

Systematics, ecomorphology, cryptic speciation and biogeography of the lizard genus *Tytthoscincus* Linkem, Diesmos & Brown (Squamata: Scincidae) from the sky-island archipelago of Peninsular Malaysia

L. LEE GRISMER^{1*}, PERRY L. WOOD, JR.², EVAN S.H. QUAH³, SHAHRUL ANUAR^{3,4}, EHWAN B. NGADI⁵, NUR AMALINA MOHD IZAM⁵ and NORHAYATI AHMAD^{5,6}

¹Herpetology Laboratory, Department of Biology, La Sierra University, 4500 Riverwalk Parkway, Riverside, , California 92515, USA

²Department of Biology, Brigham Young University, 150 East Bulldog Boulevard, Provo, Utah 84602, USA

³School of Biological Sciences, Universiti Sains Malaysia, 11800 USM, Pulau Pinang, Penang, Malaysia

⁴Center for Marine and Coastal Studies, Universiti Sains Malaysia, 11800 USM, Penang, Malaysia

⁵School of Environmental and Natural Resources Sciences, Faculty of Science and Technology, Universiti Kebangsaan Malaysia, N43600 Bangi, Selangor, Malaysia

⁶Institute for Environment and Development, (LESTARI), Universiti Kebangsaan Malaysia, 43600 Bangi, Selangor Darul Ehsan, Malaysia

Received 15 January 2017; revised 19 July 2017; accepted for publication 25 August 2017

An integrative taxonomic analysis reveals a remarkable degree of cryptic speciation between sympatric, specialized, leaf-litter species in an upland clade of the scincid genus *Tytthoscincus* across the sky-island archipelago of Peninsular Malaysia. Bayesian inference and maximum likelihood phylogenies based on the mitochondrial gene *ND2* indicate that this clade is composed of a lineage of limb, digit and tympanum-reduced, semi-fossorial species and a lineage of leaf-litter generalist bearing longer, more robust limbs and digits, and well-developed tympanae. Behavioural differences inferred from differing ecomorphologies form the basis of hypotheses proposed to account for resource partitioning at Fraser's Hill, Pahang between the sympatric leaf-litter generalist *T. bukitensis* and the new semi-fossorial species *T. kakikecil* sp. nov. However, this hypothesis does not account for the extreme case of cryptic speciation and syntopy between *T. bukitensis* and a new leaf-litter generalist *T. martae* sp. nov. at Genting Highlands, Pahang. The phylogenetic analyses also indicate there is an additional new, upland, semi-fossorial species, *T. jaripendek* sp. nov., from Cameron Highlands and a new lowland, leaf-litter generalist, *Tytthoscincus* sp., from Hulu Terengganu, Terengganu. The specific identities of the new upland populations are corroborated by morphological analyses using combinations of principal component analysis, discriminant analysis of principal components, analysis of variance, Tukey HSD (honest significant difference) tests and Welch two-way *t*-tests. The Hulu Terengganu specimen was too damaged to provide a reliable description. A biogeographic scenario inferred from a time-calibrated BEAST analysis suggests that speciation in the upland clade has been ongoing since the Upper Pliocene following repeated episodes of secondary contact associated with glacier-driven climatic oscillations generating upland forest expansion and retraction. These analyses highlight the increasing levels of herpetological diversity and endemism being discovered in the montane regions of Peninsular Malaysia and bring to light the understudied ecological complexity of Peninsular Malaysia's leaf-litter ecosystems and the growing need for its conservation.

ADDITIONAL KEYWORDS: cryptic species – ecomorphology – leaf-litter – Peninsular Malaysia – semi-fossorial – *Tytthoscincus*.

*Corresponding author. E-mail: lgrismer@lasierra.edu
[Version of Record, published on 5 October 2017; <http://zoobank.org/urn:lsid:zoobank.org:pub:31ADBE97-8DA1-47BB-969A-E5F851726453>]

INTRODUCTION

The sky-island archipelago of Peninsular Malaysia extends across a series of mountain ranges and islands and is emerging as one of the most herpetologically rich regions on the entire Thai-Malay Peninsula. This fragmented, upland ecosystem of habitat islands above 800 m in elevation is composed of hill dipterocarp and mossy forests that have yielded 38 new species of amphibians and reptiles from five different mountain systems in the last 10 years of exploration (Grismer, Grismer & Youmans, 2004; Grismer, 2006a, b, 2007, 2008; Grismer *et al.*, 2008; Wood *et al.*, 2008, 2009; Chan *et al.*, 2009, 2014; Grismer, Norhayati & Chan, 2009a; Grismer, Wood, Grismer, 2009c; Matsui *et al.*, 2009; Grismer *et al.*, 2010a, b, 2011, 2012, 2013a, b, 2014b, c, 2015a, b, 2016b; Grismer & Chan, 2010; Loredó *et al.*, 2013; Matsui, Belabut & Ahmad, 2014; Grismer & Quah, 2015; Cobos *et al.*, 2016; Davis *et al.*, 2016). Not only has this growing diversity increased levels of local upland endemism, it is beginning to reveal complex patterns of closely related co-distributed species showing remarkable degrees of syntopy (Grismer *et al.*, 2013b, 2015a; Loredó *et al.*, 2013; Grismer & Quah, 2015). Most notable in this regard are microhabitat-restricted leaf-litter taxa such as the Reed Snakes *Macrocalamus* Günther and *Calamaria* Boie (Quah *et al.*, in preparation) and the diminutive Forest Skinks *Tytthoscincus* Linkem, Diesmos, & Brown. The latter comprise a lineage of at least 13 small [snout–vent length (SVL) < 45 mm], forest floor-dwelling species that collectively extend from Sulawesi across Wallace's Line to the Philippines, Borneo, Java and Peninsular Malaysia (Linkem, Diesmos & Brown, 2011; Grismer *et al.*, 2016a). Additional molecular evidence will no doubt demonstrate that many of the diminutive skinks in Borneo, Sumatra and Thailand, currently in the genus *Sphenomorphus*, should be transferred into *Tytthoscincus*.

In general, *Tytthoscincus* have relatively elongate bodies bearing short limbs and digits that are inferred here to be adaptations for locomoting in leaf-litter (Van Damme, Aerts & Vanhooydonck, 1998, 2002; Melville & Swain, 2000; Kohlsdorf, Garland & Navas, 2001; Herrel, Meyers & Vanhooydonck, 2002; Siler & Brown, 2011). Anecdotal observations in Peninsular Malaysia indicate that *Tytthoscincus* forage within the cover of leaf-litter during the day but are occasionally seen on the surface during periods of overcast and light precipitation (Grismer, 2011). For their size, these skinks are surprisingly swift – moving in and out of rocks and root systems into which they irretrievably retreat at the slightest provocation. Species of *Tytthoscincus* are not lizards one comes across easily and considerable effort (raking leaves, turning rocks and logs, planting pitfall traps, etc.) is usually necessary for the collection

of only a few samples. Their secretive nature and ability to escape capture have contributed greatly to their low numbers in collections and a general lack of knowledge concerning their natural history. This, coupled with their relatively uniform morphology and non-descript, unremarkable, dull-brown coloration, often makes it difficult to establish species boundaries using traditional morphological characters (Grismer, 2006b, 2007, 2008; Grismer *et al.*, 2009a, b).

Recent molecular studies (Grismer *et al.*, 2016a; Karin, Bauer & Das, 2016) have demonstrated that *Tytthoscincus* is more diverse than its morphology generally indicates. Grismer *et al.* (2016a) noted that on the Thai-Malay Peninsula, there are two sequentially related monophyletic lineages: a lowland swamp-dwelling clade composed of two species from Peninsular Malaysia and Singapore and an endemic montane clade composed of nine upland species with insular derivatives. New molecular and morphological data presented herein based on collections of additional material from new localities in Peninsular Malaysia and from other known localities are used here to elucidate the phylogenetic and ecological complexity within the upland clade. We also attempt to establish a stable, phylogenetic classification by disentangling a currently erroneous taxonomy based solely on morphology (Grismer *et al.*, 2009a, b). Additionally, ecomorphological evidence will be presented that we propose contributes to a newly discovered high degree of sympatry (as many as three species at some localities) within this genus based on three new upland species discovered from the Banjaran (=mountain range) Titiwangsa and one new lowland species from the Tembat Forest Reserve, Hulu Terengganu, Terengganu. Lastly, we have expanded the molecular data set to demonstrate that Indonesian species of *Sphenomorphus* Fitzinger previously suspected of belonging to the genus *Tytthoscincus* (Linkem, 2013; Karin *et al.*, 2016) do so indeed and their formal transference is accommodated here.

MATERIAL AND METHODS

PHYLOGENETIC ANALYSIS

A data set composed of 1026 bp of the mitochondrial gene NADH dehydrogenase subunit 2 gene (*ND2*) was constructed from 36 individuals comprising all nine species of *Tytthoscincus* that comprised the ingroup plus 15 individuals from 11 other species of *Tytthoscincus* that, along with one specimen of *Larutia seribuaten-sis*, composed the outgroups based on Linkem *et al.* (2011; Table 1) and Linkem (2013). Total genomic DNA was isolated from liver or skeletal muscle from specimens stored in 95% ethanol using the Qiagen DNeasy tissue kit (Valencia, CA, USA). The *ND2* gene was amplified using a double-stranded polymerase

Table 1. GenBank accession numbers for *ND2* sequences and catalogue numbers of the voucher specimens used in this study

Species	Voucher	Locality	GenBank no.
<i>Larutia seribuatensis</i>	LSUHC 5168	West Malaysia, Johor, Pulau Tuali	HQ906968
<i>Tytthoscincus aesculeticolus</i> (paratype)	FMNH 239839	East Malaysia, Sabah Sipitang District	JF498209
<i>T. aesculeticolus</i>	SP 06913	East Malaysia, Sabah Sipitang District	JF498208
<i>T. atrigularis</i>	KU 315055	Philippines, Zamboanga City 'Province' Pasaonca Natural Park	JF497971
<i>T. atrigularis</i>	KU 315060	Philippines, Zamboanga City 'Province' Pasaonca Natural Park	JF497972
<i>T. batupanggah</i>	CAS 259189	East Malaysia, Sarawak, Gunung Penrissen	KU587723
<i>T. batupanggah</i>	ZRC 2.7123	East Malaysia, Sarawak, Gunung Penrissen	KU587725
<i>T. hallieri</i>	FMNH 230184	East Malaysia, Sabah Lahad Datu District	JF497973
<i>T. leproauricularis</i>	LSUHC 7860	East Malaysia, Sarawak, Gunung Penrissen	KU587724
<i>T. panchorensis</i> (holotype)	LSUHC 4801	West Malaysia, Penang, Bukit Panchor State Park	KU872741
<i>T. parvus</i>	RMB 4707	Indonesia, Sulawesi	JF498213
<i>T. sananus</i>	JAM 8829	Indonesia, Sanana Island	KY989394
<i>T. sibuensis</i>	LSUHC 5583	West Malaysia, Johor, Pulau Sibul	KU872743
<i>T. cf. sibuensis</i>	JAM 7233	Singapore, Nee Soon Swamp	KY989395
<i>T. temmincki</i>	BS 10263	Indonesia, Java	KY989396
<i>T. textus</i>	JAM 7497	Indonesia, Sulawesi	KY989397
Upland clade			
<i>T. bukitensis</i>	LSUHC 12750	West Malaysia, Pahang, Genting Highlands, Awana Rd.	KY989398
<i>T. bukitensis</i>	LSUHC 12237	West Malaysia, Pahang, Genting Highlands, Awana Rd.	KY989399
<i>T. bukitensis</i> (holotype)	ZRC 2.6245	West Malaysia, Pahang, Fraser's Hill, Bishops's Trail	KY989400
<i>T. bukitensis</i>	LSUHC 12686	West Malaysia, Pahang, Fraser's Hill, Jeriau	KY989401
<i>T. bukitensis</i>	LSUHC 12687	West Malaysia, Pahang, Fraser's Hill, Jeriau	KY989402
<i>T. bukitensis</i>	LSUHC 12226	West Malaysia, Pahang, Fraser's Hill, Jeriau	KY989403
<i>T. bukitensis</i>	LSUHC 11771	West Malaysia, Pahang, Fraser's Hill, Telecom Loop	KY989404
<i>T. butleri</i>	LSUHC 9206	West Malaysia, Perak, Bukit Larut	KU872732
<i>T. butleri</i>	LSUHC 12429	West Malaysia, Perak, Bukit Larut	KY989405
<i>T. butleri</i>	LSUHC 12432	West Malaysia, Perak, Bukit Larut	KY989406
<i>T. butleri</i>	LSUHC 12433	West Malaysia, Perak, Bukit Larut	KY989407
<i>T. butleri</i>	LSUHC 9204	West Malaysia, Perak, Bukit Larut	KU872731
<i>T. butleri</i>	LSUHC 12516	West Malaysia, Penang, Penang Island, Penang Hill	KY989408
<i>T. butleri</i>	LSUHC 12071	West Malaysia, Penang, Penang Island, Penang Hill	KU872733
<i>T. butleri</i>	LSUHC 11275	West Malaysia, Penang, Penang Island, Penang Hill	KY989410
<i>T. butleri</i>	LSUHC 11552	West Malaysia, Kedah, Pulau Langkawi, Gunung Raya	KU872737
<i>T. butleri</i> (holotype of <i>T. langkawiensis</i>)	LSUHC 6790	West Malaysia, Kedah, Pulau Langkawi, Gunung Raya	KU872736
<i>T. butleri</i>	LSUHC 11784	West Malaysia, Kedah, Pulau Langkawi, Gunung Raya	KY989411
<i>T. butleri</i>	LSUHC 11785	West Malaysia, Kedah, Pulau Langkawi, Gunung Raya	KU872738
<i>T. butleri</i>	LSUHC 11786	West Malaysia, Kedah, Pulau Langkawi, Gunung Raya	KU872739
<i>T. butleri</i>	LSUHC 9206	West Malaysia, Kedah, Pulau Langkawi, Gunung Raya	KU872732
<i>T. ishaki</i>	LSUHC 5165	West Malaysia, Pahang, Pulau Tioman, Gunung Kajang	KY989413

