H. yunnanensis*. The placement of other taxa were not mentioned. The genetic data presented here do not support this division, in that multiple members of Zug's (2010) proposed groups are embedded within each other (Fig. 1). Given the lack of unequivocal morphological support for these subclades and no evidence for their monophyly, we elect to follow a more robust partitioning of *Hemiphyllodactylus* based on the deep divergence (28.9%) indicated by the molecular evidence. The *typus* group as constructed here is composed of seven distinct strongly supported clades that encompass the nominal taxa *H. aurantiacus*, *H. ganoklonis*, *H. insularis*, *H. typus*, and *H. yunnanensis*, including the subspecies *H. y. dushanensis*, *H. y. jinpingensis*, *H. y. longlingensis*, and *H. y. yunnanensis* (Zhou *et al.*, 1981; Zug, 2010). Samples of *H. margarethae* from Sumatra, Indonesia, were unavailable, and we will not speculate about which group it belongs to. With the exclusion of the unisexual *H. typus*, this group extends from southern India and Sri Lanka, across Indochina, to Hong Kong. Although the relationships among the four well-supported basal lineages (A–D) composing the *typus* group remain unresolved, the considerable degree of



Figure 6. A, adult male *Hemiphyllodactylus titiwangsaensis* (LSUDPC 4506) from Cameron Highlands, Pahang, Peninsular Malaysia. B, adult female *Hemiphyllodactylus* sp. nov. 1 from Genting Highlands, Pahang, Peninsular Malaysia. C, adult male *Hemiphyllodactylus* sp. nov. 1 from Fraser's Hill, Pahang, Peninsular Malaysia.

phylogenetic substructuring within and among the seven clades that these basal lineages comprise is well supported (Fig. 1), and the taxonomic implications of this substructuring are discussed below.

Taxonomy of the typus group

Zug (2010: fig. 16) provisionally divided *H. yunnanensis* into a northern upland group (*H. yunnanensis*) from southern China and adjacent northern Southeast Asia, and a southern lowland group (*H. yunnanensis*) from Southeast Asia and Hong Kong, although no clear morphological differences were presented in support of either group. The genetic data presented here and those of Heinicke *et al.* (2011b) do not support this division. *Hemiphylloclactylus yunnanensis* s.l. is polyphyletic with respect to lineages from northern Thailand, northern Myanmar, southern Laos, and central Vietnam, as well as *H. aurantiacus* from southern India (Fig. 1).

Clade 1: This lineage is composed of an insular population from Pulau Sibul of the Seribuat Archipelago, Peninsular Malaysia, and its sister population from Pulau Enggano, off the south-west coast of Sumatra, Indonesia, and both are currently recognized as *H. typus* (Wood *et al.*, 2004; Grismer *et al.*, 2006; Zug, 2010; Grismer, 2011a, b). The Pulau Sibul population (LSUHC 5797; Fig. 7) is not *H. typus* because the only known specimen is a male and *H. typus* is parthenogenetic. Unfortunately, the specimen was lost in transit. Because this specimen is a male and is genetically distinct from all other congeners, we recognize the Pulau Sibul population as CCS *H. sp. nov. 2*. We examined two specimens recently collected from Pulau Enggano (MVZ 239345–46, Fig. 7), and conclude that they are not *H. typus* based on scalation and that MVZ 239345 is a male. Additionally, this population cannot be ascribed to *H. margarethae* from Sumatra (with a possible occurrence on Pulau Nias off the west coast of Sumatra; Zug, 2010) in that the male specimen (MVZ 239345) has a total of 42 continuous femoral and preloacal pores, whereas *H. margarethae* has a total of 29 pores, and the femoral and preloacal series are discontinuous (Zug, 2010). We consider the Pulau Enggano population as CCS *H. sp. nov. 3*. The peculiar biogeographical pattern of species from islands in the Seribuat Archipelago being more closely related to species on islands in the Sunda Shelf (hundreds of kilometres to the south), as opposed to species from Peninsular Malaysia, less than 40 km to the west, is not uncommon (for a list of species across a broad taxonomic range, see Grismer *et al.*, 2006), and is a pattern that is continuing to emerge as more phylogenies are developed.

