Repeated evolution of sympatric, palaeoendemic species in closely related, co-distributed lineages of *Hemiphyllodactylus* Bleeker, 1860 (Squamata: Gekkonidae) across a sky-island archipelago in Peninsular Malaysia

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A time-calibrated phylogenetic tree indicates that the evolution of sympatric, montane, endemic species from closely related, co-distributed lineages of the *Hemiphyllodactylus harterti* group were not the result of rapid, forest-driven, climatic oscillations of the Last Glacial Maximum, but rather the result of infrequent episodes of environmental fluctuation during the Late Miocene. This hypothesis is supported by genetic divergences (based on the mitochondrial gene *ND2*) between the three major lineages of the *H. harterti* group (17.5–25.1%), their constituent species (9.4–14.3%), and the evolution of discrete, diagnostic, morphological, and colour pattern characteristics between each species. Sister species pairs from two of the three lineages occur in sympatry on mountain tops from opposite sides of the Thai–Malay Peninsula, but the lineages to which each pair belongs are not sister lineages. A newly discovered species from Gunung Tebu, Terengganu State, *Hemiphyllodactylus bintik* **sp. nov.**, is described.

INTRODUCTION

Southeast Asia harbours 20–25% of the planet's terrestrial biodiversity in only 4% of its landmass. This extraordinary level of species richness cannot be explained by current environmental variables alone, but has arisen from repeated speciation events over millions of years, linked to the interaction of geological processes and climate (Wiens, 2004; Bird, Taylor & Hunt, 2005; Outlaw & Voelker, 2008; Reddy, 2008;

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Cannon, Morley & Bush, 2009; Woodruff, 2010; Cannon, 2012; Hall, 2012; Morley, 2012). Climatic oscillations from the Miocene to the present day have dramatically shaped and re-shaped the global distribution of ecosystems, with attendant effects on the genetics and distribution of the planet's biodiversity (Hewitt, 2004; Morley, 2012). Nowhere have these events been more pronounced than in the tropical, montane ecosystems of Southeast Asia, where cyclical, climate-driven (Bintanja, van de Wal & Oelemans, 2005; Thomas *et al*., 2009), forest dynamics have created upland refugia that act as drivers of speciation, and have resulted in extraordinarily high levels of endemism (Woodruff, 2010). Although many authors have focused on a Quaternary refugial model (especially during the Late Glacial Maximum, LGM) to account for elevated levels of upland endemism (Heaney, 1991; Meijaard, 2003; Bird *et al*., 2005; Reddy, 2008; Cannon *et al*., 2009; Cannon, 2012; Morley, 2012), molecular evidence shows that many tropical, montane species are palaeoendemics (*sensu* Tolley *et al*., 2011) that have persisted in restricted, upland refugia since before the Pliocene (Matsui *et al*., 2010; Tolley *et al*., 2011; Bell *et al*., 2012), and that species diversification generally happens along a time continuum with no clear, single, defining episode (Bell *et al*., 2010, 2012; Voelker, Outlaw & Bowie, 2010). The continuum model is supported by a broad range of genetic distances observed between co-distributed lineages bearing sister populations across a common, upland landscape (Avise & Walker, 1998; Bermingham & Moritz, 1998; Bell *et al*., 2010). Time-calibrated phylogenetic analyses can distinguish between the non-mutually exclusive, continuum, and LGM models. Allopatric sister species bearing significant genetic and discrete, morphological differences are indicative of episodes of speciation predating the Pleistocene and a lack of gene introgression during cooler, relaxed, interglacial periods. Sister species with little or no genetic and morphological differences are indicative of populations that have recently split and/or have experienced substantial introgression during periods of interglacial range expansion (Bell *et al*., 2010, 2012; Tolley *et al*., 2011; Loredo *et al*., 2013; Grismer *et al*., 2014c). Neither model, however, has been tested in a monophyletic group where different pairs of closely related, sympatric, sister lineages share the same phylogeographic pattern occurring at different nodes in the same tree.

In an integrative taxonomic analysis of the gekkonid genus *Hemiphyllodactylus* Bleeker, 1860, Grismer *et al*. (2013) referred to the two major lineages in this genus as the *typus* and *harterti* groups. The latter is a geographically circumscribed clade composed solely of rarely observed, non-vagile, montane endemics from three different mountain ranges across Peninsular Malaysia (Fig. 1). Grismer *et al*. (2013) demonstrated that two

sympatric species, *Hemiphyllodactylus harterti* Werner, 1900 and *Hemiphyllodactylus larutensis* Boulenger, 1900 in the Bintang Range on the western edge of the Thai–Malay Peninsula were not each others closest relatives, and that the latter was the sister species of *Hemiphyllodactylus tehtarik* Grismer *et al*., 2013, an upland endemic from Gunung Tebu in the Timur Range from the eastern edge of the peninsula, approximately145 km away (Fig. 1). Additional fieldwork on Gunung Tebu resulted in the discovery of another new species of *Hemiphyllodactylus*, and molecular analysis indicates that this is not the sister species of *H. tehtarik*, with which it is sympatric, but instead is most closely related to *H. harterti* from the western Bintang Range (Fig. 1). Thus, the presence of two closely related pairs of endemic, montane, sister species with identical phylogeographies provides an ideal opportunity to understand how cyclical patterns of allopatric speciation may be related to cyclical environmental fluctuations across a broad continuum of time in a shared, upland landscape of a sky-island archipelago.

MATERIAL AND METHODS
PHYLOGENETIC ANALYSES

A 1505-bp fragment of the NADH dehydrogenase subunit 2 gene (*ND2*), including the flanking transfer RNAs (tRNAmet, tRNAtrp, tRNAala, tRNAsn, and tRNAtyr) of 47 samples obtained from GenBank, was added to 41 sequenced individuals (see Grismer *et al*., 2013). Two new samples of *Hemiphyllodactylus titiwangsaensis* Zug, 2010 and one sample of the new population from Gunung Tebu were sequenced for the same fragment along with 32 taxa used as out-groups (Heinicke *et al*., 2011; Wood *et al*., 2012; Grismer *et al*., 2013; Table 1). Total genomic DNA was isolated from liver or skeletal muscle specimens stored in 95% ethanol using the Qiagen DNeasy™ tissue kit (Valencia, CA, USA). *ND2* was amplified using a double-stranded polymerase chain reaction (PCR) under the following conditions: 1.0 μl genomic DNA, 1.0 μl light strand primer, 1.0 μl heavy strand primer, 1.0 μl dinucleotide pairs, 2.0 μl 5× buffer, 1.0 μl MgCl 10× buffer, 0.18 μl Taq polymerase, and 7.5 μl H_2O. 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, 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
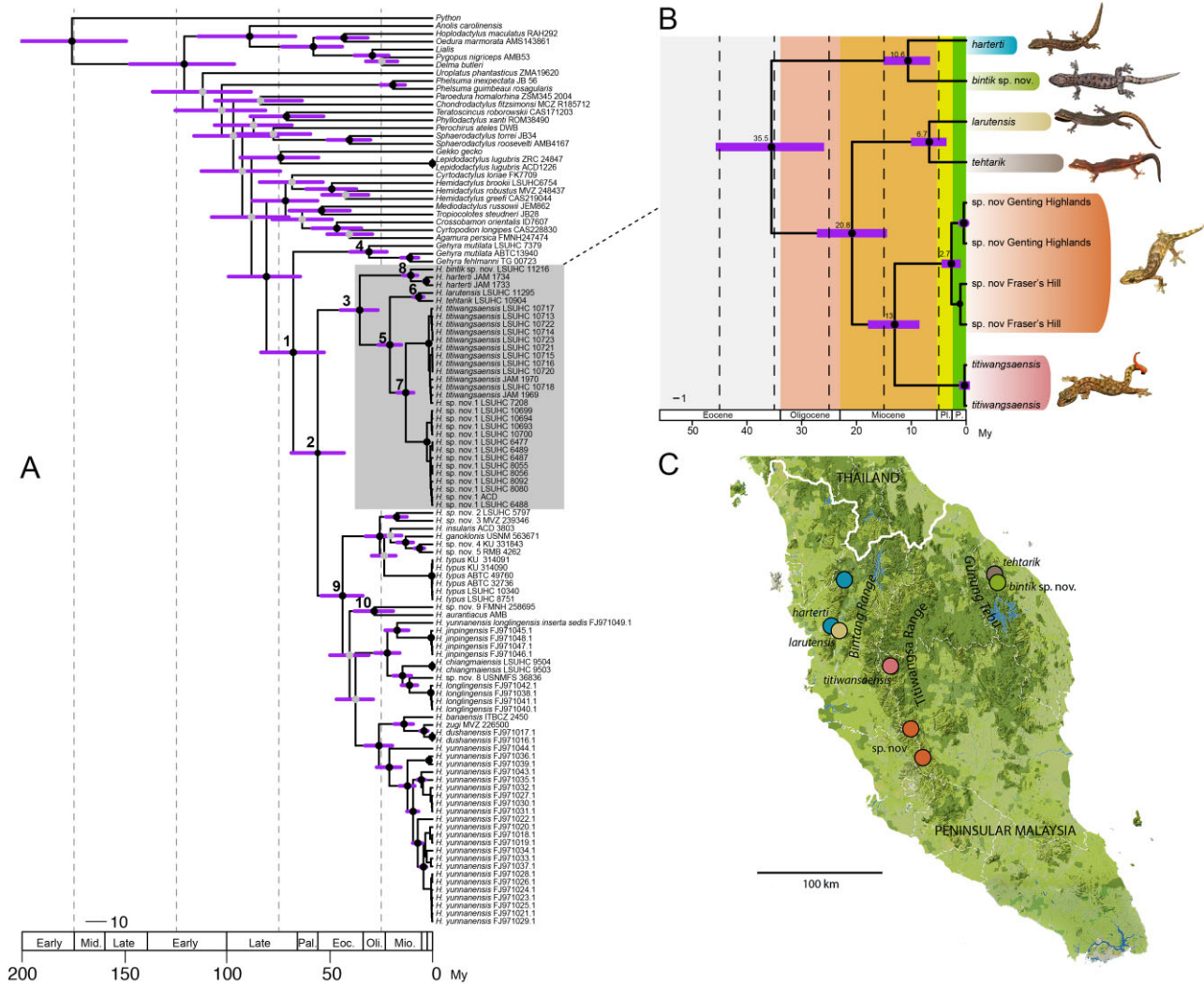
Figure 1. A, Bayesian time tree for *Hemiphyllodactylus* with 95% highest posterior density (95% HPD) intervals for major nodes represented by purple bars. Black circles at nodes are posterior probabilities ≥ 0.95; grey circles at nodes are posterior probabilities < 0.95. B, Bayesian time tree for the *Hemiphyllodactylus harterti* group. C, Distribution of the *H. harterti* group in Peninsular Malaysia.