Table 1. *Continued*

Species	Voucher	Locality	GenBank no.
<i>T. ishaki</i>	LSUHC 6150	West Malaysia, Pahang, Pulau Tioman, Gunung Kajang	Forthcoming
<i>T. ishaki</i>	LSUHC 6151	West Malaysia, Pahang, Pulau Tioman, Gunung Kajang	Forthcoming
<i>T. jaripendek</i> sp. nov. (holotype)	LSUHC 11681	West Malaysia, Pahang, Cameron Highlands, Robinson Falls	KU872745
<i>T. jaripendek</i> sp. nov. (paratype)	LSUHC 11679	West Malaysia, Pahang, Cameron Highlands, Robinson Falls	KU872746
<i>T. jaripendek</i> sp. nov. (paratype)	LSUHC 11680	West Malaysia, Pahang, Cameron Highlands, Robinson Falls	KU872747
<i>T. jaripendek</i> sp. nov. (paratype)	LSUHC 11987	West Malaysia, Pahang, Cameron Highlands, Robinson Falls	KU872748
<i>T. kakikecil</i>	LSUHC 11769	West Malaysia, Pahang, Fraser's Hill, Richmond Rd.	Forthcoming
<i>T. kakikecil</i>	LSUHC 11770	West Malaysia, Pahang, Fraser's Hill, Richmond Rd.	Forthcoming
<i>T. kakikecil</i>	LSUHC 11772	West Malaysia, Pahang, Fraser's Hill, Telecom Loop	Forthcoming
<i>T. kakikecil</i>	LSUHC 12754	West Malaysia, Pahang, Genting Highlands, Ulu Kali	Forthcoming
<i>T. perhentianensis</i> (holotype)	LSUHC 9206	West Malaysia, Terengganu, Pulau Perhentian Bear	KU872742
<i>T. temengorensis</i> (paratype)	LSUHC 9206	West Malaysia, Perak, Temengor Forest Reserve	KU872744
<i>Tytthoscincus</i> sp. nov.	LSUHC 12515	West Malaysia, Terengganu, Tembak Forest Reserve	

chain reaction (PCR) under the following conditions: 1.0 µL genomic DNA (~10–33 µg), 1.0 µL (10 µM) light strand primer (5'-AAGCAGTTGGCCCATACC-3'; Macey *et al.*, 1997), 1.0 µL (10 µM) heavy strand primer (5'-AACCAAACCCAACCTACGAAAAAT-3'; Macey *et al.*, 1997), 1.0 µL dinucleotide pairs (1.5 µM), 2.0 µL 5× buffer (1.5 µM), 1.0 µL MgCl₂ 10× buffer (1.5 µM), 0.18 µL Taq polymerase (5 U/µL) and 7.5 µL H₂O. PCR reactions were run 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 52 °C for 35 s, followed by a cycle extension at 72 °C for 35 s, for 33 cycles. All PCR products were visualized on a 1% agarose gel electrophoresis. Successfully amplified PCR products were vacuum purified using MANU 30 PCR Millipore plates and purified products were resuspended in sterile molecular 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 BYU DNA Sequencing Center. All sequences were edited in Geneious v6.1.8 (Drummond *et al.*, 2011) and aligned by eye. Mesquite v3.0.2 (Maddison & Maddison, 2015) was used to check for premature stop codons and to ensure the correct amino acid read frame.

The phylogenetic analysis applied two model-based methods: maximum likelihood (ML) and Bayesian inference (BI). The Bayesian information criterion

(BIC) implemented in IQ-TREE (Nguyen *et al.*, 2015) calculated TVM+I+G4, HKY+G4 and TPM3+G4 to be the best-fit models of evolution for the first, second and third codon positions, respectively (Kalyaanamoorthy *et al.*, 2017). ML analyses implemented in IQ-TREE employed 1000 bootstrap pseudoreplicates via the ultrafast bootstrap approximation algorithm (Minh, Nguyen & von Haeseler, 2013). A codon-partitioned Bayesian analysis was carried out in MrBayes v3.2.6 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) on CIPRES (Cyberinfrastructure for Phylogenetic Research; Miller, Pfeiffer & Schwartz, 2010) using default priors. Models of evolution used were approximated from those calculated for the ML analysis and employed GTR+I+Γ for the first and third codon positions and HKY+Γ for the second codon position. Two simultaneous runs were performed with four chains per run (three hot and one cold) using default priors. The simulation ran for four million generations, was sampled every 4000 generations from the Markov Chain Monte Carlo (MCMC) and halted after the average standard deviation split frequency was below 0.01. The first 25% of the trees were discarded as burn-in using the sumt function. Convergence of all parameters and stationarity distributions were verified and checked in Tracer v1.6 (Rambaut *et al.*, 2014). Nodes having ultrafast ML bootstrap values of 95 and BI posterior probabilities of 0.95 and above were considered well supported (Huelsenbeck *et al.*, 2001; Wilcox *et al.*, 2002; Nguyen *et al.*, 2015). Bootstrap values and posterior probabilities between 80 and 90 were considered moderately supported.

A time-calibrated BI analysis was implemented in BEAUti v1.8.0 (Bayesian Evolutionary Analysis Utility) and run on BEAST v1.8.0 (Bayesian Evolutionary Analysis Sampling Trees; Drummond *et al.*, 2012) employing an uncorrelated lognormal relaxed clock with unlinked substitution and clock models and monophyly unchecked for Taxon Sets. MCMC chains were run using a Species: Coalescence tree prior for 20 million generations and logged every 20 000 generations. It has been demonstrated that the third codon position is susceptible to substitution saturation (Zamudio, Jones & Ward, 1997; Carranza *et al.*, 2000; Grismer *et al.*, 2015a) and could contribute to overestimating node ages. However, Grismer *et al.* (2015a) noted that although third codon position saturation was evident in their study, it was not a significant factor in estimating node ages across various codon and gene partition schemes and was consistent with similar node age estimates using nuclear genes on the same taxa (Heinicke *et al.*, 2011). The run was calibrated to a 1.47% mutation rate following mean estimates by Chapple *et al.* (2012) for New Zealand skinks (*Oligosoma*) and used a lognormal prior distribution and a mean in real space with an SD of 0.05 for the ucl.d.mean of each codon. A maximum clade credibility tree using mean heights at the nodes was generated using TreeAnnotator v1.8.0 (Rambaut & Drummond, 2013) with 10% of the trees used as a burn-in. The BEAST log file was visualized and checked in Tracer v1.6.0 (Rambaut *et al.*, 2014) to ensure effective sample sizes (ESS) were above 200 for all parameters. Because ESS values for the 'prior' and 'posterior' were below 200 and the remaining parameters were considerably higher than 200 in a preliminary run using a GTR+ Γ substitution model, a re-run using the less complex HKY model was utilized because low ESS values may indicate overparameterized substitution models (Grummer, Bryson & Reeder, 2014). Importantly, however, the divergence time estimates did not differ significantly between the GTR+ Γ and the HKY models.

MORPHOLOGICAL ANALYSIS

All measurements were made with Mitutoyo digital calipers to the nearest 0.1 mm by LLG. Scale counts were made on the right side of the body when possible with a Nikon SMZ 1500 dissecting microscope. Scale terminology is adapted from Grismer *et al.* (2009a, b), Lim (1998) and Taylor (1935) and head scales are illustrated in Figure 1. Measurements and scale counts used are SVL measured from the tip of the rostral scale to the vent; head length (HL) measured from the anterior margin of the ear opening to the tip of the rostral scale; tympanum diameter (TD) measured from the anterior to the posterior margin of the auditory

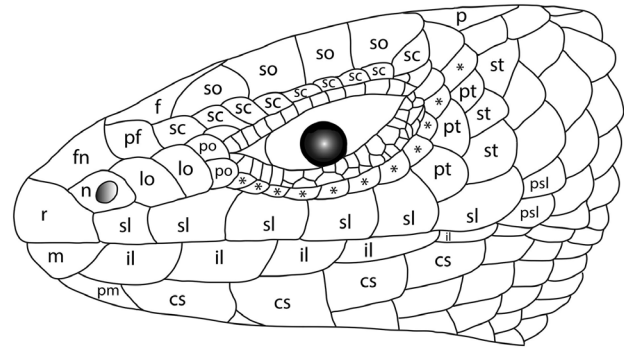


Figure 1. Generalized illustration of head terminology of *Tytthoscincus* adapted from Grismer (2009a, b), Lim (1998) and Taylor (1935). cs, chinshield; fn, frontonasal; il, infralabial; lo, loreal; m, mental; n, nasal; p, parietal; pf, prefrontal; pm, postmental; po, preorbital; psl, postsupralabial; pt, primary temporal; r, rostral; sc, superciliary; sl, supralabial; so, supraorbital; st, secondary temporal. *Subocular.

meatus; axilla–groin length (AXG) measured from the anterior margin of the hind limb at its insertion point of the body to the posterior margin of the forelimb measured at its insertion point on the body with the upper limb sections held at right angles to the body; forelimb length (FL) measured from the insertion of the forelimb on the body to the base of the third toe with the brachium held at a right angle to the body and hind limb length (HDL) measured from the insertion of the hind limb on the body to the base of the fourth toe the thigh held at a right angle to the body. Ratiometric data (TD/HL, HL/SVL, AXG/SVL, FL/SVL and HDL/SVL) from adults (SVL \geq 30 mm determined by the possession eggs or through dissection) were generated from raw measurements.

Scale counts taken were midbody scale rows (MB) counted as the number of longitudinal scale rows encircling the body at a point midway between the limb insertions; paravertebral scale rows (PV) counted as the number of scales in a line from the parietal scales to a point on the dorsum opposite the vent and ventral scale rows (VS) counted as a row of scales between the postmental and the edge of the cloacal plate. Other standard counts include superciliaries [given as two numbers, the first accounting for the anterior smaller scales followed by a second number accounting for the much larger, posteriorly projecting scales preceded by the notation of ‘’ (e.g. 8’1)], supraoculars, loreals, supralabials, infralabials and third finger and fourth toe subdigital lamellae (3FL and 4TL, respectively). Additional characters examined were the degree of contact between the parietals and supraoculars, enlargement of posterior superciliary scales, degree of contact between the prefrontal scales, presence or absence of enlarged preloacal and pectoral scales, texture of

subdigital lamellae and the degree of development of the tympanum. Colour pattern characters examined were the degree of dark, dorsolateral striping and overall ground colour.

Analyses of variance (ANOVAs) were performed to ascertain if statistically significant mean differences ($P < 0.05$) existed among the populations for the scale count and adjusted mensural data (see below). ANOVAs having P values less than 0.05 indicating that statistical differences existed were subjected to a Tukey honest significant difference (HSD) test to ascertain which population pairs differed significantly. Boxplots were generated for all characters in order to visualize trends in the data and to identify outliers.