Clade 2: This clade is composed of two sister lineages: a weakly supported Philippine and Pulau Ngercheu lineage, and a strongly supported lineage containing a population from Mindanao, Philippines, and populations of *H. typus* extending from Peninsular Malaysia to Fiji. The basal species of clade 2 are *H. insularis* from Zamboanga City Province, Mindanao (Fig. 8) and *H. ganoklonis* from Pulau Ngercheu, respectively. The sister populations from Mount Lantoy, Cebu Island, and from Pulaui Island each represent new species, as neither is embedded within any other species on the tree (Figs 1, 8), and have sequence divergences of 13.9–17.5% and 16.6–21.9%, respectively, from the other species of clade 2. The morphology of the Cebu Island specimen (KU 331843) is unique and does not align with any known taxon (Zug, 2010), and as such it is considered here as CCS *H. sp. nov. 4*. We did not examine material from Pulaui Island, and thus consider it UCS *H. sp. nov. 5*. The *H. typus* lineage contains a basal population from Mindanao that we consider as UCS *H. sp. nov. 6*, in that it shows reasonable separation (3.0% sequence divergence) from the other *H. typus* specimens, even though the specimens examined (KU 314090–91) are superficially similar to *H. typus* and require further study. Although only four specimens of the widely distributed unisexual *H. typus* were sampled, the samples covered a distance of approximately 9000 km from Penang Island, Peninsular Malaysia, in the west to Suva, Fiji, in the east, and showed a sequence divergence of only 0.1%, which is not surprising given this species is parthenogenetic and a likely human commensal. We consider this as additional support to our hypothesis that KU 314090–91 from Mindanao are not *H. typus*, even though they have less than a 5.8% sequence divergence from *H. typus*. Zug (2010) reports a bisexual population of *H. typus* from north-eastern Borneo in need of further study.

Clade 3: The phylogeny indicates *H. yunnanensis* (*sensu* Zug, 2010; clades 3–7) is polyphyletic with respect to *H. aurantiacus* and at least four undescribed species (see below), even though it is composed of a number of lineages with considerable and well-supported substructuring (Fig. 1). Zug (2010) considered *H. y. longlingensis* and *H. y. jinpingensis* (and presumably *H. y. dushanensis*, although it was not mentioned) as synonyms of a ‘monotypic’ (*sensu* Zug, 2010) *H. yunnanensis*, based on what he considered (without examination) to be a size continuum between two different states (ranging from ‘barely’ enlarged to ‘strongly’ enlarged) of the postmental and chin scales (*contra* Zhou *et al.*, 1981). The phylogeny (Fig. 1), however, indicates that *H. y. jinpingensis* and *H. y. longlingensis* form distinct lineages that are not even each other’s closest