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 centre. The primers used for amplification and sequencing are presented in Table 2.

SUBSTITUTION SATURATION AND DIVERGENCE TIME ESTIMATES

Prior to estimating divergence times, the data set was tested for substitution saturation using DAMBE 5 (Xia, 2013). The data set was pruned down to 53 individuals excluding samples with missing data. The pro-portion of invariable sites were calculated for each codon position and the tRNAs on the basis that there are different substitution rates between codon positions (e.g. first and second versus third), and it is important to incorporate this in the substitution saturation analyses. A neighbour-joining tree-building algorithm was used for each analysis, implementing default settings. Following the estimation of the distance-based tree and the proportion of invariable sites the substitution saturation test of Xia *et al.* (2003) was employed. To help mitigate and explore the potential effects of substitution saturation we applied three different partitioning schemes (partition 1, by gene, *ND2* + tRNAs; partition 2, by codon, first, second, third, +tRNAs; and partition 3, first and second sites, with no or little

Table 1. GenBank accession numbers for voucher specimens used for divergence time estimates

Voucher number	Species	Locality	GenBank accession numbers *ND2* + tRNAs
FMNH 247474	*Agamura persica*	Balochistan, Makran district, Gwadar division, Pakistan	JX440515
n/a	*Anolis carolinensis*	n/a	EU747728
MCZ R185712	*Chondrodactylus fitzsimonsi*	Gai-as spring, Namibia	JN393945
ID 7607	*Crossobamon orientalis*	Sam, Rajasthan, India	KC151975
FK 7709	*Cyrtodactylus loriae*	Milne Bay, Bunis, Papua New Guinea	EU268350
SAMA R36144	*Delma butleri*	Coonbah, New South Wales, Australia	AY134584
TG 00723	*Gehyra fehlmanni*	Imported from Malaysia	JN393948
ABTC 13940	*Gehyra insulensis*	Krakatau, Indonesia	GQ257784
LSUHC 7379	*Gehyra mutilata*	Phnom Aural, Pursat Province, Cambodia	JN393914
MVZ 215314	*Gekko gecko*	Phuket Island, Phuket, Thailnad	AF114249
MVZ 215314	*Gekko gecko*	Phuket Island, Phuket, Thailand	AF114249
LSUHC 6754	*Hemidactylus brookii*	Empangan Air Hitam, Penang, Malaysia	EU268365
CAS 219044	*Hemidactylus greefii*	Praia da Mutmba, São Tome Island, São Tome and Principe	EU268369
MVZ 248437	*Hemidactylus robustus*	40 km south of Mipur Sakro, Thatta District, Pakistan	U268376
ZRC 24847	*Lepidodactylus lugubris*	Singapore	JN393944
ACD 1226	*Lepidodactylus* sp.	Unknown	KF219759
n/a	*Lialis jicari*	Australia	AY369025
n/a	*Mediodactylus russowii*	Captive	JX440517
AMS 143861	*Oedura marmorata*	Queensland, Australia	GU459951
ZSM 345 / 2004	*Paroedura homalorhina*	Ankarana, Madagascar	EF536214
DWB (n/a)	*Perochirus ateles*	Dehpelhi Island, Pohnpei, Micronesia	JN393946
DWB (n/a)	*Perochirus ateles*	Dehpelhi Island, Pohnpei, Micronesia	JN393946
JB 56	*Phelsuma inexpectata*	Reunion (captive)	JN393939
n / a	*Phelsuma rosagularis*	Mauritius	EU423292
ROM 38490	*Phyllodactylus xanti*	Baja California Sur, Mexico	JN393940
MVZ197233	*Pygopus nigriceps*	Northern Territory, Australia	JX440518
n/a	*Python regius*	n/a	AB177878
CAS 198428	*Sphaerodactylus roosevelti*	Puerto Rico, USA	JN393943
JB 34	*Sphaerodactylus torrei*	Cuba	JX440519
CAS 228830	*Tenuidactylus longipes*	Tabas, Kharve, Yazd Prov., Iran	KC151990
CAS 171203	*Teratoscincus roborowskii*	Xinjiang, China	AF114252
JB 28	*Tropiocolotes steudneri*	Captive	JX440520
ZMA 19620	*Uroplatus phantasticus*	Vohidrazana, Madagascar	EF490800
RAH 292	*Woodworthia maculata*	Titahi Bay, New Zealand	GU459852
AMB (n/a)	*Hemiphyllodactylus aurantiacus*	Tamil Nadu, Yercaud, India	JN393933
ITBCZ 2450	*Hemiphyllodactylus banaensis*	Ba Na-Nui Chua, Vietnam	KF219783
LSUHC 11216	*Hemiphyllodactylus bintik* sp. nov.	Gunung Tebu, Terengganu, Malaysia	KJ663757
LSUHC 9503	*Hemiphyllodactylus chiangmaiensis*	Chang Mai, Thailand	KF219781
LSUHC 9504	*Hemiphyllodactylus chiangmaiensis*	Chang Mai, Thailand	KF219782
n/a	*Hemiphyllodactylus dushanensis*	Guizhou, China	FJ971016
n/a	*Hemiphyllodactylus dushanensis*	Guizhou, China	FJ971017
USNM 563671	*Hemiphyllodactylus ganoklonis*	Ngercheu, Palau	JN393950
LSUHC 10383	*Hemiphyllodactylus harterti*	Bukit Larut, Perak, Malaysia	KF219760
LSUHC 10384	*Hemiphyllodactylus harterti*	Bukit Larut, Perak, Malaysia	KF219761
KU 314962	*Hemiphyllodactylus insularis*	Mindanao, Philippines	KF219762
n/a	*Hemiphyllodactylus jinpingensis*	Yunnan, China	FJ971045
n/a	*Hemiphyllodactylus jinpingensis*	Yunnan, China	FJ971046
n/a	*Hemiphyllodactylus jinpingensis*	Yunnan, China	FJ971047
n/a	*Hemiphyllodactylus jinpingensis*	Yunnan, China	FJ971048
LSUHC 11295	*Hemiphyllodactylus larutensis*	Bukit Larut, Perak, Malaysia	KJ663758
n/a	*Hemiphyllodactylus longlingensis*	Yunnan, China	FJ971038
n/a	*Hemiphyllodactylus longlingensis*	Yunnan, China	FJ971040
n/a	*Hemiphyllodactylus longlingensis*	Yunnan, China	FJ971041
n/a	*Hemiphyllodactylus longlingensis*	Yunnan, China	FJ971042
n/a	*Hemiphyllodactylus longlingensis inserta sedis*	Yunnan, China	FJ971049
LSUHC 6487	*Hemiphyllodactylus* sp. nov. 1	Fraser's Hill, Pahang, Malaysia	KF219767
LSUHC 6488	*Hemiphyllodactylus* sp. nov. 1	Fraser's Hill, Pahang, Malaysia	KF219768
LSUHC 6489	*Hemiphyllodactylus* sp. nov. 1	Fraser's Hill, Pahang, Malaysia	KF219769
LSUHC 6477	*Hemiphyllodactylus* sp. nov. 1	Fraser's Hill, Pahang, Malaysia	KF219770
LSUHC 8055	*Hemiphyllodactylus* sp. nov. 1	Fraser's Hill, Pahang, Malaysia	KF219771
LSUHC 8056	*Hemiphyllodactylus* sp. nov. 1	Fraser's Hill, Pahang, Malaysia	KF219772
LSUHC 8080	*Hemiphyllodactylus* sp. nov. 1	Fraser's Hill, Pahang, Malaysia	KF219773
LSUHC 8092	*Hemiphyllodactylus* sp. nov. 1	Fraser's Hill, Pahang, Malaysia	KF219774
ACD XXXX	*Hemiphyllodactylus* sp. nov. 1	Fraser's Hill, Pahang, Malaysia	KF219775
LSUHC 10693	*Hemiphyllodactylus* sp. nov. 1	Genting Highlands, Pahang, Malaysia	KF219763
LSUHC 10700	*Hemiphyllodactylus* sp. nov. 1	Genting Highlands, Pahang, Malaysia	KF219764