Principal component analysis (PCA) and discriminant analysis of principal components (DAPC) were used to determine (1) the degree to which the morphological variation coincided with species boundaries delimited by the molecular phylogenetic and univariate analyses, (2) to ascertain which category of characters – discrete (scale counts) or continuous (mensural) – performed best at delimiting species and (3) whether sympatric and syntopic populations have different ecomorphologies that are separated in morphospace. PCA, implemented by the `prcomp` command in R v3.2.1 (R Core Team, 2015), searches for the best overall low-dimensional representation of significant morphological variation in the data. Characters used in the PCAs and DAPCs were discrete meristic data from the scale counts MB, PV, VS, 3FL and 4TL and the continuous mensural data from TD, HL, AXG, FL and HDL. To remove the effects of body size from the latter, we used the following equation: $X_{\text{adj}} = X - \beta(\text{SVL} - \text{SVL}_{\text{mean}})$, where X_{adj} = adjusted value, X = measured value, β = unstandardized regression coefficient for each OTU (operational taxonomic unit), SVL = measured SVL and SVL_{mean} = overall average SVL of all OTUs (Thorpe, 1975, 1983; Turan, 1999; Leonart, Salat, & Torres, 2000). All PCA data were natural log-transformed prior to analysis and scaled to their SD in order to normalize their distribution so as to ensure characters with very large and very low values did not over-leverage the results owing to intervariable non-linearity and to transform meristic and mensural data into comparable units for analysis.

To characterize clustering and separation in morphospace, a DAPC was performed to search for linear combinations of morphological variables having the greatest between-group variance and the smallest within-group variance (Jombart, Devillard & Balloux, 2010). DAPC relies on log-transformed data from the PCA as a prior step to ensure that variables analyzed are not correlated and number fewer than the sample size. Principal components (PCs) with eigenvalues greater than 1 were retained for the DAPC according to the criterion of Kaiser (1960). Separate PCA and DAPC

analyses were performed on the scale count (discrete) and mensural (continuous) data in order to ascertain which, if any category of characters, performed better at delimiting species with respect to the phylogenetic analyses. Total evidence PCA and DAPC analyses were also performed using a concatenated data set to illustrate an unbiased morphospacial relationship of the OTUs. All statistical analyses were performed using the platform R v3.2.1 (R Core Team, 2015).

Two specimens from Genting Highlands (FMNH 199945, Ulu Kali, Pahang and LSUHC 12072, Awana Road, Pahang) and one specimen from Telom Valley, Cameron Highlands (ZRC 2.5944) from which we were unable to obtain DNA sequence data did not differ discretely from some of the other species in the montane clade. In order to place them taxonomically as *conferre* (i.e. *cf.* = compared), each specimen was run separately in a concatenated PCA and DAPC. Membership probabilities were calculated based on posteriors retained from the discriminant functions of the DAPC (Jombart & Collins, 2015) using the round (`head(dapc1$posterior)`, 3) command in R v3.2.1 (R Core Team, 2015).

Specimens examined are listed in the Appendix. Museum acronyms follow Sabaj-Pérez (2010) except for the following non-standard acronyms for the Department of Wildlife and National Parks collection (DWNP), PERHILITAN, Pahang, Malaysia; La Sierra University Herpetological Collection (LSUHC), La Sierra University, Riverside, CA, USA; Langkawi Research Center of Universiti Kebangsaan Malaysia (LRCUKM) on Langkawi Island, Kedah, Malaysia; Rafe M. Brown field series (RMB), University of Kansas, Lawrence, KS, USA and Jimmy A. McGuire field series (JAM), University of California, Berkeley, CA, USA.

RESULTS

MOLECULAR ANALYSES

The ML and the BI analyses produced trees with non-conflicting topologies and the ML topology is presented here with Bayesian posterior probabilities and ultrafast ML bootstrap values placed at the nodes, respectively (Fig. 2). The molecular analyses corroborate some of the earlier morphological hypotheses of species designation (Grismer, 2006b; Grismer *et al.*, 2009a, b) by indicating that *Tytthoscincus ishaki* Grismer, *T. perhentianensis* Grismer, Wood, & Grismer and *T. temengorensis* Grismer, Norhayati, & Chan are not nested within other species. The analyses similarly corroborate the species designation of *T. butleri* (Boulenger) from Bukit Larut, Perak but indicate that it is paraphyletic with respect to *T. langkawien-sis* Grismer from the Langkawi Archipelago, Kedah

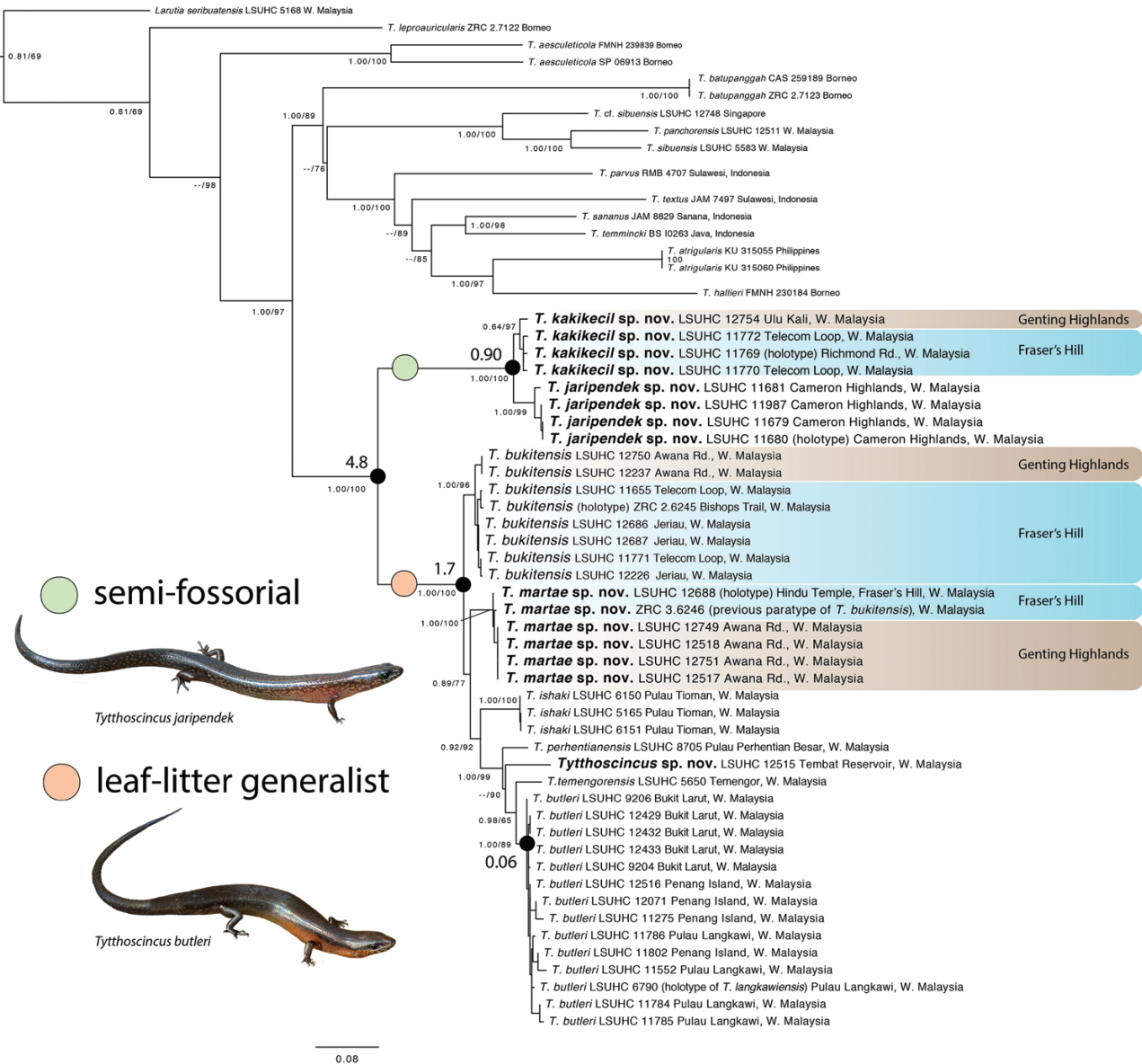


Figure 2. Maximum likelihood phylogram depicting the relationships of species within the genus *Tyttoscincus* with Bayesian posterior probabilities and ultrafast ML bootstrap values, respectively, labelled at the nodes. Black circles denote time-calibrated nodes labelled in millions of years before present.

(Grismer, 2008) and a newly discovered population of *Tyttoscincus* from Pulau Pinang (Penang Island, Malaysia). However, these three allopatric populations have an uncorrected pairwise sequence divergence no greater than 2.04% among them and correspondingly extremely short branch lengths (Fig. 2). Considering this, and that there are no discrete morphological differences nor statistically different mean values of any character separating these populations from one another (Table 2) and that they completely overlap in the PCA and DAPC analyses (Fig. 3), the Penang Island population is considered conspecific with *T.*

butleri and *T. langkawiensis* Grismer, 2008 becomes a junior synonym of *T. butleri* (Boulenger, 1912) by way of nomenclatural priority.

The molecular analyses also indicate there are two well-supported (BI 1.00/ML 100) major lineages within the upland clade of *Tyttoscincus* (Fig. 2). The first is composed of two semi-fossorial sister species (see below for the morphological designation of this ecomorph): the newly discovered population *T. jaripendek* sp. nov. (see description below) from Cameron Highlands, Pahang and a new species, *T. kakikecil* sp. nov. (see description below) from Fraser’s Hill and Ulu Kali,

Table 2. Summary statistics and scale counts of the three allopatric populations of *Tytthoscincus butleri*

	Pulau Langkawi	Bukit Larut	Penang Island
Supralabials	6	6	6
Infralabials	5 (10) or 6 (1)	5	5
Supraoculars	4	4	4
Frontoparietal contacting supraoculars	2, 3, 4	2, 3, 4	2, 3, 4
Superciliaries	9·1	9·1	9·1
Prefrontals in contact	Yes	Yes	Yes
Loreals	1 (1) or 2 (10)	1 (1) or 2 (7)	2
Tympanum deeply recessed and pigmented	Yes	Yes	Yes
Pectoral scales enlarged	No – weakly	Weakly – yes	Yes
Lamellae texture	Keeled	Keeled	Keeled
Midbody scales	32–38	32–35	30–35
Mean	34.9	33.7	32.3
SD	±1.87	±1.11	±2.51
<i>n</i>	11	7	3
Paravertebral scales	60–72	65–72	64–75
Mean	68.5	69.2	70.3
SD	±3.24	±2.28	±5.69
<i>n</i>	11	7	3
Ventral scales	63–72	63–69	68–73
Mean	67.6	66.4	69.67
SD	±3.41	±2.15	±2.89
<i>n</i>	11	7	3
3rd finger lamellae	7	7	7
Mean	7	7	7
SD	±0.0	±0.0	±0.0
<i>n</i>	11	7	3
4th toe lamellae	10–13	10–13	10–12
Mean	11.5	11.7	11.0
SD	±0.82	±0.95	±1.00
<i>n</i>	11	7	3
TD/HL	0.13–0.16	0.13–0.16	0.13–0.14
Mean	0.14	0.14	0.13
SD	±0.01	±0.01	±0.01
<i>n</i>	8	7	3
HL/SVL	0.20–0.22	0.19–0.22	0.19–0.22
Mean	0.21	0.21	0.20
SD	±0.01	±0.01	±0.01
<i>n</i>	8	7	3
AXG/SVL	0.53–0.57	0.52–0.56	0.50–0.58
Mean	0.54	0.54	0.54
SD	±0.01	±0.02	±0.04
<i>n</i>	8	7	3
FL/SVL	0.22–0.28	0.23–0.26	0.22–0.23
Mean	0.24	0.24	0.23
SD	±0.02	±0.01	±0.01
<i>n</i>	8	7	3
HDL/SVL	0.33–0.40	0.34–0.38	0.33–0.37
Mean	0.35	0.36	0.35
SD	±0.02	±0.01	±0.02
<i>n</i>	8	7	3
Maximum SVL	40.1	40.9	38.0

All measurements are in millimetres. AXG, axilla–groin length; FL, forelimb length; HDL, hind limb length; HL, head length; SVL, snout–vent length; TD, tympanum diameter.