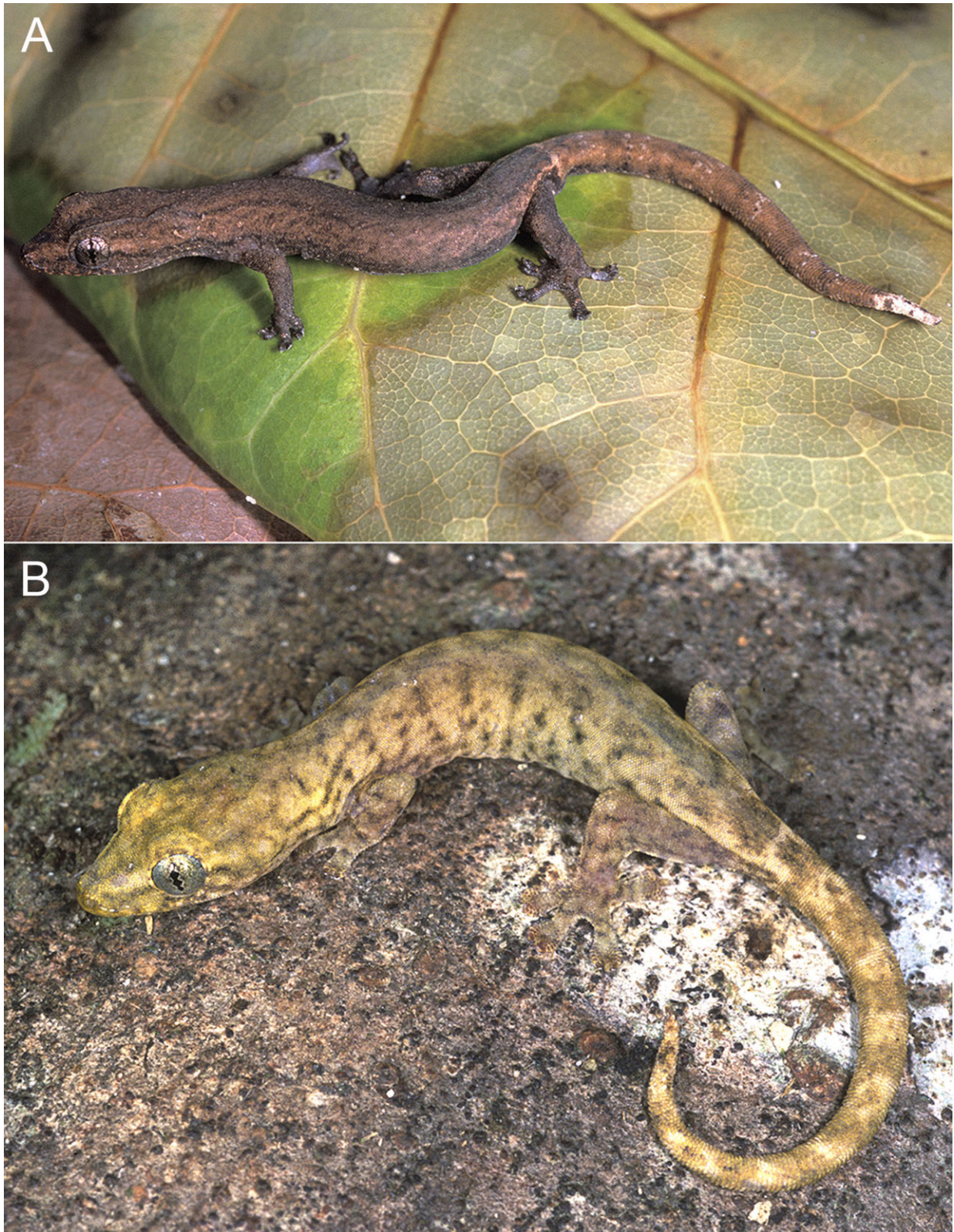


Figure 7. A, adult male *Hemiphyllodactylus* sp. nov. 2 (LSUHC 5759) from Pulau Sibul, Johor, Malaysia; photo by L. Grismer. B, adult female *Hemiphyllodactylus* sp. nov. 3 (MVZ 239345) from Pulau Enggano, Sumatra, Indonesia; photo by J. McGuire.



Figure 8. A, adult male *Hemiphyllodactylus* sp. nov. 5 (PNM 7666) from Palau Island; photo by R.M. Brown. B, adult male *Hemiphyllodactylus insularis* (KU uncatalogued) from Pasonanca, Zamboanga, Western Mindanao, Philippines. C, adult female *Hemiphyllodactylus* sp. nov. 4 (KU 331843) from Mount Lanoy, Municipality of Argao, Cebu Province, Philippines; photo by R.M. Brown.