Table 1. *Continued*

Voucher number	Species	Locality	GenBank accession numbers *ND2* + tRNAs
LSUHC 10699	*Hemiphyllodactylus* sp. nov. 1	Genting Highlands, Pahang, Malaysia	KF219765
LSUHC 10694	*Hemiphyllodactylus* sp. nov. 1	Genting Highlands, Pahang, Malaysia	KF219766
LSUHC 5797	*Hemiphyllodactylus* sp. nov. 2	Pulau Sibu, Johor, Malaysia	JN393936
MVZ 239346	*Hemiphyllodactylus* sp. nov. 3	Pulau Enggano, Sumatra	KF219776
KU 331843	*Hemiphyllodactylus* sp. nov. 4	Cebu Island, Philippines	KF219777
RMB 4262	*Hemiphyllodactylus* sp. nov. 5	Palaui Island, Philippines	KF219778
KU 314090	*Hemiphyllodactylus* sp. nov. 6	Mindanao, Philippines	KF219779
KU 314091	*Hemiphyllodactylus* sp. nov. 6	Mindanao, Philippines	KF219780
USNM-FS 36836	*Hemiphyllodactylus* sp. nov. 7	Mandalay, Pyin Oo Lwin, Myanmar	JN393949
FMNH 258695	*Hemiphyllodactylus* sp. nov. 8	Champasak, Pakxong, Laos	JN393935
LSUHC 10904	*Hemiphyllodactylus tehtarik*	Gunung Tebu, Malaysia	KF219784
LSUHC 10717	*Hemiphyllodactylus titiwangsaensis*	Cameron Highlands, Malaysia	KF219785
JAM 1969	*Hemiphyllodactylus titiwangsaensis*	Cameron Highlands, Pahang, Malaysia	KJ663760
JAM 1970	*Hemiphyllodactylus titiwangsaensis*	Cameron Highlands, Pahang, Malaysia	KJ663759
LSUHC 10713	*Hemiphyllodactylus titiwangsaensis*	Cameron Highlands, Pahang, Malaysia	KF219786
LSUHC 10714	*Hemiphyllodactylus titiwangsaensis*	Cameron Highlands, Pahang, Malaysia	KF219787
LSUHC 10722	*Hemiphyllodactylus titiwangsaensis*	Cameron Highlands, Pahang, Malaysia	KF219788
LSUHC 10723	*Hemiphyllodactylus titiwangsaensis*	Cameron Highlands, Pahang, Malaysia	KF219789
LSUHC 10718	*Hemiphyllodactylus titiwangsaensis*	Cameron Highlands, Pahang, Malaysia	KF219790
LSUHC 7208	*Hemiphyllodactylus titiwangsaensis*	Cameron Highlands, Pahang, Malaysia	KF219791
LSUHC 10721	*Hemiphyllodactylus titiwangsaensis*	Cameron Highlands, Pahang, Malaysia	KF219792
LSUHC 10716	*Hemiphyllodactylus titiwangsaensis*	Cameron Highlands, Pahang, Malaysia	KF219793
LSUHC 10720	*Hemiphyllodactylus titiwangsaensis*	Cameron Highlands, Pahang, Malaysia	KF219794
LSUHC 10715	*Hemiphyllodactylus titiwangsaensis*	Cameron Highlands, Pahang, Malaysia	KF219795
JAM 1969	*Hemiphyllodactylus titiwangsaensis*	Cameron Highlands, Pahang, Malaysia	KJ663759
JAM 1970	*Hemiphyllodactylus titiwangsaensis*	Cameron Highlands, Pahang, Malaysia	KJ663760
ABTC 32736	*Hemiphyllodactylus typus*	Fiji Suva	GQ257745
ABTC 49760	*Hemiphyllodactylus typus*	Papua New Guinea	GQ257744
LSUHC 10340	*Hemiphyllodactylus typus*	Pulau Pinang, Penang, Malaysia	KF219796
LSUHC 8751	*Hemiphyllodactylus typus*	Tasik Chini, Phanag, Malaysia	KF219797
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971018
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971019
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971020
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971021
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971022
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971023
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971024
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971025
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971026
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971027
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971028
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971029
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971030
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971031
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971032
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971033
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971034
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971035
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971036
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971037
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971039
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971043
n/a	*Hemiphyllodactylus yunnanensis*	Yunnan, China	FJ971044
MVZ 226500	*Hemiphyllodactylus zugi*	Vinh Phu, Vietnam	KF219798

Abbreviations are as follows: ABTC, Australian Biological Tissue Collection; ACD, Arvin C. Diesmos field collection; AMB, Aaron M. Bauer; AMS, Australian Museum, Sydney; CAS, California Academy of Sciences; DWB, Donald W. Buden; FK, Fred Kraus field series; FMNH, Field Museum of Natural History; ID, Indraneil Das field series; ITBCZ, Institute of Tropical Biology Collection of Zoology; JAM, Jimmy A. McGuire field series; JB, Jon Boone; KU, Kansas University Museum of Natural History; LSUHC, La Sierra University Herpetological Collection; MCZ, Museum of Comparative Zoology, Harvard University; MVZ, Museum of Vertebrate Zoology (Berkeley); RAH, Rod Hitchmough; RMB, Rafe M. Brown field series; ROM, Royal Ontario Museum; TG, Tony Gamble; USNM, United States National Museum; USNM-FS, United States National Museum, Field Series; ZMA, Zoological Museum, Amsterdam; and ZSM, Zoologische Staatssammlung, München. n/a, catalogue number not available.

Table 2. Primers used for polymerase chain reaction (PCR) amplification and sequencing reactions

Primer name	Primer citation		Sequence
L4437b	(Macey & Schulte, 1999)	External	5′-AAGCAGTTGGGCCCATACC-3′
CyrtintF1	(Siler *et al.*, 2010)	Internal	5′-TAGCCYTCTCYTCYATYGCCC-3′
CyrtintR1	(Siler *et al.*, 2010)	Internal	5′-ATTGTKAGDGTRGCYAGGSTKGG-3′
H5934	(Macey & Schulte, 1999)	External	5′-AGRGTGCCAATGTCTTTGTGRTT-3′

Specific amplification conditions are presented in the materials and methods.

Table 3. Uncorrected pairwise sequence divergences (p-distances) in *Hemiphyllodactylus*, based on based on *ND2* and flanking transfer RNAs calculated in MEGA 5.22 (Tamura *et al.*, 2011)

	H. bintik sp. nov.	*H. harterti*	*H. larutensis*	**H. sp. nov. 1**	*H. titiwangsaensis*	*H. tehtarik*
H. bintik sp. nov.	–					
H. harterti	0.132	–				
H. larutensis	0.230	0.234	–			
H. sp. nov. 1	0.231	0.249	0.175	–		
H. titiwangsaensis	0.226	0.242	0.186	0.143	–	
H. tehtarik	0.243	0.251	0.094	0.181	0.191	–

substitution saturation). It has been well documented that the third codon position and portions of the tRNAs are susceptible to substitution saturation (Zamudio, Jones & Ward, 1997; Carranza, Arnold & Mateo J. Lopez-Jurado, 2002a; Brandley *et al.*, 2011), and may overestimate node age estimates.

To estimate divergence times, a fossil-calibrated chronogram for the genus *Hemiphyllodactylus* was constructed based on *ND2* and its flanking tRNAs. Partitioning schemes 1–3 were used to explore the effects of substitution saturation on node age estimates. All models of molecular evolution follow that of Grismer *et al.* (2013). We applied a Yule tree prior and an uncorrelated lognormal clock implemented in BEAST 1.8 (Drummond *et al.*, 2012). Fossil calibrations follow Heinicke *et al.* (2011). The divergence between *Sphaerodactylus roosevelti* Grant, 1931 and *Sphaerodactylus torrei* Barbour, 1914 was calibrated (exponential, mean = 3, offset = 15) from the amber-preserved fossil *Sphaerodactylus* from Hispanola, dated to 15–20 Mya (Iturralde-Vinent & MacPhee, 1996). The divergence between *Oedura* and *Woodworthia* was calibrated (exponential, mean = 17, offset = 16) from a fossil from New Zealand '*Hoplodactylus*', dated to 16–19 Mya (Lee *et al.*, 2009). The divergence between *Pygopus* and *Lialis* was calibrated (exponential, mean = 10, offset = 20) from the fossil *Pygopus*, dated to 20–22 Mya (Hutchinson, 1998). The root height of the tree was calibrated (normal, mean = 200, SD = 13) from the estimates of divergence of gekkotans from other squamates (Vidal & Hedges, 2005; Hugall, Foster &

Lee, 2007; Jonniaux & Kumazawa, 2008). Markov chain Monte Carlo (MCMC) for 1×10^8 generations were sampled every 1×10^4 steps, and each partitioning scheme was run ten times to ensure that the parameters were converging on the same space. Step size was considered sufficient to generate effective sample sizes (ESSs) greater than 200. To assess convergence, log files were visualized in TRACER 1.5 (Drummond *et al.*, 2012) to assess the stationarity of the likelihood scores. Multiple runs per partitioning scheme that converged on the same tree space were combined using LogCombiner 1.8 (Drummond *et al.*, 2012) and sampled at a lower frequency, with an end result of 1×10^4 trees after a 10% burn-in per run. A maximum clade credibility tree (MCC) using mean heights was constructed for each partitioning scheme using TreeAnotator 1.8.0 (Drummond *et al.*, 2012). Pairwise sequence divergences (Table 3) were calculated in MEGA 5.22 (Tamura *et al.*, 2011).

MORPHOLOGICAL ANALYSES

For the descriptive work, colour notes were taken using digital images of specimens prior to preservation. The terminology and methodology involving the evaluation of mensural and meristic characters follows Grismer *et al.* (2014c). Mensural data were taken with Mitutoyo dial calipers to the nearest 0.1 mm under a Nikon SMZ 1500 dissecting microscope on the left side of the body, where appropriate: snout–vent length (SVL), taken from the tip of the 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 rostrum. Meristic character states, evaluated on the holotype and comparative material (see Appendix; Zug, 2010), were: the number of scales contacting the nares (circumnasal scales); the number of scales between the supranasals (postrostrals); the numbers of supralabial and infralabial scales counted from the largest scale immediately posterior to the dorsal inflection of the posterior portion of the upper jaw to the rostral and mental scales, respectively; the number of longitudinal ventral scales at 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 precloacal and femoral pores (i.e. the contiguous or discontinuous rows of femoral and precloacal scales bearing pores); and the number of cloacal spurs. Colour pattern characters evaluated were: 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 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; LSUDPC refers to the La Sierra University Digital Photo Collection. Other acronyms follow Sabaj-Pérez (2014).

RESULTS

TAXONOMY

The morphological analysis indicates that the newly discovered Gunung Tebu population is diagnosable from all other *Hemiphyllodactylus* by a number of morphological and colour pattern characters (see below and Table 4). The molecular analysis indicates that it is phylogenetically embedded within the *harterti* group (*sensu* Grismer *et al*., 2013), and within this group it is the sister species of *H. harterti* (Fig. 1). As such, it is described below as a new species.

HEMIPHYLLODACTYLUS BINTIK SP. NOV.
SPOTTED DWARF GECKO
CICAK KERDIL BERINTIK

Holotype
Adult male (LSUHC 11216) collected by Chan Kin Onn on 2 July 2013 at 800 m a.s.l. on Gunung Tebu, Terengganu, Peninsular Malaysia (05°36.11′N, 102°36.19′S).

Diagnosis
Hemiphyllodactylus bintik sp. nov. can be separated from all other species of *Hemiphyllodactylus* by the unique combination of: a maximum SVL of 36.6 mm; seven chin scales extending transversely from unions of second and third infralabials and posterior margin of mental; enlarged postmental scales; five circumnasal scales; three scales between supranasals (= postrostrals); 11 supralabials; 12 infralabials; 17 longitudinally arranged dorsal scales at midbody contained within one eye diameter; seven longitudinally arranged ventral scales at midbody contained within one eye diameter; lamellar formula on hand 2443; lamellar formula on foot 3444; dorsal body pattern consisting of dark, squarish, paravertebral blotches; postsacral mark cream-coloured, lacking anteriorly projecting arms; and caecum and oviducts unpigmented. These characters and potentially diagnostic morphometric characters are scored across all species in Table 4.