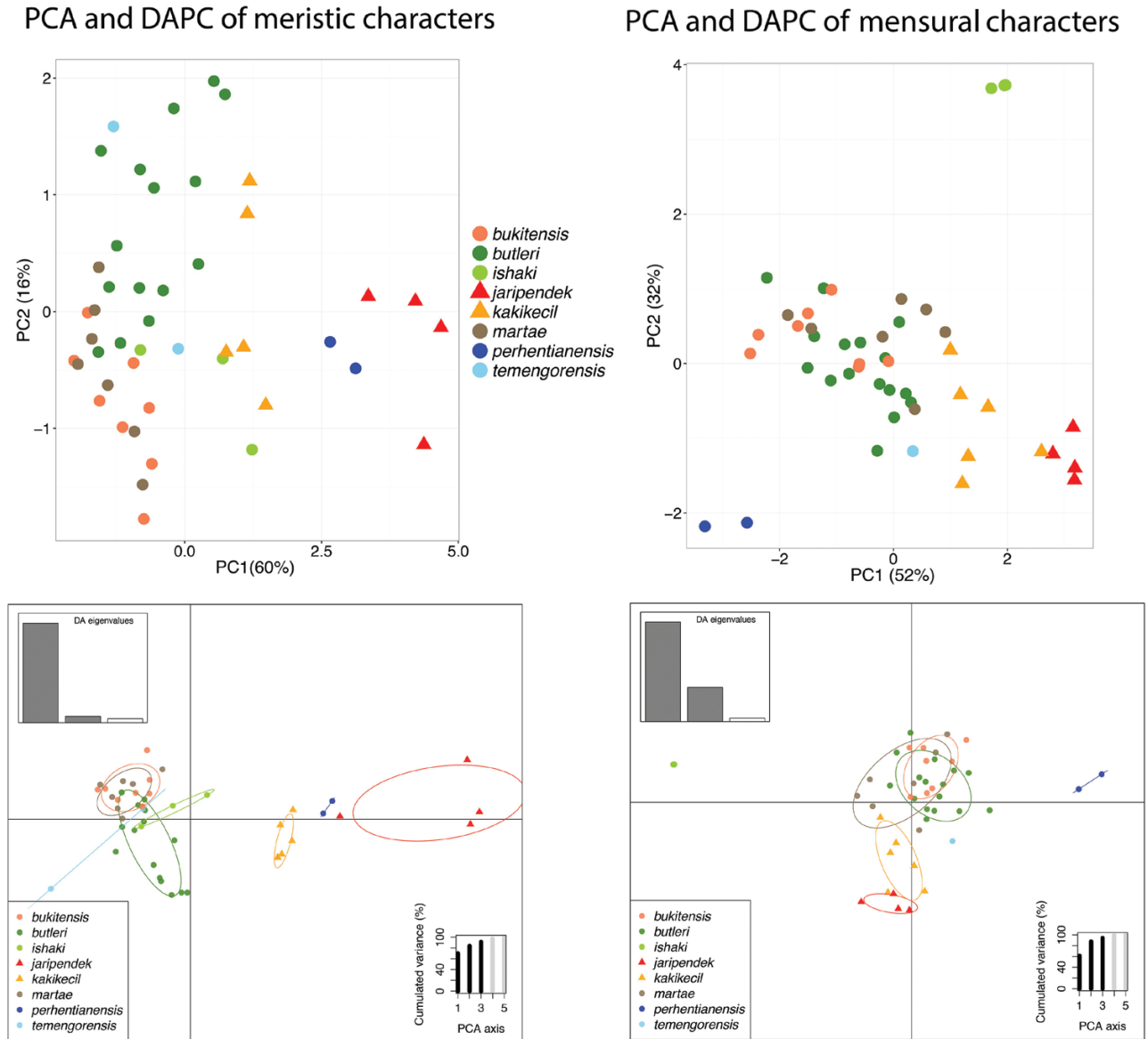


Figure 3. Principal component analysis (PCA) and discriminant analysis of principal components (DAPC) analyses of scale count and adjusted mensural data.

Genting Highlands, Pahang. Together, these two species comprise the sister group to the second major lineage consisting of leaf-litter generalists (see below for the morphological designation of this ecomorph). This lineage is composed of *T. bukitensis*, a new species *T. martae* sp. nov. (see description below) from Awana Road, Genting Highlands, Pahang; *T. ishaki*; *T. perhentianensis*; *T. temengorensis* and *T. butleri*. Additionally, expanded genetic sampling demonstrates that *T. bukitensis* is not endemic to Fraser’s Hill (Grismer, 2007), but extends as far south to at least Awana Road in Genting Highlands and as such, is syntopic with *T. martae* sp. nov. (Fig. 2). Lastly, the analyses demonstrate that the Tembat Forest Reserve population from

Hulu Terengganu, Terengganu represents a fourth new species, *Tyttthoscincus* sp. nov. However, this specimen died in a pitfall trap and subsequent predation by insects left it damaged beyond description.

The expanded molecular data set confirmed that *Sphenomorphus sananus* (Kopstein), *S. temmincki* (Duméril & Bibron) and *S. textus* (Müller) should be included in the genus *Tyttthoscincus* as previously hypothesized by Linkem *et al.* (2011) and Linkem (2013) being that they are embedded within the phylogeny of *Tyttthoscincus* (Fig. 2) and are thus transferred herein.

Using a limited taxon set and a ML analysis, Karin *et al.* (2016) demonstrated that *Tyttthoscincus*

batupanggih Karin, Das & Bauer and *T. leproauricularis* Karin, Das & Bauer were part of a monophyletic group that included species from Sulawesi and Borneo. Increased taxon sampling from Sulawesi and Peninsular Malaysia and the additional use of a BI analysis here indicate that the group to which *T. batupanggih* and *T. leproauricularis* belong is paraphyletic with respect to the montane clade from Peninsular Malaysia. *Tyrrhoscincus batupanggih* is the sister species of a monophyletic group composed of *T. atrigularis*, *T. hallieri* and *T. parvus* as Karin *et al.* (2016) indicated but now included in that group are *T. panchorensis* Grismer, Muin, Wood, Anuar, & Linkem, *T. sibuensis* Grismer, *T. textus*, *T. sananus*, *T. cf. sibuensis* and *T. temmincki* (Fig. 2). Karin *et al.* (2016) placed *T. leproauricularis* as the sister species to *T. aesculeticola* but the analyses herein show it to be the potential sister lineage to a clade containing all other *Tyrrhoscincus* although this relationship is only weakly supported (0.81/69).

MORPHOLOGICAL ANALYSES

The PCA and DAPC for the continuous, adjusted mensural characters are largely consistent with the molecular analyses in that they indicate little to no overlap between the semi-fossorial and fossorial species (Fig. 3). PC1 and PC2 account for 84% of the total variation and load most heavily for AXG and FL along PC1 (52% of the total variation) and for TD along PC2 (32% of the total variation) (Table 3). Boxplots for these characters show that *T. jaripendek* sp. nov. and *T. kakikecil* sp. nov. along with *T. temengorensis* have relatively longer trunk lengths (AXG) than all other species; that along with *T. temengorensis* and *T. perhentianensis*, they have relatively shorter FL than all other species; and they have the relatively smallest tympanae of all species (Fig. 4). The DAPC further characterizes these results (Fig. 3). These characters are commonly correlated with a fossorial lifestyle (see below).

The PCA and DAPC for the discrete, meristic characters (scale counts) do not coincide as well with the molecular analyses as the mensural data in that *T. perhentianensis* clusters between the semi-fossorial species *T. jaripendek* sp. nov. and *T. kakikecil* sp. nov. (Fig. 3). PC1 and PC2 account for 76% of the total variation and load most heavily for the number of subdigital lamellae on the third finger (3FL), fourth toe (4TL) and paravertebral scales (PV) along PC1 (60% of the total variation) and for MB along PC2 (16% of the total variation; Table 4). The boxplots for 3TL and MB show that *T. jaripendek* sp. nov. and *T. kakikecil* sp. nov. along with *T. perhentianensis* have fewer lamellae (=shorter third toes) than all other species and that *T. jaripendek* sp. nov. and *T. kakikecil* sp. nov. have fewer MB than all other species (Fig. 5). These results are further characterized in the DAPC (Fig. 3). Shorter digits are commonly correlated with a fossorial lifestyle (see below).

The concatenated PCA and DAPC analyses are the preferred analyses in that they performed best overall with respect to the molecular analyses in that there was unequivocal separation between the semi-fossorial and fossorial species as well as clear separation among other combinations of the leaf-litter generalist species (Fig. 6). More precisely, the PCA analysis demonstrates that the upland clade of *Tyrrhoscincus* is composed of two non-overlapping, distinctive, ecomorphological lineages along PC1 that are referred to here as the semi-fossorial and the leaf-litter generalist lineages (Fig. 1). PC1 accounts for 44% of the total variation and loads most heavily for characters related to a reduction in limb length and number of digital lamellae (FL, HDL, 3FL and 4TL; Figs 4, 5; Table 5) – characters commonly correlated with a fossorial lifestyle. Ordination of PC1 and PC2 show complete separation of the semi-fossorial species *T. jaripendek* sp. nov. and *T. kakikecil* sp. nov., the leaf-litter generalists *T. perhentianensis* and *T. ishaki* from each other and all other species. The leaf-litter generalists *T. temengorensis* clusters separately from all other species except *T. butleri*. The limbs of *T. jaripendek*

Table 3. Summary statistics and principal component scores for scaled ratiometric characters

	PC1	PC2	PC3	PC4	PC5
SD	1.606044	1.270911	0.670349	0.549558	0.232432
Proportion of variance	0.515880	0.323040	0.089870	0.060400	0.010800
Cumulative proportion of variance	0.515880	0.838920	0.928790	0.989200	1.000000
Eigenvalues	2.579378	1.615215	0.449368	0.302014	0.054025
AXG	-0.518408	-0.214519	0.507062	0.615025	0.223311
TD	-0.163549	-0.656511	-0.706972	0.179008	0.101942
HL	-0.451126	-0.413177	0.289974	-0.730316	-0.091236
FL	-0.541198	0.335782	-0.256324	0.131888	-0.715024
HDL	-0.456174	0.489398	-0.305438	-0.197345	0.648195

AXG, axilla–groin length; FL, forelimb length; HDL, hind limb length; HL, head length; TD, tympanum diameter.