relatives, in that *H. y. longlingensis* forms a clade with populations from Central Myanmar and north-western Thailand, which are shown below to be distinct species themselves (i.e. not *H. yunnanensis sensu* Zug, 2010). Zhou *et al.* (1981) separated these two subspecies on the basis of the former having subdigital scissor formulae of 3-4-4-4 on the hand and 4-5-5-5 on the foot, as opposed to 3-3-3-3 on the hand and 3-4-4-4 on the foot in the latter, and they have a mean sequence divergence between them of 18.6% (Table 3). Furthermore, based on Zhou *et al.* (1981), these non-reticulating lineages come from disjunct upland populations in different mountain ranges that extend for approximately 1200 km across southern China, from Longling County, Yunnan Province, in the west to Dayaoshan, Guangxi Province, in the east (Zhou *et al.*, 1981; Fig. 2). One outlying individual of *H. y. longlingensis* (FJ971049.1) does not group with other *H. y. longlingensis* specimens, but instead forms a distant (18.4% sequence divergence) sister lineage relationship with *H. y. jinpingensis* (Fig. 2). Unfortunately we were unable to examine this specimen or to determine from the authors its provenance, and thus we leave its species status as *insertae sedis*. With the exception of this outlying individual, recognizing the subspecies of *H. yunnanensis* as species-level taxa is more consistent with the genetic, morphological, and biogeographic data, and does not misrepresent their evolutionary history by recognizing a polyphyletic *H. yunnanensis*.

Clade 4: Clade 4 is the sister lineage to clade 3, and is composed of a basal lineage from Chiang Mai, Thailand, and its sister lineages from Pyin-Oo-Lwin, Mandalay Division, Myanmar, and *H. longlingensis* from southern China (Zhou *et al.*, 1981; Fig. 1). Neither the Chiang Mai nor Mandalay populations are phylogenetically imbedded within *H. longlingensis*, to which they are related, or imbedded within *H. yunnanensis*, with which they are currently considered conspecific (Zug, 2010). Additionally, they bear substantial sequence divergences between them and the other lineages of clades 3 and 4 (18.6–18.8%; Table 6). We have examined nine specimens (Appendix) from Chiang Mai, and have found that they are morphologically distinct from all other *Hemiphyllodactylus* (L. L. Grismer, P. L. Wood, M. Cota, unpubl. data), and recognize them here as CCS *H. sp. nov. 7* (Fig. 9). We have examined only colour photos of a specimen from Mandalay (Fig. 9), but given its phylogenetic position within clade 4 and its 13.5% sequence divergence from its sister species *H. longlingensis*, we consider this population as UCS *H. sp. nov. 8*.

Clade 5: The species status of *H. aurantiacus* from southern India and Sri Lanka (Figs 2, 10) is well supported in the phylogeny, and corroborates Zug's (2010) continued recognition of this taxon as a species-level lineage (*contra* Smith, 1935), based on morphology. A specimen catalogued as *H. yunnanensis* (FMNH 258695) from Pakxong District, Champasak Province, in southern Laos, and recognized by Zug (2010) as '*H. yunnanensis*' is the sister lineage to *H. aurantiacus* (Fig. 1). Based on the considerable sequence divergence (23.1%) between these lineages, the significant distributional gap between southern India and Champasak, Laos (~3000 km; Fig. 2), and the distinct morphology of this population (B. L. Stuart, unpubl. data), we consider this lineage as CCS *H. sp. nov. 9*, and we predict that geographically intervening species within this clade will eventually be discovered. Heinicke *et al.* (2011b) have previously considered this population to be a distinct species.

Clade 6: Clade 6 is composed of a basal lineage from Ba Na-Nui Chua Nature Reserve, Hoa Vang District, Da Nang City, in central Vietnam ('*H. yunnanensis*'; Zug, 2010), and the sister species *H. zugi* from Vinh Phuc Province in northern Vietnam (Zug, 2010) and *H. dushanensis* from Guizhou Province in southern China (Nguyen *et al.* 2013; Zhou *et al.*, 1981; Figs 1, 2). Based on morphology (V. T. Ngo, L. L. Grismer, H. Pham, P. L. Wood, unpubl. data), the Ba Na-Nui Chua Nature Reserve population (Fig. 10) cannot be ascribed to any known species of *Hemiphyllodactylus*, and it has a 16.7% sequence divergence from other lineages in clade 6. Thus, we consider it here to be CCS *H. sp. nov. 10*.