Description of holotype
Adult male: head triangular in dorsal profile, depressed, distinct from neck; lores and interorbital regions flat; rostrum moderate in length (NarEye/HeadL 0.33); prefrontal region flat to weakly concave; canthus rostralis smoothly rounded, barely discernable; snout moderate, rounded in dorsal profile; eye large; ear opening round, small; eye to ear distance greater than diameter of eye; rostral wider than high, partially divided dorsally, bordered posteriorly by large supranasals; three internasals (= postnasals); external nares bordered anteriorly by rostral, dorsally by supranasal, posteriorly by two postnasals, ventrally by first supralabial (= circumnasals 3R,L); 11 (R,L) square supralabials tapering to below posterior margin of orbit; 12 (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 and slightly raised; dorsal superciliaries flat, rectangular, subimbricate; mental triangular, bordered

Table 4. Diagnostic and potentially diagnostic (colour pattern and morphometric ratios) characters (bold) separating *Hemiphyllodactylus bintik* **sp. nov.** from all other nominal taxa of *Hemiphyllodactylus*

	H. aurantiacus	*H. banaensis*	*H. chiangmaiensis*	*H. engganoensis*	*H. ganoklonis*	*H. harterti*	*H. insularis*	*H. larutensis*	*H. margarethae*	*H. titiwangsaensis**	*H. typus**	*H. yunnanensis**	*H. tehtarik*	*H. zugi*	*H. bintik* sp. nov.
Max SVL	37.9	**51.0**	**41.2**	37.3	34.2	39	37.3	**52.2**	46.9	**62.1**	**46.1**	49.3	40.4	46.6	36.6
Chin scales	**10–14**	6–7	**8–12**	6	**9–12**	6–8	**8–14**	6–10	6–11	**8,9**	**9–14**	6–11	**8**	**9–12**	7
Postmentals distinctly enlarged (1) or not (0)	**0**	1	1	**0**	**0**	1	**0**	1	1	1	1	1	1	1	1
Circumnasal scales	**2–4**	**3**	3,4	5	**2–4**	2–5	**1–4**	3–5	**2 or 3**	**3**	1–5	**2–4**	5r,l	**2 or 3**	5
Scales between supranasals	3–6	**4–11**	1–3	3 or 4	3–5	3–4	2–4	3	2–4	1–3	1–5	2–5	3	3–5	3
Supralabial scales	10–13	9–12	9–11	**12**	8–11	10–11	9–13	9,10	10–13	9–11	9–14	8–13	11	10–13	11
Infralabial scales	8–12	**9–11**	9–12	12	**8–10**	**10–11**	**9–11**	**7–10**	9–12	**8–10**	7–13	8–12	**10**	**10 or 11**	12
Dorsal scales	11–17	17–20	11–21	**24 or 25**	11–18	14–19	13–18	13–20	11–17	14–19	12–19	9–18	18	**20–22**	17
Ventral scales	**8–12**	**9–12**	6–10	**14**	**9–12**	6–14	**8–14**	7–13	6–12	7–9	**8–14**	6–12	**12**	**15 or 16**	7
Lamellar formula on hand	2222	3444, 4554	3333, 3433	4554/4454	3443	3333	3333		4444	3444	3444	3333	3333	3444	2443
Lamellar formula on foot	2232/2233	4555	3333, 3444	4555	3444	3343	3444		4555	4555	4454	3444	3454	4555	3444
Subdigital lamellae on first finger	3,4	**5**	3,4	**4 or 5**	3–5	**3**	2–5	3,4	4–8	4–6	4,5	4–6	**5**	4 or 5	4
Subdigital lamellae on first toes	4,5	5	**3,4**	4 or 5	3–5	**4**	3–6	3–5	4–7	5–8	5,6	4–7	5	4 or 5	5
Precloacal and femoral pore series separate (1) or continuous (0)	1	0	0	0	1	0	1	0	1	0	1 or 0	1	–	0	–
Precloacal and femoral pores	16–25	18–21	17–25	42	16–28	42–45	17–38	27–36	0–29	17–39	0–26	11–25	0	18–21	–
Cloacal spurs on each side	1–3	1	1	5	1–4	1,2	0–3	2,3	1,2	1–4	1–5	0–2	3	1	1
Subcaudals enlarged, plate-like (1) or not (0)	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	**0**	1	1	1	1	–	1	1	1	1	1	1
Light postocular or trunk spots (1) or absent (0)	1	1	1	0	1	1	1	1	–	1	1	1	0	1	0

Character														
Dark dorsolateral stripe on trunk present (1) or not (0)	0	1	0	0	1	0	0	1,0	–	0	0	0	0	0
Dorsal pattern unicolor (1) or not (0)	0	0	0	0	0	1	0	0	–	0	0	**0**	**0**	1
Dark dorsal transverse blotches (1) or not (0)	1	1	1	1	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	1	0	1	0	0	0	0
Postsacral mark brown or orange (2), outer edge yellow or red (1), outer edge red (0)	2	0	1	0	1	1	0	0	1	0	0	2	2	0
Postsacral mark lacking anterior arms (1) or arms present (0)	1	0	0	1	0	1	1	0	1	0	1	0	**0**	1
Caecum pigmented (1) or not (0)	1	0	1	0	1	1	1	0	0	1	0	1	0	0
Gonads pigmented (1) or not (0)	1	0	1	–	1	1	1	0,1	0	1	0	1	0	0
Trunk/SVL	0.44–0.51	0.44–0.49	0.46–0.56	0.49–0.51	0.49–0.57	0.48–0.53	0.45–0.58	0.46–0.51	0.40–0.54	0.40–0.65	0.40–0.55	0.42–0.50	**0.50–0.56**	0.49
HeadL/SVL	0.21–0.26	0.22–0.24	**0.25–0.43**	**0.24–0.26**	0.20–0.23	0.22–0.24	0.21–0.24	0.21–0.26	0.21–0.26	0.18–0.24	0.21–0.26	0.23–0.27	0.21–0.24	0.23
HeadW/SVL	**0.15–0.16**	0.18–0.23	**0.16**	**0.12–0.15**	**0.12–0.15**	0.16–0.18	0.12–0.18	**0.15–0.17**	0.15–0.19	**0.10–0.16**	0.14–0.22	0.16–0.19	0.17–0.18	0.18
HeadW/HeadL	**0.57–0.79**	0.41–0.80	**0.62–0.67**	0.65–0.85	**0.53–0.65**	0.65–0.85	0.54–0.82	**0.63–0.73**	**0.66–0.79**	**0.51–0.77**	0.59–0.83	**0.64–0.73**	**0.74–0.79**	0.80
SnEye/HeadL	0.34–0.42	0.23–0.49	0.41–0.43	0.36–0.45	0.28–0.34	0.41–0.48	0.26–0.44	0.39–0.51	0.29–0.35	0.34–0.48	0.34–0.46	**0.26–0.32**	**0.43–0.49**	0.41
NarEye/HeadL	0.27–0.33	0.22–0.25	**0.29–0.30**	0.23–0.24	0.28–0.34	0.28–0.33	0.27–0.42	0.27–0.36	0.29–0.35	0.24–0.40	0.26–0.35	0.20–0.32	0.29–0.39	0.33
EyeD/HeadL	0.22–0.28	0.13–0.24	0.23–0.24	0.23–0.28	0.22–0.25	0.22–0.30	0.23–0.32	0.22–0.28	0.16–0.25	0.20–0.32	0.22–0.29	0.21–0.30	–	–
SnW/HeadL	0.14–0.20	0.13–0.17	**0.13–0.15**	0.13–0.17	**0.13–0.19**	0.15–0.22	0.14–0.21	**0.11–0.15**	0.15–0.19	0.11–0.21	0.11–0.22	0.14–0.21	**0.16**	0.17
EyeD/NarEye	0.69–0.96	0.68–0.81	0.77–0.82	0.73–0.95	0.81–1.00	0.74–0.95	0.74–0.81	0.66–0.90	0.47–0.81	0.61–1.06	0.63–1.00	0.68–0.94	**0.72**	0.74
SnW/HeadW	0.21–0.30	0.2–0.24	0.20–0.24	0.20–0.37	0.23–0.32	0.20–0.32	0.18–0.21	**0.22–0.28**	0.16–0.34	0.21–0.31	0.15–0.36	0.16–0.34	**0.20**	0.21–23

Diagnostic and potentially diagnostic characters are set in bold; –, data unavailable.

*Taxa containing multiple undescribed species, but encompassed within the taxonomy of Zug (2010).

laterally by first infralabials and posteriorly by two large postmentals; each postmental bordered laterally by a single sublabial; no row of smaller scales extending transversely from juncture of second and third infralabials and contacting mental; seven chin scales; gular scales small, subimbricate, grading posteriorly into slightly larger, subimbricate, throat and pectoral scales that grade into slightly larger, subimbricate ventrals.

Body somewhat elongate (Trunk/SVL 0.49), dorsoventrally compressed; ventrolateral folds absent; dorsal scales small, granular, 17 scales contained within one eye diameter; ventral scales, flat, subimbricate much larger than dorsal scales, seven scales contained within one eye diameter; no enlarged, precloacal scales; no pore-bearing femoral or precloacal pore-bearing scales; forelimbs short, robust in stature, covered with flat, subimbricate scales dorsally and ventrally; palmar scales flat, subimbricate; all digits except digit I well developed; digit I vestigial, clawless; distal, subdigital lamellae of digits II–V undivided, angular, and U-shaped; lamellae proximal to these transversely expanded; lamellar formula of digits II–V 2443 (R,L); four transversely expanded lamellae on digit I; claws on digits II–V well developed, unsheathed; distal portions of digits strongly curved, terminal joint free, arising from central

portion of lamellar pad; hindlimbs short, more robust than forelimbs, covered with flat, juxtaposed scales dorsally, and by larger, flat subimbricate scales ventrally; plantar scales low, flat, subimbricate; all digits except digit I well developed; digit I vestigial, clawless; distal, subdigital lamellae of digits II–V undivided, angular, and U-shaped; lamellae proximal to these transversely expanded; lamellar formula of digits II–V 3444 (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 rectangular in cross-section; posterior one-half (16 mm) of tail regenerated; all caudal scales flat, imbricate, not forming distinct caudal segments. Morphometric data are presented in Table 4.