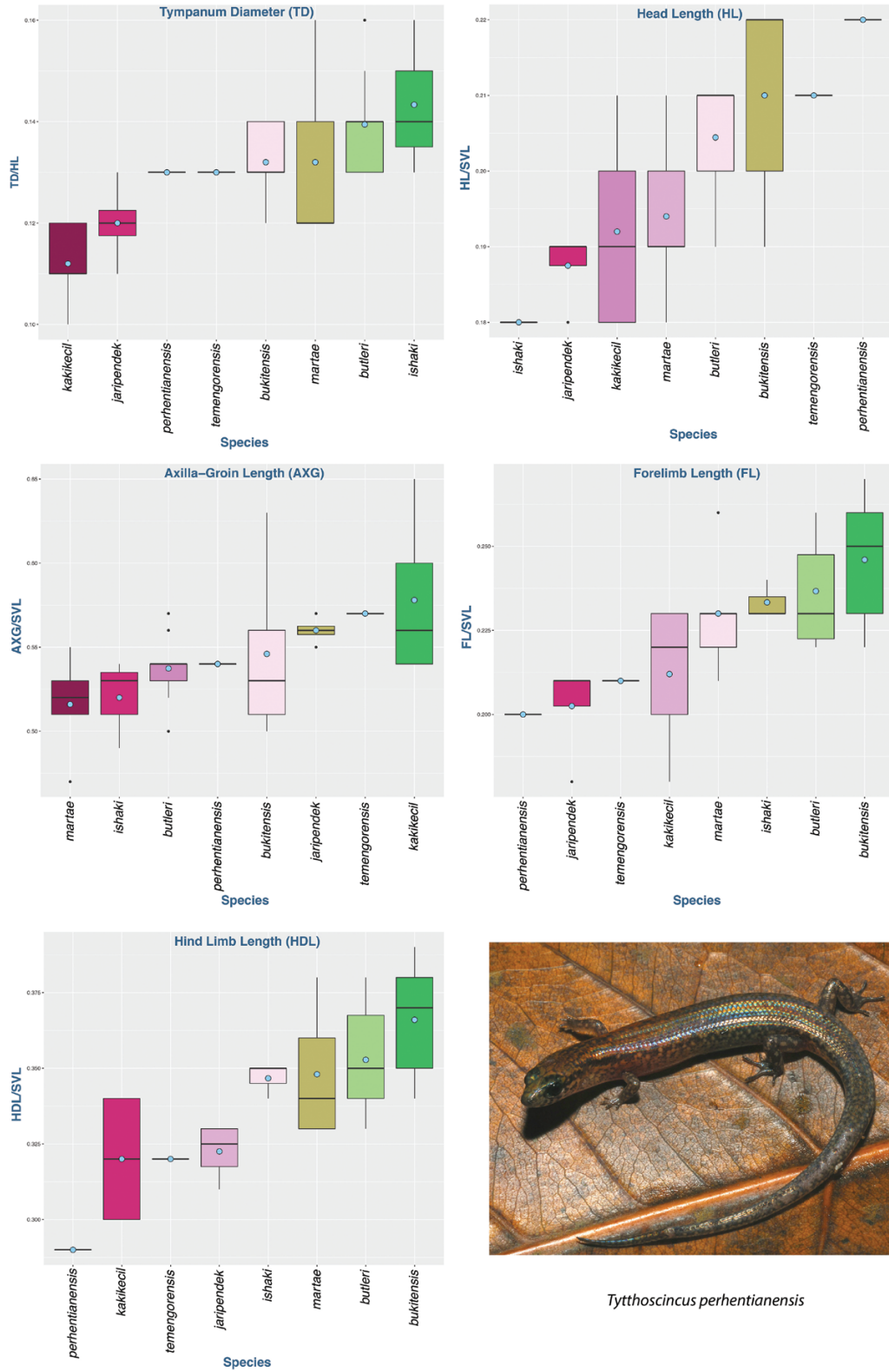


Figure 4. Boxplots of the ratiometric data.

Table 4. Summary statistics and principal component scores for meristic characters

	PC1	PC2	PC3	PC4	PC5
SD	1.734939	0.906664	0.789836	0.588183	0.445139
Proportion of variance	0.602	0.16441	0.12477	0.06919	0.03963
Cumulative proportion of variance	0.602	0.76641	0.89118	0.96037	1
Eigenvalues	3.010012	0.822039	0.623841	0.345959	0.198149
MB	-0.388991	0.634759	-0.463629	0.476040	-0.064813
PV	-0.443814	-0.567318	0.093480	0.542347	0.422256
VS	-0.391034	0.340741	0.838640	0.020419	-0.165086
3FL	-0.504837	0.118398	-0.165947	-0.661859	0.515292
4TL	-0.493909	-0.380930	-0.213200	-0.201920	-0.724375

FL, forelimb length; MB, midbody scale rows; PV, paravertebral scale rows; TL, toe subdigital lamellae; VS, ventral scale rows.

sp. nov. and *T. kakikecil* sp. nov. are also much less robust than those of the other species and they have extremely reduced, shallow, pigmented tympanae (Fig. 7). Varying combinations of *T. bukitensis*, *T. butleri*, *T. martae* sp. nov. and *T. temengorensis* overlap along PC1 and/or PC2.

The PC2 accounts for an additional 19% of the total variation (Fig. 6) and loads heavily for reduced tympanae (TD), shortened head (HL) and a longer trunk (AXG; Figs 4, 5; Table 5) – characters commonly correlated with a fossorial lifestyle. The PC3 accounts for an additional 10% of the total variation and loads heavily for ventral scales (VS; Table 5). The first eight PCs had eigenvalues ranging from 0.17 to 4.44 and accounted for 98% of the total variance (Table 5) and the first three of these were retained for the DAPC analysis. The DAPC analysis also shows exclusive clustering among the semi-fossorial species *T. jaripendek* sp. nov. and *T. kakikecil* sp. nov., the leaf-litter generalists *T. perhentianensis* and *T. ishaki*, as well as broad overlap among *T. butleri*, *T. bukitensis*, *T. martae* sp. nov. and *T. temengorensis* (Fig. 6).

The morphological analyses support the molecular analyses further in the specific recognition of the newly discovered populations from Cameron Highlands (*T. jaripendek* sp. nov.) and its sister species from Fraser's Hill and Genting Highlands (*T. kakikecil* sp. nov.) being that each of them is discretely and statistically diagnosable from each other and all other species of *Tytthoscincus* in the montane clade (Tables 6, 7; Fig. 2). Additionally, they have a 4.0% uncorrected pairwise sequence divergence between them. The other new species from Fraser's Hill and Genting Highlands (*T. martae* sp. nov.) is statistically diagnosable from most species in the montane clade and clusters separately from them in the concatenated PCA and DAPC. It is statistically separated from *T. butleri*, *T. ishaki* and *T. perhentianensis* but not *T. temengorensis* and *T. bukitensis* although it does cluster separately from *T. temengorensis* in the PCA and DAPC (Table 5; Fig. 6). The phylogenetic analysis indicates that considering *T. bukitensis* and *T. martae* sp. nov. conspecific would render the former paraphyletic (Fig. 2).

TAXONOMY

The molecular phylogeny combined with the morphological data indicate that the sister lineages *T. jaripendek* sp. nov. from Cameron Highlands and *T. kakikecil* sp. nov. from Cameron Highlands, Fraser's Hill and Genting Highlands warrant species recognition. The molecular phylogeny also suggests that *T. martae* sp. nov., from Fraser's Hill and Genting Highlands, also warrants species recognition even though its morphological separation from *T. bukitensis* is less clear (see below).

ORDER SQUAMATA OPPEL, 1811

FAMILY SCINCIDAE GRAY, 1825

GENUS *TYTTHOSCINCUS* LINKEM,
DIESMOS & BROWN, 2011

TYTTHOSCINCUS JARIPENDEK SP. NOV.

CAMERON HIGHLANDS FOREST SKINK

MENGGARUNG HUTAN CAMERON HIGHLANDS

(FIG. 8; TABLE 8)

Tytthoscincus sp. Grismer *et al.* 2016a: 236.

Holotype: Adult male (LSUHC 11680) collected at Robinson's Falls, Cameron Highlands, Pahang, Peninsular Malaysia (N 04°27.959', E 101°23.129'; 1411 m in elevation) by Evan S. H. Quah and L. Lee Grismer on 26 April 2014.

Paratypes: LSUHC 11679, 11681 and 11987 all bear the same collection data as the holotype except the latter was collected on 4 September 2014.

Diagnosis: *Tytthoscincus jaripendek* sp. nov. can be differentiated from all other species of *Tytthoscincus* in the montane clade by having the combination of 8'1 superciliaries; a shallow, pigmented tympanic depression; no enlarged pectoral scales; 28–30 midbody

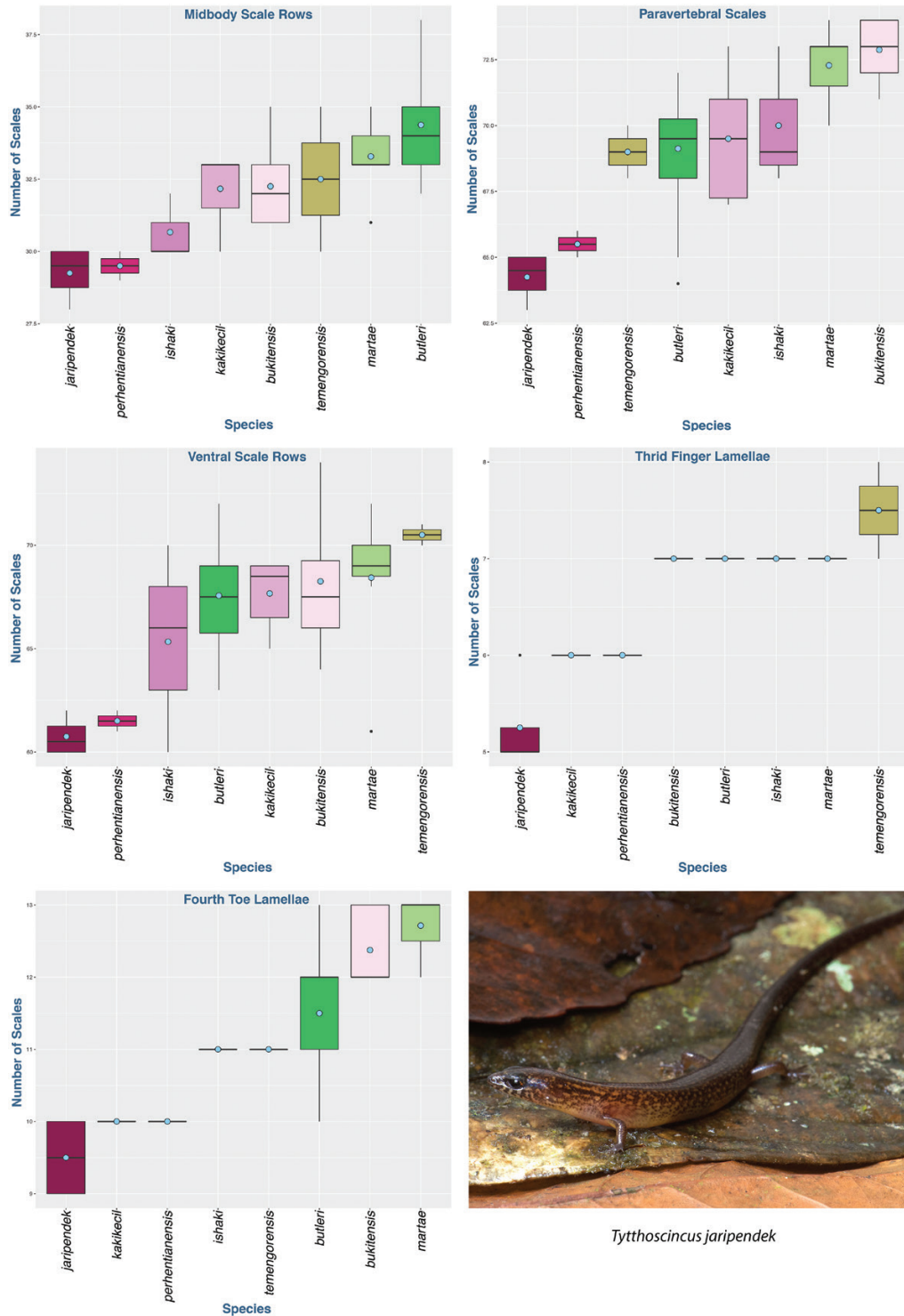
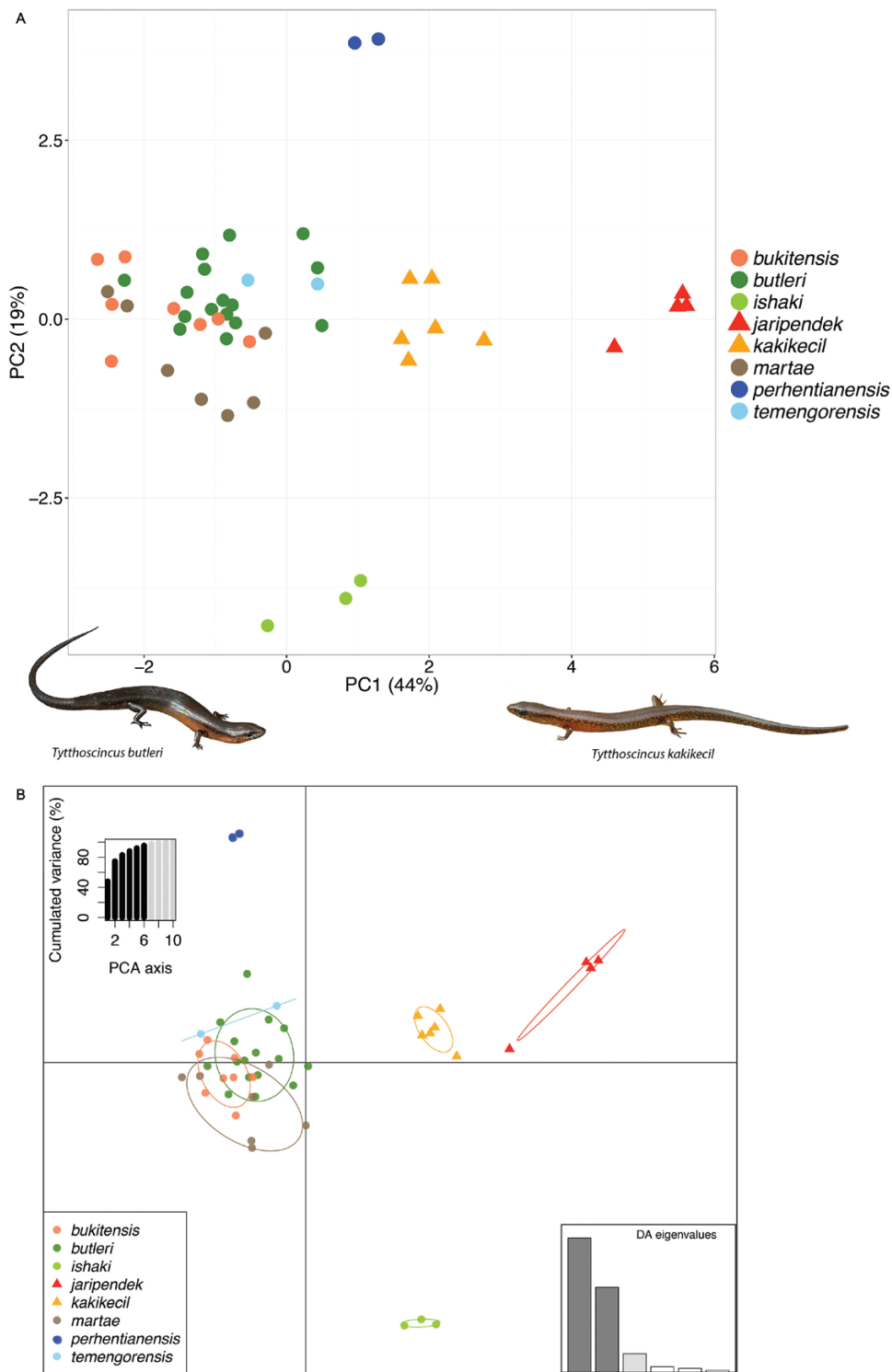