Clade 7: Clade 7 comprises *H. yunnanensis s.s.*, and is what Zhou *et al.* (1981) considered to be *H. y. yunnanensis*. The phylogeny (Fig. 1) indicates that there is considerable substructuring within this lineage, with perhaps as many as five additional species. We were unable to ascertain the exact localities of the specimens in Figure 1, nor did we examine material from southern China. Unlike other species of *Hemiphyllodactylus*, *H. yunnanensis s.s.* still contains a large number of undescribed species scattered throughout the vast fragmented uplands of southern China.

DISCUSSION

It is a well-established fact that the world's biodiversity is woefully underestimated (Mora *et al.*, 2011), and that most species with broad distributions across environmentally heterogeneous regions are rarely a single species, but rather complexes of generally



Figure 9. A, *Hemiphyllodactylus* sp. nov. 7 (LSUDPC 6668) from Chiang Mai, Chiang Mai Province, Thailand; photo by P.L. Wood. B, *Hemiphyllodactylus* sp. nov. 8 (USNM 570374) from Pyin-Oo-Lwin, Mandalay Division, Myanmar; photo by G. Zug.

cryptic species. This is especially true in tropical regions such as Southeast Asia, the dynamic and complex environmental history of which (Hall, 1998, 2001, 2002, 2012; Woodruff, 2003, 2010; Bird, Taylor & Hunt, 2005; Outlaw & Volker, 2008; Reddy, 2008; Cannon, Morley & Bush, 2009; Cannon, 2012; Gower *et al.*, 2012; Morley, 2012; Richardson, Costion & Muellner, 2012) has contributed greatly to the phylogenetic and phylogeographic structuring of a number of wide-ranging clades thought previously to be single species (e.g. Matsui *et al.*, 2005; Stuart, 2006; Inger, Stuart & Iskandar, 2009; Wood *et al.*, 2009, 2010; Grismer *et al.*, 2010b, 2012a; Malhotra *et al.*, 2011; Brown *et al.*, 2012; Johnson *et al.*, 2012; Nishikawa *et al.*, 2012; Loredó *et al.*, 2013). The infu-

sion of a molecular phylogenetic data set into the morphology-based classification of the wide-ranging genus *Hemiphyllodactylus* not only contributes to this growing body of knowledge, but highlights the inherent tendency of morphological data sets to underestimate biodiversity in taxonomic revisions of widespread groups. Zug's (2010) characterization of *Hemiphyllodactylus* as a 'low diversity taxon' is emblematic of this problem, in that this group's diversity was underestimated conservatively by as much as 113–162%. The molecular phylogeny of *Hemiphyllodactylus* (Fig. 1) facilitated an independent test of the morphology-based taxonomy (Zug, 2010), identified a minimum of ten (perhaps as many as 13) additional lineages for consideration of