Coloration before preservation (Fig. 2)
Top of head, body, and limbs nearly unicolour beige; ground colour of anterior, dorsal caudal region dull yellow; dark postorbital and paired, paroccipital stripes present; a pair of short, dark paravertebral stripes on nape; dorsum overlain with paired, dark, slightly offset, squarish, paravertebral markings that meet medially to form a pre- and postsacral band; large, dark, lateral markings on anterior half of original tail; posterior half
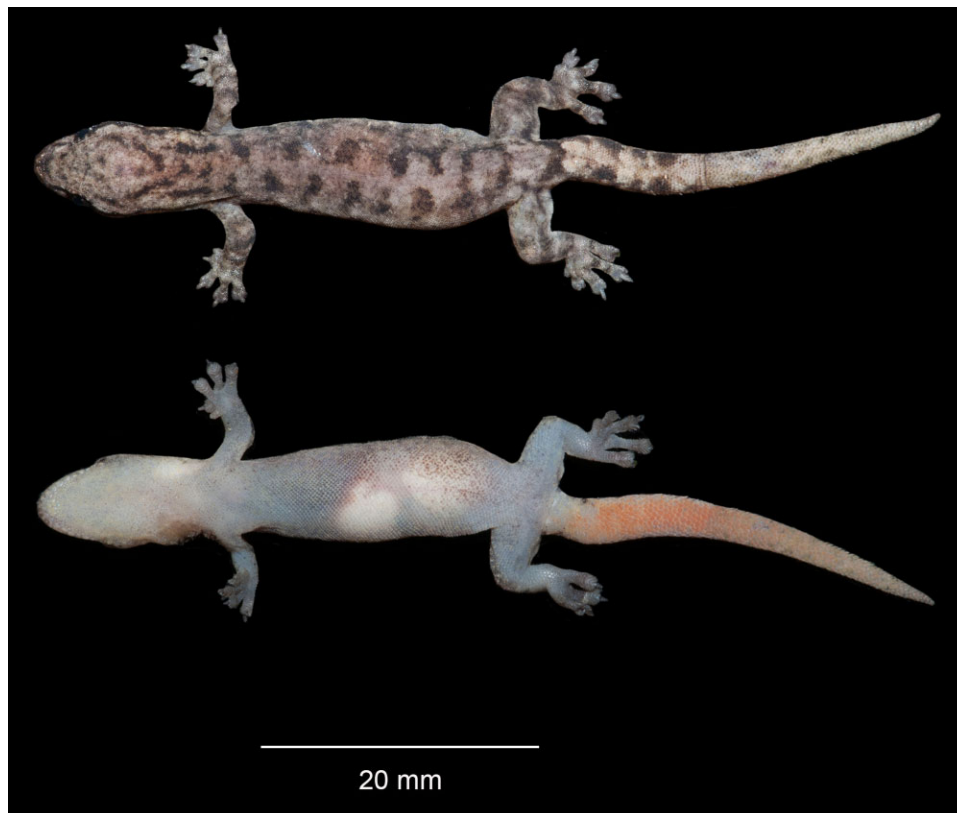

Figure 2. Dorsal and ventral view of the holotype of *Hemiphyllodactylus bintik* **sp. nov.** (LSUHC 11216).

of tail regenerated, nearly unicolour; flanks and dorsal surfaces of limbs darkly mottled; ventral surfaces of head, neck, body, and limbs whitish, semi-transparent; subcaudal region orange, more so on original portion of tail.

Distribution

Hemiphyllodactylus bintik sp. nov. is known only from the type locality of Gunung Tebu, Terengganu, Peninsular Malaysia (Fig. 1), but is expected to range more widely throughout the mountain range.

Natural history

Hemiphyllodactylus bintik sp. nov. was collected at 01:00 h during heavy rain while moving along the upper surface of a fallen log in hill dipterocarp forest (Fig. 3). *Hemiphyllodactylus tehtarik*, with which it is sympatric, was found in a riparian area at Punca Air. These two species may avoid competition by exploiting different microhabitats. The holotype is carrying two eggs, indicating that the reproductive season extends into July.

Etymology

The specific epithet '*bintik*' is a Malaysian word for 'spot', and refers to the spotted dorsal pattern of this species.

Comparisons

The molecular analysis indicates that *H. bintik* sp. nov. is embedded within the *harterti* group. It can be distinguished from all other species in that group in having 12 infralabial scales, as opposed to between seven and 11, and by having a finger formula of 2443, as opposed to 3333 or 3444, and a toe formula of 3444, as opposed to 4555, 3454, or 3343. It can be distinguished from all other species in that group except *H. harterti* in having a maximum SVL of less than 40 mm. It differs from *H. titiwangsaensis* and *H. tehtarik* in having seven as opposed to eight or nine chin scales. It can be separated from *H. titiwangsaensis*, *H. harterti*, and *H. larutensis* by lacking, as opposed to having, light postocular spots. *Hemiphyllodactylus bintik* sp. nov. lacks the dark, dorsal, transverse blotches found in *H. titiwangsaensis* and the unicolour dorsal pattern seen in *H. tehtarik* and *H. larutensis*. Additionally, it lacks

Figure 3. Habitat at the type locality of ***Hemiphyllodactylus bintik* sp. nov.**, Gunung Tebu, Terenganu, Peninsular Malaysia.

Table 5. Results from tests of substitution saturation for each partitioning scheme, based on the reduced data set with no missing data and only fully resolved sites implemented in DAMBE 5 (Xia *et al*., 2003; Xia & Lemey, 2009; Xia, 2013)

Nucleotide positions	Number of OTUs	Iss	Iss.cSym	T	DF	P	General conclusion
1st	4	0.148	4.139	65.183	5	**0.0000**	LS
1st	8	0.193	6.084	74.700	5	**0.0000**	LS
1st	16	0.241	1.711	18.351	5	**0.0000**	LS
1st	32	0.257	9.542	155.397	5	**0.0000**	LS
2nd	4	0.232	0.783	22.104	295	**0.0000**	LS
2nd	8	0.249	0.736	18.239	295	**0.0000**	LS
2nd	16	0.260	0.686	15.838	295	**0.0000**	LS
2nd	32	0.259	0.684	16.173	295	**0.0000**	LS
3rd	4	0.743	0.783	1.401	327	0.1621	SS
3rd	8	0.767	0.736	1.162	327	0.2462	US
3rd	16	0.777	0.686	3.741	327	**0.0002**	VP
3rd	32	0.771	0.684	3.823	327	**0.0002**	VP
1 + 2pos	4	0.326	0.805	23.461	592	**0.0000**	LS
1 + 2pos	8	0.321	0.765	20.681	592	**0.0000**	LS
1 + 2pos	16	0.334	0.744	18.878	592	**0.0000**	LS
1 + 2pos	32	0.343	0.718	17.409	592	**0.0000**	LS
tRNAs	4	0.148	4.139	65.183	5	**0.0000**	LS
tRNAs	8	0.193	6.084	74.700	5	**0.0000**	LS
tRNAs	16	0.241	1.711	18.351	5	**0.0000**	LS
tRNAs	32	0.257	9.542	155.397	5	**0.0000**	LS

Testing for whether the observed index of substitution saturation (Iss) is significantly lower than the critical value of substitution saturation assuming a symmetrical tree (Iss.cSym) and using a two-tailed test. Significant *P*-values are presented in bold. Abbreviations: LS, little saturation; SS, substantial saturation; VP, very poor for phylogenetics; US, useless sequences; OTUs, operational taxonomic units.
***If Iss < Iss.cSym with a significant *P* value = little saturation; not significant= substantial saturation. If Iss > Iss.cSym and a significant *P* value = useless sequence; not significant = very poor for phylogenetics. Proportion of invariable sites (P_{inv}): first position P_{inv} = 0.06697, second position P_{inv} = 0.10067, third position P_{inv} = 0.00643, tRNAs P_{inv} = 0.0000, first and second position P_{inv} = 0.09535.

the anteriorly projecting arms of the postsacral marking found in the latter two species. Within the *harterti* group, *H. bintik* sp. nov. is most closely related to *H. harterti*, from which it is further separated by having four as opposed to three subdigital lamellae on the first finger, and having five as opposed to four subdigital lamellae on the first toe. These two species also have a 13.2% uncorrected pairwise sequence divergence between them (Table 3). Grismer *et al*. (2013) noted that a divergence of at least 5.0% in *Hemiphyllodactylus* was consistent with discrete, diagnostic, morphological differences delimiting species boundaries. Additional diagnostic characters separating *H. bintik* sp. nov. from members of the *typus* group are listed in Table 4.

SUBSTITUTION SATURATION AND PARTITIONING STRATIGIES

A test for substitution saturation for each codon position indicated that there is little saturation in all of the codon positions and tRNAs, except for the third

codon position, which was substantially saturated and contained very poor sequences for phylogenetics (Table 5). The node age estimates based on the different partitioning schemes were very similar, and there was no dramatic difference. Saturation was not considered to be a significant factor in estimating node ages, and the exclusion of the third codon position did not result in a marked change in node age estimates as compared with the other partitioning schemes (Fig. 4; Table 6). Partitioning scheme 2 was the preferred scheme used to estimate divergence times within *Hemiphyllodactylus*, based on the criteria that its recovered node ages were younger, and the 95% highest posterior density (95% HPD) intervals were smaller, when compared with the other partitioning schemes (see Fig. 4, Table 6).