Figure 5. Boxplots of the scale count data.

scales (MB); 63–65 paravertebral scales; 60–62 ventral scales; keeled, subdigital lamellae; five or six subdigital lamellae on the third finger; nine or ten subdigital lamellae on the fourth toe; TD/HL = 0.11–0.13; HDL/SVL = 0.18–0.19; AXG/SVL = 0.55–0.57; FL/SVL =

0.18–0.21; HDL/SVL = 0.31–0.33 and a maximum SVL of 33.9 mm (Table 6). All non-ratiometric characters are presented in all other *Tyttoscincus* and species of *Sphenomorphus* suspected of being *Tyttoscincus* in Grismer *et al.* (2016a: 237) and Karin *et al.* (2016: 416).



Downloaded from https://academic.oup.com/zoolinmean/article/183/3/635/4349658 by guest on 25 April 2024

Figure 6. A, concatenated principle component analysis (PCA) of the montane clade of *Tyttoscincus* showing separation of the semi-fossorial species (triangles) and the leaf-litter generalists (circles) along axis PC1. B, concatenated discriminant function of principle component analysis (DAPC) emphasizing interspecific variation and complete separation of the semi-fossorial species from one another and the leaf-litter generalists.

Table 5. Summary statistics and principal component scores for meristic and scaled ratio-metric variables

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
SD	2.107388	1.395620	1.014235	0.888918	0.783016	0.719016	0.565513	0.411946	0.349538	0.225295
Proportion of variance	0.444110	0.194780	0.102870	0.079020	0.061310	0.051700	0.031960	0.016970	0.012220	0.005080
Cumulative proportion of variance	0.444110	0.638880	0.741750	0.820770	0.882080	0.933780	0.965740	0.982710	0.994920	1.000000
Eigenvalues	4.441085	1.947756	1.028673	0.790175	0.613114	0.516984	0.319579	0.169699	0.122177	0.050758
MB	-0.303549	0.035739	-0.343574	0.549427	-0.487490	-0.325005	0.173186	-0.318962	0.090920	-0.058284
PV	-0.321171	-0.214824	-0.172704	-0.604050	0.086622	-0.391133	0.210385	-0.307255	-0.395894	0.010386
VS	-0.261003	-0.081636	-0.641692	0.074810	0.440500	0.471684	-0.221627	-0.187923	0.079655	-0.023302
3TL	-0.413132	-0.140872	-0.019955	0.136672	-0.139177	0.311290	0.363137	0.612392	-0.408808	-0.010529
4FL	-0.384368	-0.132103	-0.020961	-0.433226	-0.382836	0.060766	-0.181724	0.224593	0.640385	0.053585
TD	0.055018	0.575580	-0.391448	-0.097530	0.266474	-0.399060	0.203116	0.440121	0.179600	-0.073900
HL	-0.187674	0.574420	-0.000883	-0.114987	-0.307726	0.094936	-0.573638	-0.028975	-0.424818	0.086714
AXG	-0.241444	0.482122	0.308350	-0.122662	0.053034	0.376710	0.480371	-0.372963	0.164776	-0.239593
FL	-0.406735	0.079774	0.299189	0.219141	0.358316	-0.177021	-0.020664	-0.028813	0.105362	0.720126
HDL	-0.395209	-0.092507	0.318901	0.188388	0.313002	-0.277125	-0.332015	0.092727	0.021455	-0.635613

AXG, axilla-groin length; FL, forelimb length; HL, head length; HDL, hind limb length; MB, midbody scale rows; PV, paravertebral scale rows; TD, tympanum diameter; TL, toe subdigital lamellae; VS, ventral scale rows.

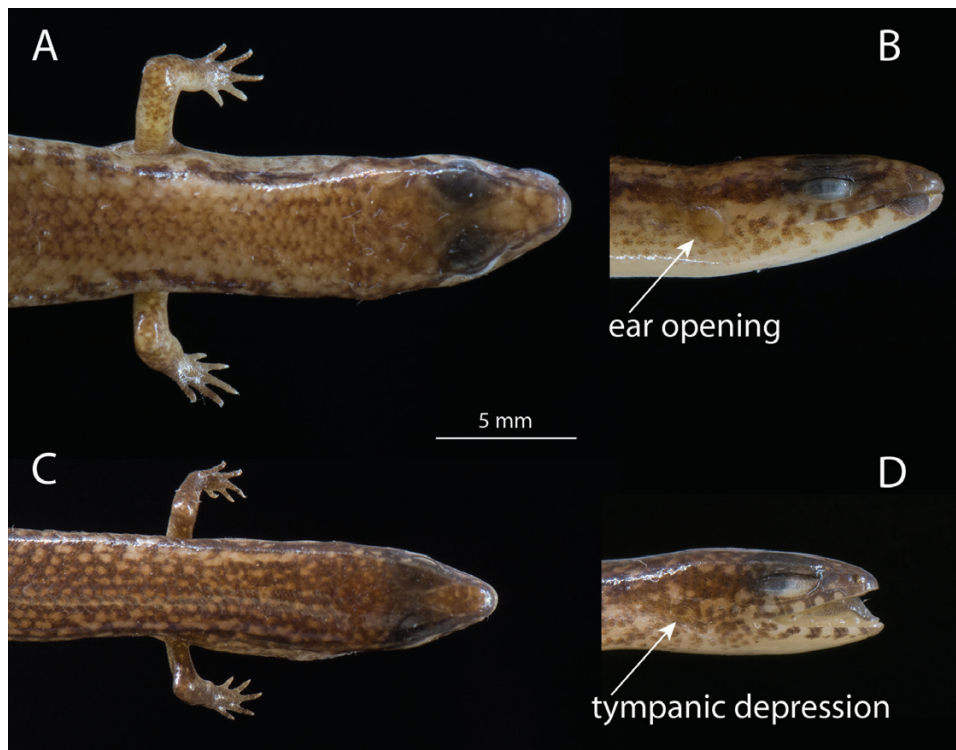


Figure 7. A, B, dorsal and lateral views of the anterior portion of the body and head, respectively, of the leaf-litter generalist *Tytthoscincus butleri* (LSUHC 9204) showing its more robust forelimbs and deeply set, well-developed tympanum. C, D, dorsal and lateral views of the anterior portion of the body and head, respectively, of the semi-fossorial *Tytthoscincus kakikecil* sp. nov. (LSUHC 11769) showing its more gracile forelimbs and shallow, poorly developed tympanic depression.

Description of holotype: Adult male, SVL 32.2 mm; tail length 38.0 mm; AXG 18.4 mm; HL 6.1 mm; head width 3.7 mm; snout to anterior margin of foreleg 11.2 mm; rostral wider than long, in broad contact with frontonasal; frontonasal wider than long; prefrontals large, broadly contacting on midline; frontal elongate, diamond-shaped, in contact with first two supraoculars; four supraoculars; frontoparietals in contact posterior to frontal, contacting second, third and fourth supraoculars anterolaterally and parietals and interparietal posteriorly; interparietal diamond-shaped, large, slightly projecting posteriorly, eyespot in posterior projection; parietals large, in medial contact posterior to interparietal, contacting fourth supraocular anteriorly; enlarged nuchal scales absent; nasals small, widely separated, trapezoidal, contacting rostral anteriorly, frontonasal dorsally, first loreal posteriorly, first supralabial ventrally; nostril in centre of nasal; supranasals absent; two loreals, posterior loreal taller than wide; upper and lower preocular present; lower preocular followed by a series of suboculars; eight superciliaries, posterior superciliary elongate and projecting dorsomedially; six supralabials, third, fourth and fifth below eye; two postsupralabials; two primary temporals; three secondary

temporals, uppermost not contacting parietals; lower eyelid transparent, scaly, no enlarged central window; mental twice as wide as long; single, large postmental, contacting first infralabial on each side; two enlarged pairs of chinshields posterior to postmental, anterior pair contacting medially, posterior pair widely separated posteriorly by a single scale; anterior and posterior chinshield pairs contacting first, second and third infralabials; five infralabials; external ear opening 0.8 mm wide, approximately one-half diameter of eyeball, subcircular, lacking anterior lobules; and tympanum very shallow, pigmented.

Body scales smooth, cycloid, imbricate; ventral scales slightly larger than dorsal scales; 28 longitudinal scale rows around midbody; 65 paravertebral scales (PV); 60 ventral scales (VS); slightly enlarged median preloacal scales overlapping outer preloacal scales; tail slightly compressed laterally; subcaudals slightly larger than dorsal caudals; limbs very thin, short (FL/SVL = 0.21; HDL/SVL = 0.33), widely separated when adpressed; scales of dorsal surface slightly larger than those of ventral surface; palmar and plantar scales slightly raised; and digits short, scales of dorsal surfaces in a single row, subdigital lamellae bicarinate, five on third finger, ten on fourth toe.