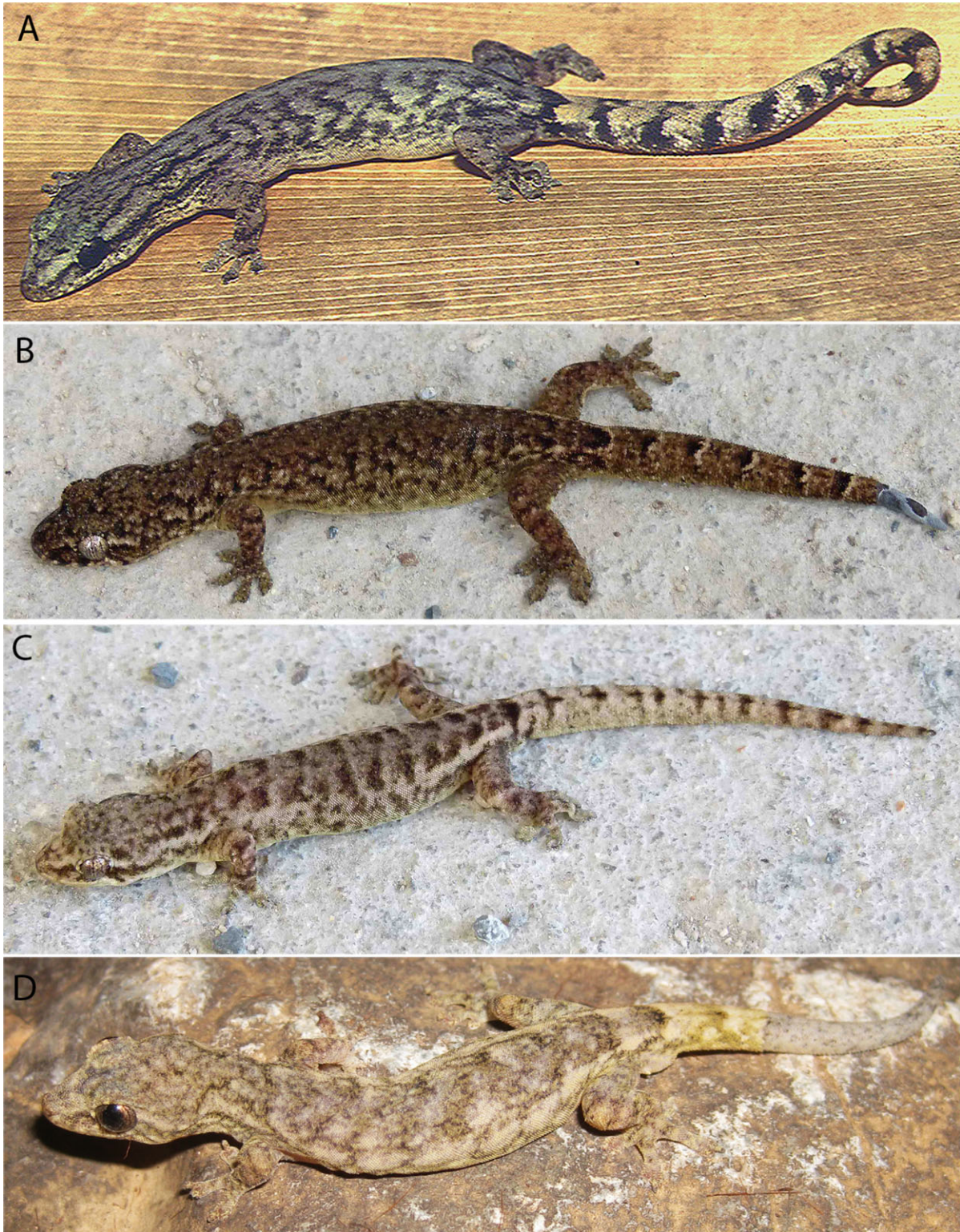


Figure 10. A, adult *Hemiphyllodactylus auriantiacus* (LSUDPC 7006) from Yercaud, Salem District (Shevaroyan Hill Range), Tamil Nadu, India. B, adult *Hemiphyllodactylus* sp. nov. 10 (ITBCZ 2450). C, male *Hemiphyllodactylus* sp. nov. 10 (LSUDPC 6675) from Ba Na-Nui Chua Nature Reserve, Hoa Vang District, Da Nang City Province, Vietnam; photos B and C by Ngo Van Tri. D, adult male *Hemiphyllodactylus zugii* (LSUDPC 8089) from Cao Bang Province, Vietnam; Photo by T. Q. Nguyen and T. Lehmann.

species-level designation, and resulted in a less subjective and more stable classification upon which others can build. Some (i.e. Isaac, Mallet & Mace, 2004) posit that studies such as these: (1) result in taxonomic inflation because they tend to use lineage-based species concepts as opposed to a more 'stable' biological species concept; (2) impede macroevolutionary studies because they generate asymmetric taxonomies across groups, making them incomparable; and (3) generate unnecessary challenges for conservation efforts. We argue that rather than inflating taxonomies, an integrative approach based on a unified lineage concept (de Queiroz, 1998) actually reveals the true structure of biodiversity, and will ultimately enhance conservation efforts by bringing to the forefront the entities (i.e. species, management units, etc.) in actual need of conserving. The resulting taxonomies are not only more species rich, but are more stable because they are inextricably bound to methodologically and conceptually less biased molecular data sets, and are delivered from the pluralistic outdated biological species concept that is difficult or impossible to apply to allopatric lineages, and often misrepresents the history (e.g. see Frost & Kluge, 1994).