PHYLOGENY AND DIVERGENECE TIMES

The transpeninsular, phylogeographic sister species relationship between *H. larutensis* and *H. tehtarik* is
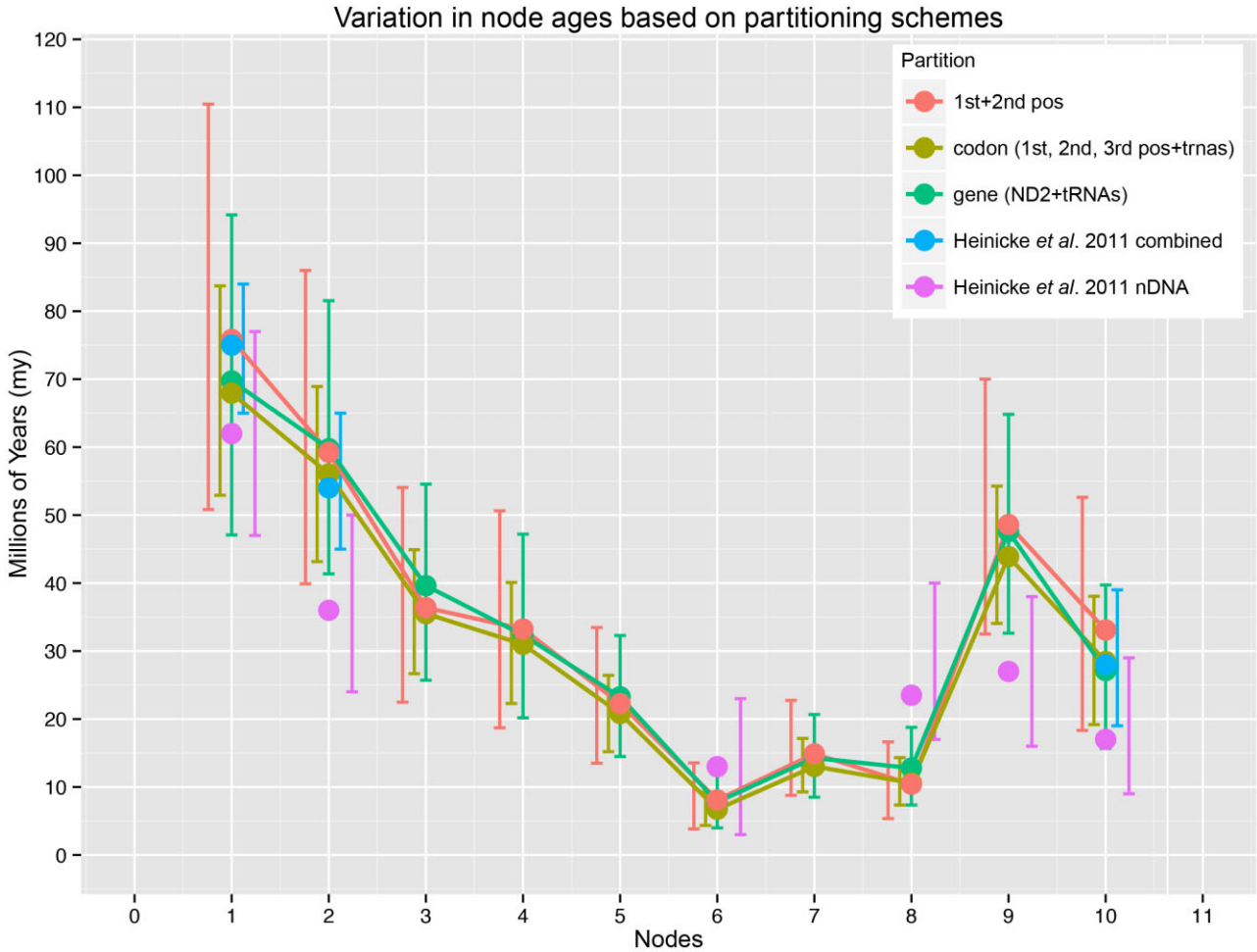
Figure 4. The results of the different partitioning schemes on node age estimates. When applicable, node age estimates from Heinicke *et al.* (2011) for nuclear DNA (nDNA) only and combined mitochondrial (mtDNA) and nDNA were included for comparative purposes.

Table 6. Estimated mean divergence time estimates and 95% highest posterior density (95% HPD) intervals for the partitioning schemes of *Hemiphyllodactylus*, with estimated dates of Heinicke *et al.* 2011

Node	Gene (*ND2* + tRNAs)	Codon (1st, 2nd, 3rd positions + tRNAs)	Codon (1st + 2nd positions)	Heinicke *et al.* 2011 nDNA	Heinicke *et al.* 2011 combined
1	69.75 (47.08–94.17)	67.95 (52.92–83.73)	75.85 (50.83–110.46)	62 (47–77)	75 (65–84)
2	59.78 (41.36–81.55)	56.06 (43.16–68.92)	59.25 (39.89–86)	36 (24–50)	54 (45–65)
3	39.62 (25.71–54.56)	35.51 (26.68–44.91)	36.38 (22.48–54.07)	–	–
4	32.36 (20.18–47.2)	30.99 (22.29–40.1)	33.24 (18.71–50.64)	–	–
5	23.27 (14.49–32.29)	20.81 (15.2–26.43)	22.27 (13.49–33.47)	–	–
6	7.79 (3.99–11.82)	6.73 (4.35–9.29)	8.1 (3.84–13.55)	–	–
7	14.28 (8.5–20.67)	13.03 (9.28–17.15)	14.88 (8.77–22.75)	13 (3–23)	–
8	12.78 (7.35–18.78)	10.6 (7.35–14.33)	10.41 (5.35–16.64)	23.5 (17–40)	–
9	47.58 (32.63–64.83)	43.9 (34.07–54.27)	48.61 (32.5–70.01)	27 (16–38)	–
10	27.13 (15.68–39.73)	28.48 (19.18–38.06)	33.1 (18.33–52.62)	17 (9–29)	28 (19–39)

–, indicates that the data was not available or comparable with this study. Mean node age estimates are followed by the minimum and maximum node age estimates, respectively.

mirrored by the same phylogeographic pattern in the sister species *H. harterti* and *H. bintik* sp. nov. (Fig. 1). That is, species from opposing mountain ranges 145 km away are more closely related to each other than they are to species with whom they are sympatric. Additionally, these two species-pair lineages are not each other's closest relatives, rather the *H. tehtarik–H. larutensis* lineage is the sister lineage to the *H. titwangsaensis–H.* sp. nov. species pair from the geographically intervening Titiwangsa Range (Fig. 1).

Heinicke *et al*. (2011) pruned *ND2* sequences from their data set, noting that potentially high rates of substitution saturation in mitochondrial markers could inflate divergence time estimates (but see Carranza *et al*., 2000, 2002; Carranza & Arnold, 2012). Using only nuclear markers (*RAG-1* and *PDC*), Heinicke *et al*. (2011) revealed a deep, phylogenetic divergence within *Hemiphyllodactylus* that was calculated to have occurred during the Eocene (mean divergence time of ~36 Mya). Jonniaux & Kumazawa (2008), however, showed that under multiple combinations of gene and taxon choice, mitochondrial data performed robustly in estimating deep divergences between Gekkotan families and more shallow divergences among eublepharid genera [although Heinicke *et al*. (2011), without explanation, stated that the divergence times of Jonniaux & Kumazawa (2008) were significantly overestimated]. Using a much more inclusive data set, Grismer *et al*. (2013) recovered the same, deep divergence within *Hemiphyllodactylus*. Our fossil-calibrated data set includes only *ND2*, and our mean estimated divergence time for this split is 56.1 Mya, significantly older than that of Heinicke *et al*. (2011) based on their exclusively nuclear DNA data, and potentially indicative of oversaturation or slowly evolving nuclear genes. However, our estimated node age for *Hemiphyllodactylus* only differs by 2 million years compared with Heinicke *et al*.'s (2011) combined data set results (Heinicke *et al*., 2011: table 2; Fig. 4; Table 6). Additionally, at a more shallow region in the tree, our mean divergence time estimate of the split between *H. titiwangsaensis* and *H.* sp. nov. (13.0 Mya) falls well within the range of that reported by Heinicke *et al*. (2011; ~23–3 Mya, mean ~13 Mya), and the mean node ages are nearly identical (Fig. 4, node 7). We consider this as evidence that our remaining estimates of divergence times at other shallow regions in the tree are legitimate estimates as well. Mean divergence time estimates between the three species pairs range well in to the Miocene (15.2–26.4 Mya; Fig. 1), significantly predating the climate-driven, cyclical expansions and contractions of montane forests from the Late Pliocene onwards (Woodruff, 2010). Mean divergence time estimates for the split between the *harterti–bintik* lineage and the remainder of the Malaysian *Hemiphyllodactylus* minus the *H. typus* group (35.51 Mya), and the subsequent split between the *tehtarik–larutensis* and *H. titwangsaensis–H.* sp. nov. lineages (20.81 Mya), indicate their constituent species are most likely to be remnants of palaeoendemic lineages that have persisted in stable, upland refugia since at least the Oligocene.

DISCUSSION

Globally, montane tropical rainforests are renowned for their high levels of endemism (Blackburn & Measey, 2009; Bell *et al*., 2010; Grismer *et al*., 2010; Grismer, 2011; Tolley *et al*., 2011), and this is becoming even more evident in Southeast Asia where recent research in the upland regions of Peninsular Malaysia has yielded 21 new, co-distributed species of amphibians and reptiles across five different mountain systems in only 8 years (Grismer, 2006a, b, 2007, 2008; Grismer *et al*., 2006, 2008, 2009b, 2010, 2011, 2012, 2013, 2014a, b, c; Wood *et al*., 2008, 2009; Chan *et al*., 2009, 2010, 2014; Grismer, Norhayati & Chan, 2009a; Grismer & Chan, 2010; Johnson *et al*., 2012; Loredo *et al*., 2013). It is noteworthy, however, that the phylogeographic relationships of these species bear no overarching pattern, indicating that a single historical event cannot account for speciation across this broad, upland landscape of sky-island archipelagos (Grismer *et al*., in prep.).

Time-calibrated phylogeographic studies have demonstrated that speciation in tropical, montane forests is not solely the result of oscillating, climatic events of the Late Pleistocene, but have emerged along a significantly longer time continuum, and that some upland species have existed in isolated refugia as palaeoendemics since the Miocene (Vences *et al*., 2009; Tolley *et al*., 2011; Bell *et al*., 2012). This appears to be the case with the six species of the *H. harterti* group that are restricted to mountaintops across Peninsular Malaysia. The evolution of the *bintik–harterti* and *tehtarik–larutensis* lineages followed by the speciation within each lineage on the *same* mountain ranges is consistent with a pre-Plio–Pleistocene, climatic fluctuation model. We cannot be certain if speciation within each of these lineages was simultaneous or sequential (estimated mean divergence time of 10.6 Mya for *harterti–bintik* and 6.73 Mya for *larutensis–tehtarik*) because of significant overlap in the 95% HPD values (Fig. 1). Speciation within the *H. titiwangsaensis–H* sp. nov. lineage also occurred around the same time (13.03 Mya), but in an intervening mountain range (Fig. 1). The time frames of these speciation events significantly pre-date the dramatic and frequent climatic oscillations (~50; Woodruff, 2010) of the Pleistocene.