Table 6. Scale counts, summary statistics and morphometric ratios of selected characters of the montane clade of *Tyttthoscincus* from Peninsular Malaysia

	<i>butleri</i>	<i>bukitensis</i>	<i>jaripendek</i> sp. nov.	<i>temengorensis</i>	<i>perhentianensis</i>	<i>ishaki</i>	<i>kakikecil</i> sp. nov.	<i>martae</i> sp. nov.	<i>cophias</i>
Supralabials	6	6	6	6	6	6	6	6	6
Infralabials	5, 6	5	5	5, 6	5, 6	5, 6	5, 6	5, 6	6
Superciliaries	9.1	8.1, 9.1, 9.2, 10.2	8.1	9.1	9.1	8.1, 9.1, 9.2	8.1, 9.1, 10.2	8.1, 9.1, 10.2	8.1
Loreals	1, 2	2	1, 2	2	2	1, 2	2	2	2
Tympanum	DWD	DWD	SPD	DWD	DWD	DWD	DWD	DWD	SPD
Pectoral scales	Yes (10), no (11)	Yes (9), no (1)	No	Yes	Yes	No	Yes	Yes	Yes
enlarged									
Lamellae texture	Keeled	Keeled	Keeled	Smooth	Smooth	Keeled	Keeled	Keeled	Keeled
Midbody scales	32–38	31–35	28–30	29, 30	29, 30	30–32	31–35	31–35	23
Mean	34.2	32.5	29.3	29.5	29.5	30.7	33.3	33.3	23.0
SD	±1.8	±1.3	±1.0	±0.7	±0.7	±1.1	±1.3	±1.3	±0.0
<i>n</i>	20	8	4	2	2	3	7	7	1
Paravertebral scales	60–75	71–74	63–65	65, 66	65, 66	68–73	70–74	70–74	56
Mean	68.9	72.9	64.3	65.5	65.5	70.0	72.3	72.3	56.0
SD	±3.4	±1.2	±1.0	±0.7	±0.7	±2.6	±2.2	±1.4	±0.0
<i>n</i>	20	8	4	2	2	3	7	7	1
Ventral scales	62–73	64–74	60–62	61, 62	61, 62	60–70	61–72	61–72	56
Mean	67.6	68.3	60.6	61.5	61.5	65.3	68.4	68.4	56.0
SD	±3.1	±3.5	±1.0	±0.7	±0.7	±5.0	±3.5	±3.5	±0.0
<i>n</i>	20	8	4	2	2	3	7	7	1
3rd finger lamellae	6–8	7	5 or 6	7, 8	6	7	7	7	5
Mean	7	7	5.1	7.5	6	7.0	7	7	5.0
SD	±0.4	±0.0	±0.5	±0.7	±0.0	±0.0	±0.0	±0.0	±0.0
<i>n</i>	20	8	4	2	1	3	7	7	1
4th toe lamellae	10–13	12 or 13	9 or 10	11	10	11	12 or 13	12 or 13	10
Mean	11.6	12.4	9.5	11	10	11.0	12.7	12.7	10.0
SD	±0.8	±0.5	±0.6	±0.0	±0.0	±0.0	±0.5	±0.5	±0.0
<i>n</i>	20	8	4	1	1	3	7	7	1
TD/HL	0.13–0.16	0.12–0.16	0.11–0.13	0.13	0.13–0.14	0.13–0.16	0.12–0.16	0.12–0.16	0.15
Mean	0.14	0.14	0.12	0.13	0.14	0.14	0.13	0.13	0.15
SD	±0.01	±0.01	±0.01	±0.0	±0.01	±0.2	±0.01	±0.02	±0.0
<i>n</i>	18	8	4	2	2	3	7	7	1
HL/SVL	0.19–0.21	0.19–0.24	0.18–0.19	0.21–0.23	0.22–0.23	0.18	0.18–0.21	0.18–0.26	0.15
Mean	0.20	0.22	0.19	0.22	0.23	0.18	0.19	0.21	0.15
SD	±0.01	±0.02	±0.01	±0.1	±0.1	±0.0	±0.01	±0.03	±0.0
<i>n</i>	18	8	4	2	2	3	6	7	1

Table 6. Continued

	<i>butleri</i>	<i>bukitensis</i>	<i>jaripendek</i> sp. nov.	<i>temengorensis</i>	<i>perhentianensis</i>	<i>ishaki</i>	<i>kakikecil</i> sp. nov.	<i>martae</i> sp. nov.	<i>cophias</i>
AXG/SVL	0.50–0.57	0.48–0.63	0.55–0.57	0.50–0.57	0.54–0.55	0.49–0.54	0.52–0.65	0.47–0.55	0.58
Mean	0.54	0.53	0.56	0.54	0.55	0.52	0.57	0.51	0.58
SD	±0.02	±0.05	±0.01	±0.5	±0.1	±0.03	±0.05	±0.03	±0.0
<i>n</i>	16	8	4	2	2	3	6	7	1
FL/SVL	0.22–0.28	0.22–0.27	0.18–0.21	0.21–0.22	0.20–0.21	0.23–0.24	0.18–0.23	0.21–0.26	0.17
Mean	0.24	0.25	0.20	0.22	0.21	0.23	0.21	0.24	0.17
SD	±0.02	±0.02	±0.02	±0.01	±0.1	±0.01	±0.02	±0.02	±0.0
<i>n</i>	18	8	4	2	2	3	6	7	1
HDL/SVL	0.33–0.40	0.34–0.40	0.31–0.33	0.32–0.38	0.29–0.30	0.34–0.35	0.30–0.34	0.33–0.38	0.28
Mean	0.36	0.37	0.32	0.35	0.30	0.35	0.32	0.35	0.28
SD	±0.02	±0.02	±0.01	±0.0	±0.1	±0.01	±0.02	±0.02	±0.0
<i>n</i>	18	8	4	2	2	3	6	7	1
Maximum SVL	40.9	42.6	33.9	35.5	30.0	41.0	36.2	44.0	35.9

All measurements are in millimetres; paired values indicate counts taken on the right and left sides, respectively. AXG, axilla–groin length; HDL, hind limb length; HL, head length; *n*, sample size; SFD, tympanum shallow, poorly developed to nearly absent and pigmented; SVL, snout–vent length; TD, tympanum diameter.

Coloration: Overall dorsal ground colour of head, body, limbs and tail dark brown; head speckled with light-coloured markings; labials distinctly banded; anterior of flanks to posterior margin of jaws dull-orange bearing irregularly shaped, dark speckles and elongate markings; dorsum, posterior portion of flanks and tail bearing small, light-coloured spots; limbs faintly mottled; ventral surfaces dull-yellow, immaculate; lateral margin of gular region stippled with dark brown; and palmar and plantar surfaces, subtibial, subforearm and subcaudal regions heavily stippled with dark brown.

Variation: The paratypes closely approach the holotype in all aspects of coloration except for LSUHC 11987 which has considerably more gular stippling and is darker dorsally overall. Meristic variation is presented in Table 8.

Distribution: *Tytthoscincus jaripendek* sp. nov. is known only from the type locality at Robinson's Falls, Cameron Highlands, Pahang, Peninsular Malaysia (Fig. 9) but is likely to range more widely across the Cameron Highlands plateau.

Natural history: *Tytthoscincus jaripendek* sp. nov. inhabits leaf-litter in hill dipterocarp forests at 1411 m in elevation (Fig. 10). All specimens were collected by raking leaves that had accumulated at the foot of an earthen bank. Specimens were collected both day and night and during periods of heavy rain.

Etymology: The specific epithet *jaripendek* is derived from the Malay words *jari* meaning finger and *pendek* meaning short and refers to this species' short digits as indicated by its low numbers of subdigital lamellae.

Comparisons: *Tytthoscincus jaripendek* sp. nov. can be differentiated from all other species of *Tytthoscincus* of the montane clade (Table 6), except its sister species *T. kakikecil* sp. nov., by having a shallow, pigmented tympanic depression vs. a well-developed, deeply recessed, non-pigmented tympanum. From *T. kakikecil* sp. nov., it differs discretely and statistically by having 63–65 vs. 67–73 paravertebral scales, 60–62 vs. 65–69 ventral scales (Tables 6, 7), and statistically significant differences in the mean number of paravertebral scales, ventral scales, 3TL and FL/SVL (Tables 6, 7). From all other species except *T. perhentianensis*, it differs further in having fewer midbody scales (28–30 vs. 30–38 collectively). *Tytthoscincus jaripendek* sp. nov. also bears statistically significant mean differences of all ten characters in varying combinations across all other species (Table 7). Meristic and body shape trends of these characters among species in the montane clade are presented in Figures 4 and 5.

Table 7. Matrix of species pairs having significantly different ($P < 0.05$) mean values of varying combinations of meristic and scaled ratiometric characters based on a Tukey HSD test

	<i>bukitensis</i>	<i>butleri</i>	<i>ishaki</i>	<i>jaripendek</i>	<i>kakikecil</i>	<i>martae</i>	<i>perhentianensis temengorensis</i>
<i>bukitensis</i>	*						
<i>butleri</i>	MB, PV	*					
<i>ishaki</i>	AXG, TD, HL	AXG, VMB, TD, HL	*				
<i>jaripendek</i>	MB, PV, VS, 3TL, 4TL, AXG, HL, FL, HDL	MB, PV, VS, 3TL, 4TL, AXG, HL, FL, HDL	PV, 3TL, TD, HL, FL, HDL	*			
<i>kakikecil</i>	PV, 3TL, 4TL, AXG, HL, FL, HDL	3TL, 4TL, AXG, HL, FL, HDL	TD, HL, HDL	PV, VS, 3TL, FL	*		
<i>martae</i>		PV, 4TL	4TL, TD, AXG, HL, FL	MB, PV, VS, 3TL, 4TL, AXG, FL, HDL	3TL, 4TL, TD, HL, HDL	*	
<i>perhentianensis</i>	AXG, PV, 3TL, HL	MB, 3TL, 4TL, AXG	AXG, TD, HL	3TL, AXG, HL, FL, HDL	AXG, HL	PV, 3TL, 4TL, AXG, TD	*
<i>temengorensis</i>	3TL, HDL	3TL	AXG, TD, HL	VS, 3TL, AXG	3TL, AXG	3TL, HL, AXG	*

AXG, axilla-groin length; FL, forelimb length; HDL, hind limb length; HL, head length; MB, midbody scale rows; PV, paravertebral scale rows; TD, tympanum diameter; TL, toe subdigital lamellae; VS, ventral scale rows.

TYTTTHOSCINCUS KAKIKECIL SP. NOV.

FRASER'S HILL FOREST SKINK

MENGKARUNG HUTAN BUKIT FRASER

(FIG. 11; TABLE 9)

Holotype: Adult male (LSUHC 11769) collected along Richmond Road, Frasers's Hill, Pahang, Peninsular Malaysia (N 03°42.590', E 101°44.236'; 1271 m in elevation) by Evan S. H. Quah on 27 September 2013.

Paratypes: LSUHC 11770 and 11772 collected on the Telecom Loop Road, Fraser's Hill, Pahang, Peninsular Malaysia (N 03°43.112', E 101°45.158'; 1305 m in elevation) by Evan S. H. Quah and L. Lee Grismer on 27 September 2013. LSUHC 12754 collected at Ulu Kali, Genting Highlands, Pahang, Peninsular Malaysia (N 03°25.759', E 101°47.328'; 1670 m in elevation) by Evan S. H. Quah and L. Lee Grismer on 22 June 2016.

Additional specimens examined: FMNH 19945 from Ulu Kali, Genting Highlands and ZRC 2.5944 from Telom Valley, Cameron Highlands, Pahang, Peninsular Malaysia.

Diagnosis: *Tytthoscincus kakikecil* sp. nov. can be differentiated from all other species of *Tytthoscincus* in the montane clade by having the combination of 8 1, 9 1 or 9 2 superciliaries; a shallow, pigmented tympanic depression; enlarged pectoral scales; 30–33 midbody scales; 67–73 paravertebral scales; 65–69 ventral scales; keeled, subdigital lamellae; six subdigital lamellae on the third finger; ten subdigital lamellae on the fourth toe; TD/HL = 0.10–0.12; HL/SVL = 0.18–0.21; AXG/SVL = 0.52–0.65; FL/SVL = 0.18–0.23; HDL/SVL = 0.30–0.34; and a maximum SVL of 36.2 mm (Table 6). All non-ratiometric characters are scored across all other *Tytthoscincus* and species of *Sphenomorphus* suspected of being *Tytthoscincus* in Grismer *et al.* (2016a: 237) and Karin *et al.* (2016: 416).

Description of holotype: Adult male, SVL 30.8 mm; original tail 33.9 mm; AXG 19.9 mm; HL 6.2 mm; head width 3.4 mm; snout to anterior margin of foreleg 10.6 mm; rostral wider than long, in broad contact with frontonasal; frontonasal wider than long; prefrontals large, in broad contact on midline; frontal elongate, diamond-shaped, in contact with first two supraoculars; four supraoculars; frontoparietals in contact posterior to frontal, contacting second, third and fourth supraoculars anterolaterally and parietals and interparietal posteriorly; frontoparietals non-overlapping; interparietal diamond-shaped, large, slightly projecting posteriorly, eyespot in posterior projection; parietals large, in medial contact posterior to interparietal, contacting fourth supraocular anteriorly; enlarged nuchal scales absent; nasals small, widely separated, trapezoidal, contacting rostral anteriorly, frontonasal dorsally, first loreal posteriorly, first supralabial



Figure 8. Holotype of *Tytthoscincus jaripendek* sp. nov. (LSUHC 11680) from Robinson Falls, Cameron Highlands, Pahang, Peninsular Malaysia.

ventrally; nostril in centre of nasal; supranasals absent; two loreals taller than wide, posterior loreal smallest; upper and lower preocular present; lower preocular followed by a series of suboculars; nine superciliaries, posterior superciliary elongate and projecting dorsomedially; six supralabials, third, fourth and fifth below eye; two postsupralabials; three primary temporals; three secondary temporals, uppermost not contacting parietals; lower eyelid transparent, scaly, no enlarged central window; mental twice as wide as long; single, large postmental, contacting first infralabial on each side; two enlarged pairs of chin shields posterior to postmental, anterior pair contacting medially, posterior pair widely separated posteriorly by a single scale; anterior and posterior chinshield pairs contacting first, second and third infralabials; five infralabials; external ear opening 0.6 mm less than one-half diameter of eye, subcircular, lacking anterior lobules; tympanum very shallow, pigmented.