Recent taxonomic work across the broad spectrum of life is revealing that nature is considerably more diverse than a polytypic species concept (Mayr, 1963) would lead us to believe. And if we are to forward a sincere effort in an attempt to stem the biodiversity crisis, we need to know upon what to focus our efforts. The very broad distribution (from the Mascarene Islands to Hawaii) and generally conserved morphology of *Hemiphyllodactylus* illustrates the limits of a morphological taxonomy in the delimitation of species boundaries for such groups. Considerable work on this group is still necessary before we gain a clear understanding of its diversity. The genetics of many of the known populations from Vietnam, Laos, Cambodia, Thailand, and throughout the islands of Indonesia, for example, remain unsampled. As additional material becomes available, we will use the phylogenetic taxonomy hypothesized here as a foundation upon which to build future taxonomies. Infusing this taxonomy with molecular estimates of phylogeny allows for a more fine-grained analysis and greater potential for discovering species-level lineages and distinct management units that may be of special concern and in need of conservation (Hodkinson *et al.*, 2012).

ACKNOWLEDGEMENTS

For assistance in the field we thank A. Alonso, A. Cobos, B. Beltran, C. Ogle, C. Thompson, A.C. Diesmos, C. D. Siler, and M. Yusof. For the loan of specimens we are indebted to Kelvin K.P. Lim (ZRC).

We thank the Terengganu State Forestry Department for their permission to conduct research in Gunung Tebu Forest Reserve. We are grateful for the generosity of M. Heinicke and A. Bauer for providing us with unpublished sequence divergence data for a number of gekkonid species. The Philippine fieldwork was supported by a National Science Foundation grant (DEB 0743491) to RMB; we thank the Philippine Department of Environment and Natural Resources for research permits. A research pass (40/200/19 SJ.1105) was issued to LLG by the Economic Planning Unit, Prime Minister's Department, Malaysia. This research was supported in part by grants to LLG from the College of Arts and Sciences, La Sierra University, Riverside, California, and by a Universiti Sains Malaysia grant 815075 to Shahrul Anuar. DNA sequencing was supported by J. W. Sites Jr and the department of biology at Brigham Young University. Fieldwork for Evan S. H. Quah in Malaysia was partially supported by the USM Fellowship Scheme.

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APPENDIX

The following specimens were examined. Museum acronyms follow those of Sabaj-Pérez (2010).

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 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 Terjung Titikerawang LSUHC 10342. *Hemiphyllodactylus* cf. *yunnanensis*. Cambodia; Pursat Province, Phnom Samkos, LSUHC 8242. *Hemiphyllodactylus* sp. nov. 1. Malaysia: Pahang, Fraser's Hill, LSUHC 6477, 6487–89, 8055–57, 8080, 8092; Genting Highlands, LSUHC 10693–94, 10699–700. *Hemiphyllodactylus* sp. nov. 2. Malaysia, Johor, Pulau Sibul, LSUHC 5797. *Hemiphyllodactylus* sp. nov. 3. Indonesia, Sumatra, Bengkulu Province, Pulau Enggano, MVZ 236345–46. *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. 6. Philippines: Agusan del Sur Province, Municipality of San Francisco, Barangay Kaim, KU 314090–91.

Hemiphyllodactylus sp. nov. 7. Thailand: Chiang Mai Province, Chiang Mai, NSMNH 15192–200. *Hemiphyllodactylus* sp. nov. 9. Laos: Champasak Province, Pakxong District, FMNH 258696. *Hemiphyllodactylus* sp. nov. 10. Vietnam: Da Nang Province, Hoa Vang District, Ba Na-Nui Chua Nature Reserve, ITBCZ 2450, 2461–69.