Highland landscapes in Peninsular Malaysia have been a prominent, tectonically stable feature since the Miocene (Hall, 2012), when overall temperatures began to rise (Morley, 2012). As such, cooler montane regions

would have offered a stable refuge from the warmer lowlands during the infrequent periods of climatic flux that persisted into the early Pliocene (Zachos *et al.*, 2001; Morley, 2012). These fluctuations may have resulted in the sequential evolution of the three upland lineages of *Hemiphyllodactylus*, followed by Late Miocene speciation events within each lineage. This is not the case, however, for all montane endemics in Peninsular Malaysia. For example, pareatid snakes of the genus *Asthenodipsas* Peters, 1864 occupy many of the same allopatric, upland forests as the species of the *H. harterti* group. The two Malaysian species *Asthenodipsas vertebralis* (Boulenger, 1900) and *Asthenodipsas lasgalenensis* Loredo *et al.*, 2013 are well separated genetically (7.8–8.4% based on cytochrome *b*) and morphologically (Loredo *et al.*, 2013), yet occur in sympatry in at least three isolated, upland localities on two different mountain ranges (Loredo *et al.*, 2013:Fig. 4); however, there is no detectable, significant, intraspecific morphological variation in either species, and intraspecific genetic distances are less than 1.0% across 210 km of uninhabitable terrain. This strongly suggests that the isolation event(s) separating the montane populations of each species were very recent (during the LGM), and that these populations are likely to have introgressed during interglacial periods when cooler temperatures were amenable to downslope migration and range expansion (Loredo *et al.*, 2013). Grismer *et al.* (2014c) suggested that the low levels of genetic differentiation between populations of the colubrid snake *Lycodon butleri* Boulenger, 1900 from the Bintang and Titiwangsa ranges resulted from the same processes. Such is the case for other species of commonly observed, vagile amphibians and reptiles distributed across these same mountain ranges (Grismer, Quah & Wood, unpubl. data), suggesting that the ability to disperse may lead to introgression during periods of glacial maxima, and that life history may play a significant role in shaping phylogeographic and community structure (see Bell *et al.*, 2010; Johnson *et al.*, 2012; Scheffers *et al.*, 2013).

Studying the effects of climate change on the genetic structure and distribution of biodiversity will help us to navigate the potential, pending crisis of global warming; however, it is important to understand that there is not one overarching scenario that fits all groups, and the search for a single, explanatory model is not realistic. This is especially true in Peninsular Malaysia where the unique phylogeographic patterns of many upland endemics are a consequence of their unique and varied evolutionary histories coupled with their unique and varied life histories (Grismer, Quah & Wood, unpubl. data). Understanding this inextricable relationship will provide insight as to how climate change may affect the trajectory of phylogeographic change.

REFERENCES

Avise JC, Walker D. 1998. Phylogeographic effects on avian populations and the speciation process. *Proceedings of the Royal Society of London B* **265:** 457–463.

Bell RC, MacKenzie JB, Hickerson MJ, Chavarría KL, Cunningham M, Williams S, Mortitz C. 2012. Comparative multi-locus phylogeography confirms multiple vicariance events in co-distributed rainforest frogs. *Proceedings of the Royal Society B Biological Series* **279:** 991–999.

Bell RC, Parra JL, Tonione M, Hoskin CJ, MacKenzie JB, Williams SE Moritz C. 2010. Patterns of persistence and isolation indicate resilience to climate change in montane rainforest lizards. *Molecular Ecology* **19:** 2531–2544.

Bermingham E, Moritz C. 1998. Comparative phylogeography: concepts and applications. *Molecular Ecology* **7:** 367–369.

Bintanja R, van de Wal SW, Oelemans J. 2005. Modeled atmospheric temperatures and global sea levels of the past million years. *Nature* **437:** 125–128.

Bird MI, Taylor D, Hunt C. 2005. Paleoenvironments of insular Southeast Asia during the last glacial period: a savanna corridor in Sundaland? *Quaternary Science Reviews* **24:** 228–2242.

Blackburn DC, Measey GJ. 2009. Dispersal to or from an African biodiversity hotspot? *Molecular Ecology* **18:** 1904–1915.

Brandley MC, Wang Y, Guo X, de Oca ANM, Fería-Ortíz M, Hikida T, Ota H. 2011. Accommodating heterogenous rates of evolution in molecular divergence dating methods: an example using intercontinental dispersal of *Plestiodon* (*Eumeces*) lizards. *Systematic Biology* **60:** 3–15.

Cannon CH. 2012. Quaternary dynamics of Sundaland forests. In: Gower DJ, Johnson KG, Richardson JE, Rosen BR, Rüber L, Williams ST, eds. *Biotic evolution and environmental change in Southeast Asia*. The Systematics Association Special Volume 82. Cambridge: Cambridge University Press, 115–137.

Cannon CH, Morley RJ, Bush ABG. 2009. The current refugial rainforests of Sundaland are unrepresentative of their biogeographic past and highly vulnerable to disturbance. *Proceedings of the National Academy of Sciences of the United States of America* **106:** 11188–11193.

Carranza S, Arnold EN. 2012. A review of the geckos of the genus *Hemidactylus* (Squamata: Gekkonidae) from Oman based on morphology, mitochondrial and nuclear data, with descriptions of eight new species. *Zootaxa* **3378:** 1–95.

Carranza S, Arnold EN, Mateo JA, Geniez P. 2002. Relationships and evolution of the North African geckos, *Geckonia* and *Tarentola* (Reptilia: Gekkonidae), based on mitochondrial and nuclear DNA sequences. *Molecular Phylogenetics and Evolution* **23:** 244–256.

Carranza S, Arnold EN, Mateo J. Lopez-Jurado L. 2000. Long-distance colonization and radiation in gekkonid lizards, *Tarentola* (Reptilia: Gekkonidae), revealed by mitochondrial DNA sequences. *Proceedings of the Royal Society B: Biological Sciences* **267:** 637–649.

Chan KO, Grismer LL, Anuar S, Quah E, Muin MA, Savage AE, Grismer JL, Norhayati A, Remegio A-C, Greer LF. 2010. A new endemic Rock Gecko *Cnemaspis* Strauch 1887 (Squamata: Gekkonidae) from Gunung Jerai, Kedah, northwestern Peninsular Malaysia. *Zootaxa* **2576:** 59–68.

Chan KO, Grismer LL, Norhayati A, Belabut D. 2009. A new species of *Gastrophrynoides* (Anura: Microhylidae): an addition to apreviously monotypic genus and a new genus for Peninsular Malaysia. *Zootaxa* **2142:** 63–68.

Chan KO, Wood Jr PL, Anuar S, Muin MA, Quah ESH, Sumarli XYA, Grismer LL. 2014. A new species of upland Stream Toad of the genus *Ansonia* Stoliczka, 1870 (Anura: Bufonidae) from northeastern Peninsular Malaysia. *Zootaxa* **3764:** 427–440.

Drummond AJ, Suchard MA, Xie D, Rambaut A. 2012. Bayesian Phylogenetics with Beauti and the Beast 1.7. *Molecular Biology and Evolution* **29:** 1969–1973.

Grismer LL. 2006a. A new species of *Ansonia* Stoliczka, 1872 (Anura: Bufonidae) from Central Peninsular Malaysia and a revised taxonomy for *Ansonia* from the Malay Peninsular. *Zootaxa* **1327:** 1–21.

Grismer LL. 2006b. Two new species of skinks (Genus *Sphenomorphus* Fitzinger 1843) from the Seribuat Archipelago, West Malaysia. *Herpetological Natural History* **9:** 151–162.

Grismer LL. 2007. A new species of small montane forest floor skink (Genus *Sphenomorphus* Fitzinger 1843) from southern peninsular Malaysia. *Herpetologica* **63:** 544–551.

Grismer LL. 2008. A new species of insular skink (Genus *Sphenomorphus* Fitzinger 1843) from the Langkawi Archipelago, Kedah, West Malaysia with the first report of the herpetofauna of Pulau Singa Besar and an updated checklist of the herpetofauna of Pulau Langkawi. *Zootaxa* **1691:** 53–56.

Grismer LL. 2011. *Lizards of peninsular Malaysia, Singapore and their adjacent archipelagos. Their description, distribution, and natural history*. Franfurt am Mai: Edition Chimaira, 1–728.

Grismer LL, Chan KO. 2010. Another new rock gecko (genus *Cnemaspis* Strauch 1887) from Pulau Langkawi, Kedah, Peninsular Malaysia. *Zootaxa* **2419:** 51–62.

Grismer LL, Chan KO, Grismer JL, Wood PL Jr, Norhayati A. 2010. A checklist of the herpetofauna of the Banjaran Bintang, Peninsular Malaysia. *Russian Journal of Herpetology* **17:** 147–160.

Grismer LL, Grismer JL, McGuire JM. 2006. A new species of pitviper of the genus *Popeia* (Squamata: Viperidae) from Pulau Tioman, Pahang, West Malaysia. *Zootaxa* **1305:** 1–19.

Grismer LL, Grismer JL, Wood JPL, Chan KO. 2008. The distribution, taxonomy, and redescription of the geckos *Cnemaspis affinis* (Stoliczka 1887) and *C. flavolineata* (Nicholls 1949) with descriptions of a new montane species and two new lowland, karst-dwelling species from Peninsular Malaysia. *Zootaxa* **1931:** 1–24.

Grismer LL, Norhayati A, Chan KO. 2009a. A new, diminutive, upland *Sphenomorphus* Fitzinger 1843 (Squamata; Scincidae) from the Belum-Temengor Forest Complex, Peninsular Malaysia. *Zootaxa* **2312:** 27–38.

Grismer LL, Norhayati A, Chan KO, Belabut D, Muin MA, Wood PL Jr, Grismer JL. 2009b. Two new diminutive species of *Cnemaspis* Strauch 1887 (Squamata: Gekkonidae) from Peninsular Malaysia. *Zootaxa* **2019:** 40–56.

Grismer LL, Quah ESH, Anuar S, Muin MA, Wood PL Jr. 2014c. A diminutive new species of cave-dwelling Wolf Snake (Colubridae: *Lycodon* Boie, 1826) from Peninsular Malaysia. *Zootaxa* **3815:** 51–67.

Grismer LL, Quah ESH, Muin MA, Siler CD, Grismer JL, Chan KO, Wood PL Jr, Shahrul AM, Norhayati A. 2011. A new species of legless skink of the genus *Larutia* (Böhme) from Pulau Pinang, Peninsular Malaysia with a phylogeny of the genus. *Zootaxa* **2799:** 29–40.

Grismer LL, Wood PL Jr, Cota M. 2014a. A new species of *Hemiphyllodactylus* Bleeker, 1860 (Squamata: Gekkonidae) from northwestern Thailand. *Zootaxa* **3760:** 67–68.

Grismer LL, Wood PL Jr, Anuar S, Muin MA, Quah ESH, McGuire JA, Brown RA, Ngo VT, Pham H. 2013. Integrative taxonomy uncovers high levels of cryptic species diversity in *Hemiphyllodactylus* Bleeker, 1860 (Squamata: Gekkonidae) and the description of a new species from Peninsular Malaysia. *Zoological Journal of the Linnean Society* **169:** 849–880.

Grismer LL, Wood PL Jr, Anuar S, Quah ESH, Muin MA, Mohamad M, Chan KO, Sumarli AS-I, Loredo AI, Heinz HM. 2014b. The phylogenetic relationships of three new species of the *Cyrtodactylus pulchellus* complex (Squamata: Gekkonidae) from poorly explored regions in northeastern Peninsular Malaysia. *Zootaxa* **3768:** 359–381.

Grismer LL, Wood PL Jr, Anuar S, Riyanto A, Norhayati A, Muin MA, Sumontha M, Grismer JL, Quah ESH, Pauwels OSA. 2014c. Systematics and natural history of Southeast Asian Rock Geckos (genus *Cnemaspis* Strauch, 1887) with descriptions of eight new species from Malaysia, Thailand, and Indonesia. *Zootaxa* **3880:** 1–147.

Grismer LL, Wood PL Jr, Quah ESH, Shahrul A, Muin MA, Sumontha M, Norhayati A, Bauer AM, Wangkulangkul S, Grismer JL, Pauwels OSG. 2012. A phylogeny and taxonomy of the Thai-Malay Peninsula Bent-toed Geckos of the *Cyrtodactylus pulchellus* complex (Squamata: Gekkonidae): combined morphological and molecular analyses with descriptions of seven new species. *Zootaxa* **3520:** 1–55.

Hall R. 2012. Sundaland and Wallacea: geology, plate tectonics and paleogeography. In: Gower DJ, Johnson KG, Richardson JE, Rosen BR, Rüber L, Williams ST, eds. *Biotic Evolution and Environmental Change in Southeast Asia*. The Systematics Association Special Volume 82. Cambridge: Cambridge University Press, 32–78.

Heaney LR. 1991. A synopisis of climatic and vegetational change in Southeast Asia. *Climate Change* **19:** 53–61.

Heinicke MP, Greenbaum E, Jackman TR, Bauer AM. 2011. Phylogeny of a trans-Wallacean radiation (Squamata, Gekkonidae, *Gehyra*) supports a single early colonization of Australia. *Zoologica Scripta* **40:** 584–602.

Hewitt GM. 2004. Genetic consequences of climatic oscillations in the Quaternary. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **359:** 183–195.

Hugall AF, Foster R, Lee MSY. 2007. Calibration Choice, Rate Smoothing, and the Pattern of Tetrapod Diversification According to the Long Nuclear Gene Rag-1. *Systematic Biology* **56:** 543–563.

Hutchinson MN. 1998. The first fossil pygopodid (Squamata, Gekkota), and a review of mandibular variation in living species. *Memoirs of the Queensland Museum* **41:** 355–366.

Iturralde-Vinent MA, MacPhee R. 1996. Age and paleogeographical origin of dominican amber. *Science* **273:** 1850–1852.

Johnson CB, Quah ESH, Anuar S, Muin MA, Wood PL Jr, Grismer JL, Greer LF, Chan KO, Norhayati A, Bauer AM, Grismer LL. 2012. Phylogeography, geographic variation, and taxonomy of the Bent-toed Gecko *Cyrtodactylus quadrivirgatus* Taylor, 1962 from Peninsular Malaysia with the description of a new swamp dwelling species. *Zootaxa* **3406:** 39–58.

Jonniaux P, Kumazawa Y. 2008. Molecular Phylogenetic and Dating Analyses Using Mitochondrial DNA Sequences of Eyelid Geckos (Squamata: Eublepharidae). *Gene* **407:** 105–115.

Lee MS, Hutchinson MN, Worthy TH, Archer M, Tennyson AJ, Worthy JP, Scofield RP. 2009. Miocene skinks and geckos reveal long-term conservatism of New Zealand's lizard fauna. *Biology Letters* **5:** 833–837.

Loredo AI, Wood PL Jr, Quah ESH, Anuar SH, Greer L, Norhayati A, Grismer LL. 2013. Cryptic speciation within *Asthenodipsas vertebralis* (Boulenger, 1900) (Squamata: Pareatidae), the description of a new species from Peninsular Malaysia, and the resurrection of *A. tropidonotus* (Lidth de Jude, 1923) from Sumatra: an integrative taxonomic analysis. *Zootaxa* **3664:** 505–524.

Macey J, Schulte J. 1999. Molecular phylogenetics, trna evolution, and historical biogeography in anguid lizards and related taxonomic families. *Molecular Phylogenetics and Evolution* **12:** 250–272.

Matsui M, Tominaga A, Liu W, Khonsue W, Grismer LL, Diesmos AC, Das I, Sudin A, Yambun P, Yong H, Sukumaran J, Brown RM. 2010. Phylogenetic relationships of *Ansonia* from Southeast Asia as inferred from mitochondrial DNA sequences: systematic and biogeographic implications (Anura: Bufonidae). *Molecular Phylogenetics and Evolution* **54:** 561–570.

Meijaard E. 2003. Mammals od south-east Asian islands and their Late Pleistocene environments. *Journal of Biogeography* **30:** 1245–1257.

Morley RJ. 2012. A review of the Cenozoic paleoclimate history of Southeast Asia. In: Gower DJ, Johnson KG, Richardson JE, Rosen BR, Rüber L, Williams ST, eds. *Biotic evolution and environmental change in Southeast Asia*. The Systematics Association Special Volume 82. Cambridge: Cambridge University Press, 79–114.

Outlaw DC, Voelker G. 2008. Pliocene climatic change in insular Southeast Asia as an engine of diversification in *Ficedula* flycatchers. *Journal of Biogeography* **35:** 739–752.

Reddy S. 2008. Systematics and biogeography of the shrike-babblers (*Pteruthius*): species limits, molecular phylogenetics, and diversification patterns across southern Asia. *Molecular Phylogenetics and Evolution* **47:** 54–72.

Sabaj-Pérez M. 2014. Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an Online Reference. *Version* **5**.

Scheffers BR, Phillips BL, Laurance WF, Sodhi NS, Diesmos A, Williams SE. 2013. Increasing arboreality with altitude: a novel biogeographic dimension. *Proceedings of the Royal Society B* **280:** 1–9.

Siler CD, Oaks JR, Esselstyn JA, Diesmos AC, Brown RM. 2010. Phylogeny and biogeography of Philippine Bent-toed Geckos (Gekkonidae: Cyrtodactylus) contradict a prevailing model of Pleistocene diversification. *Molecular Phylogenetics and Evolution* **55:** 699–710.

Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S. 2011. MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution* **28:** 2731–2739.

Thomas AL, Henderson GM, Deschamps P, Yokoyama Y, Mason AJ, Bard E, Hamelin B, Durand N, Camion G. 2009. Penultimate deglacial sea level timing from uranium/thorium dating of Tahitian corals. *Science* **324:** 1186–1189.

Tolley KA, Colin RT, Measey GJ, Menegon M, Branch WR, Matthee C. 2011. Ancient forest fragmentation or recent radiation? Testing refugial speciation models in chameleons within an African biodiversity hot spot. *Journal of Biogeography* **38:** 1748–1760.

Vences M, Wollenberg KC, Vieites DR, Lees DC. 2009. Madagascar as a model region of species diversification. *Trends in Ecology and Evolution* **24:** 456–465.

Vidal N, Hedges SB. 2005. The phylogeny of squamate reptiles (lizards, snakes, and amphisbaenians) inferred from nine nuclear protein-coding genes. *Comptes Rendus Biologies* **328:** 1000–1008.

Voelker G, Outlaw RK, Bowie RCK. 2010. Pliocene forest dynamics as a primary driver of African bird speciation. *Global Ecology and Biogeography* **19:** 111–121.

Wiens JJ. 2004. Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. *Evolution* **58:** 193–197.

Wood PL Jr, Grismer LL, Norhayati A, Chan KO, Bauer AM. 2009. Two new montane species of *Acanthosaura* GRAY,

1831 (Squamata: Agamidae) from Peninsular Malaysia. *Zootaxa* **2012:** 28–46.

Wood PL Jr, Grismer LL, Norhayati A, Juliana S. 2008. Two new species of torrent dwelling toads *Ansonia* Stoliczka 1872 (Anura: Bufonidae) from Peninsular Malaysia. *Herpetologica* **64:** 321–340.

Wood PL Jr, Heinicke MP, Jackman TR, Bauer AM. 2012. Phylogeny of bent-toed geckos (*Cyrtodactylus*) reveals a west to east pattern of diversification. *Molecular phylogenetics and evolution* **65:** 992–1003.

Woodruff DS. 2010. Biogeography and conservation in Southeast Asia: how 7 million years of repeated environmental fluctuations affect today's patterns and the future of the remaining refugial-phase biodiversity. *Biodiversity Conservation* **19:** 919–941.

Xia X. 2013. DAMBE5: a comprehensive software package for data analysis in molecular biology and evolution. *Molecular Biology and Evolution* **30:** 1720–1728.

Xia X, Lemey P. 2009. Assessing substitution saturation with DAMBE. In: Lemey P, Salemi M, Vandamme A-M, eds. *the phylogenetic handbook: a practical approach to DNA and protein phylogeny, 2nd edn*. Cambridge: Cambridge University Press, 615–630.

Xia X, Xie Z, Salemi M, Chen L, Wang Y. 2003. An index of substitution saturation and its application. *Molecular Phylogenetics and Evolution* **26:** 1–7.

Zachos JC, Pagani M, Sloan L, Thomas E, Billups K. 2001. Trends, rhythms, and abberations in global climate 65 Ma to present. *Science* **292:** 686–693.

Zamudio KR, Jones KB, Ward RH. 1997. Molecular systematics of short-horned lizards: biogeography and taxonomy of a widespread species complex. *Systematic Biology* **46:** 284–305.

Zug GR. 2010. Speciation and dispersal in a low diversity taxon: the Slender geckos *Hemiphyllodactylus* (Reptilia, Gekkonidae). *Smithsonian Contributions to Zoology* **631:** 1–70.

APPENDIX

The following specimens were examined. Museum acronyms follow Sabaj-Pérez (2014).

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. *Hemphyllodactylus 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 Sibu LSUHC 5797. *Hemiphyllodactylus engganoensis*. 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 chiangmaiensis*. Thailand: Chiang Mai Province, Chiang Mai NSMNH 15192–200. *Hemiphyllodactylus* sp. nov. 9. Laos: Champasak Province, Pakxong District FMNH 258696. *Hemiphyllodactylus banaensis*. Vietnam: Da Nang Province, Hoa Vang District, Ba Na-Nui Chua Nature Reserve ITBCZ 2450, 2461–69.