Body scales smooth, cycloid, imbricate; ventral scales slightly larger than dorsal scales; 33 longitudinal scale rows around midbody; 73 paravertebral scales; 65 ventral scales; slightly enlarged preloacal scales; tail slightly compressed laterally; subcaudals same size as dorsal caudals; limbs very thin, short (FL/SVL = 0.22; HDL/SVL = 0.32), widely separated when adpressed; scales of dorsal surface slightly larger than those of ventral surface; palmar and plantar scales slightly raised; and digits short, scales of dorsal surfaces in a single row, subdigital lamellae bicarinate, ten on fourth toe; six on third finger.

Coloration: Overall dorsal ground colour of head, body, limbs and tail brown; head speckled with light-coloured markings; labials bearing light centres; dorsum, posterior portion of flanks and tail bearing small, light-coloured spots; limbs mottled; anterior of flanks to posterior margin of jaws dull-orange bearing irregularly shaped speckles and elongate markings; all ventral surfaces dull-yellow, immaculate; lateral margin of gular region stippled with dark brown; and palmar and plantar surfaces, subtibial, subforearm and subcaudal regions heavily stippled with dark brown.

Variation: The paratypes closely approach the holotype in all aspects of coloration except LSUHC 12754 is considerably darker in overall in dorsal coloration (Fig. 11). Meristic variation is presented in Table 9.

Distribution: *Tytthoscincus kakikecil* sp. nov. is known from the town of Fraser's Hill at Richmond Road and the Telecom Loop and from the upper elevations of Genting Highlands at Ulu Kali, Pahang, Peninsular Malaysia (Fig. 9).

Natural history: *Tytthoscincus kakikecil* sp. nov. inhabits leaf-litter in hill dipterocarp and mossy forests from at least 1305–1670 m in elevation (Fig. 12). All specimens at Fraser's Hill were collected by raking leaves that had accumulated on earthen banks along the road or by turning rocks and logs buried in leaf-litter. LSUHC 12754 from Genting Highlands was found abroad at night in a dirt parking lot next to a rubbish

Table 8. Meristic and ratiometric characters of the type series of *Tytthoscincus jaripendek* sp. nov.

	LSUHC 11679	LSUHC 11680	LSUHC 11681	LSUHC 11987
	Paratype	Holotype	Paratype	Paratype
Supralabials	6	6	6	6
Infralabials	5	5	5	5
Supraoculars	4	4	4	4
Frontoparietal contacting supraoculars 2, 3 and 4	Yes	Yes	Yes	Yes
Superciliaries	8`1	8`1	8`1	8`1
Prefrontals in contact	Yes	Yes	Yes	No
Loreals	1	2	1	1
Tympanum shallow, pigmented	Yes	Yes	Yes	Yes
Midbody scale rows	29	28	30	30
Dorsal scales striated	No	No	Weakly	No
Paravertebral scale rows	64	65	65	63
Ventral scale rows	61	60	62	60
Enlarged pectoral scales	Yes	Yes	Yes	Yes
Enlarged precloacal scales	Yes	Yes	Yes	Yes
3rd finger lamellae	5	5	5	6
4th toe lamellae	9	10	9	10
Lamellae texture	Keeled	Keeled	Keeled	Keeled
HL	6.2	6.1	6.2	6.3
TD	0.8	0.8	0.7	0.7
TD/HL	0.12	0.13	0.12	0.11
HL/SVL	0.19	0.19	0.18	0.19
AXG	18.6	18.4	18.8	18.5
AXG/SVL	0.56	0.57	0.55	0.56
FL	6.6	6.6	6.2	7.0
FL/SVL	0.2	0.21	0.18	0.21
HDL	10.7	10.8	10.5	10.9
HDL/SVL	0.32	0.33	0.31	0.33
SVL	32.9	32.2	33.9	32.7
Sex	Male	Male	Female	Female

AXG, axilla–groin length; FL, forelimb length; HDL, hind limb length; HL, head length; SVL, snout–vent length; TD, tympanum diameter.

pile on the edge of a mossy forest that we presume to be its natural habitat (as opposed to the rubbish pile).

Etymology: The specific epithet *kakikecil* is derived from the Malay words *kaki* meaning leg or foot and *kecil* meaning small and refers to this species' diminutive limbs.

Comparisons: *Tytthoscincus kakikecil* sp. nov. can be differentiated from all other species of *Tytthoscincus* of the montane clade (Table 6), except its sister species *T. jaripendek* sp. nov., by having a shallow, pigmented tympanic depression vs. a well-developed, deeply recessed, weakly pigmented tympanum. From *T. jaripendek* sp. nov., it differs by having 67–73 vs. 63–65 paravertebral scales; 65–69 vs. 60–62 ventral scales; having as opposed to lacking enlarged pectoral scales; and having statistically significant differences in the mean number of PV, VS, 3TL and FL/SVL (Tables 6, 7).

Tytthoscincus kakikecil sp. nov. also bears statistically significant mean differences of all ten characters in varying combinations across all other species (Table 6). Meristic and body shape trends of these characters among species in the montane clade are presented in Figures 4 and 5.

Remarks: *Tytthoscincus kakikecil* sp. nov. is known from separate populations at Fraser's Hill (LSUHC 11769–70, 11772) and Ulu Kali, Genting Highlands (LSUHC 12754, FMNH 19945), ~38 km apart (Fig. 8). We were unsuccessful in obtaining DNA sequences from FMNH 19945, also from Ulu Kali. Sly (1976) considered this specimen to be *T. butleri* but provided no character evidence and Grismer (2011), who did not examine the specimen, considered it to be *T. bukitensis* based on the fact that *T. butleri* occurs in different mountain range and *T. bukitensis* occurs 38 km to the north across habitable

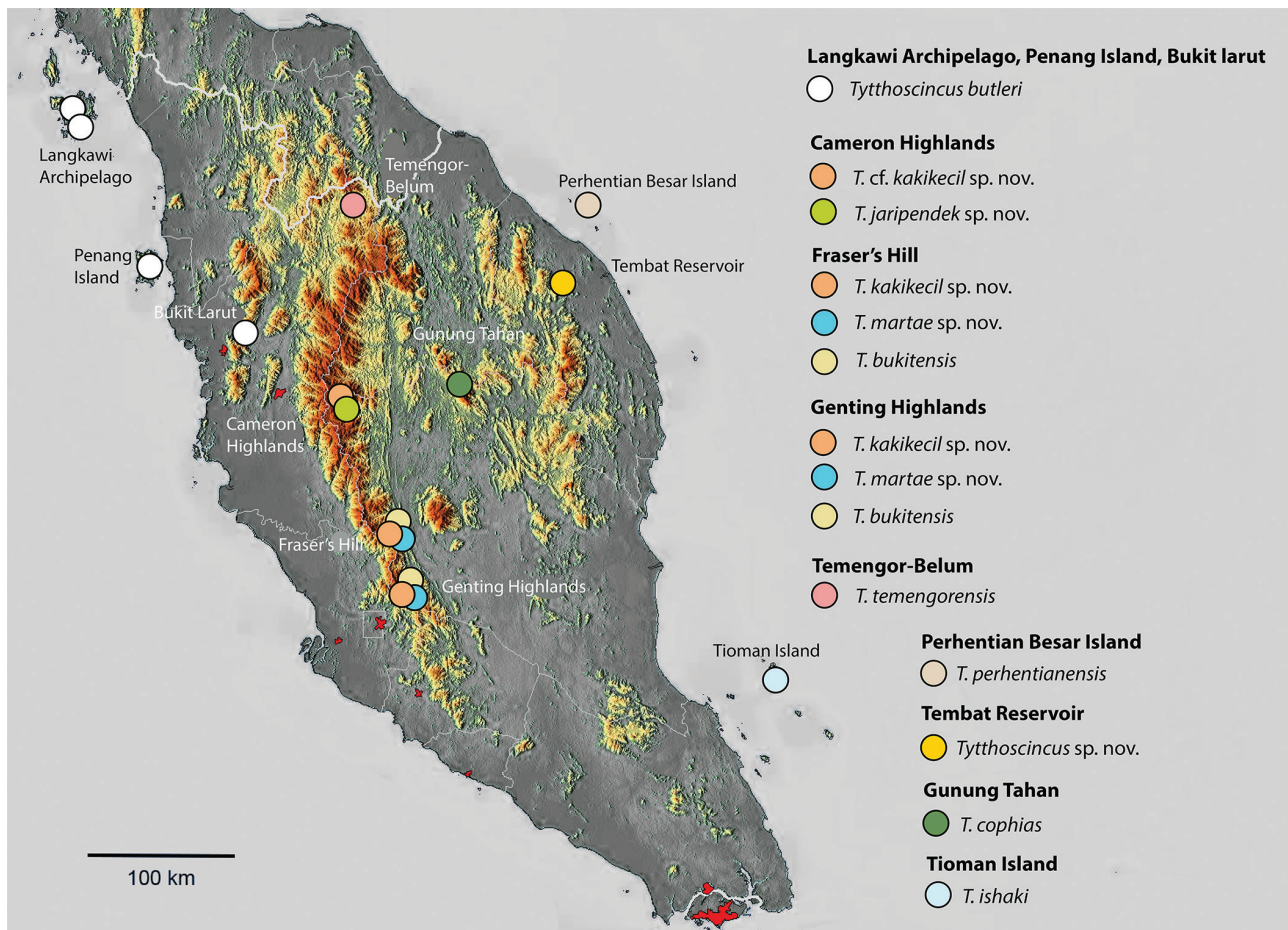


Figure 9. Distribution of the species of the montane clade of *Tytthoscincus* in Peninsular Malaysia.

terrain (multiple point measurements made from Google Earth along an elevation profile) at Fraser's Hill in the same mountain range. FMNH 19945 plotted next to a sequenced specimen of *T. kakikecil* sp. nov. from Ulu Kali (LSUHC 12754) in the PCAs and DAPCs. Furthermore, based on probability estimates generated from retained posteriors from the concatenated DAPC, FMNH 19945 clustered with *T. kakikecil* sp. nov. with a 72% probability. However, these populations (Fraser's Hill and Ulu Kali) differ discretely in their numbers of midbody scales (33 vs. 30 or 31, respectively), TD (TD/HL = 0.10–0.11 vs. 0.12, respectively), HL (HL/SVL = 0.19–0.21 vs. 0.18, respectively) and HDL (HDL/SVL = 0.30–0.32 vs. 0.34, respectively). But, based on a Welch two-sample *t*-test, only the means of the HDL/SVL ratios are significantly different ($P = 0.035$). In the absence of molecular data, it would be tempting to consider these populations as separate species regardless of their small sample sizes – an error that has been made before with species of *Tytthoscincus* (e.g. Grismer, 2007, 2008). However, the molecular data estimate these two populations have only a 1.9% sequence divergence between them and they cluster

tightly together in the concatenated PCA and DAPC (Fig. 2). This shallow divergence across ~38 km of habitable terrain is in stark contrast to the 6.2% divergence found between individuals of *T. martae* sp. nov. (LSUHC 12749, 12751) and *T. bukitensis* (LSUHC 12750) found only a few meters apart at Awana Road, Genting Highlands (see below). This suggests gene flow still exists between these populations and the morphological differences are due to small sample sizes ($n = 3$ for Fraser's Hill and $n = 2$ for Genting Highlands) and/or sampling error. We predict that data from additional specimens from both localities and the intervening regions will most probably eclipse their current morphological differences.

***TYTTHOSCINCUS MARTAE* SP. NOV.**

HINDU TEMPLE FOREST SKINK
MENGKARUNG HUTAN KUIL HINDU

(FIG. 13; TABLE 10)

Holotype: Adult male (LSUHC 12688) collected at the Hindu Temple 1.2 km south of the town of Fraser's Hill



Figure 10. Microhabitat of *Tytthoscincus jaripendek* sp. nov. at Robinson Falls, Cameron Highlands, Pahang, Peninsular Malaysia.



Figure 11. Type specimens of *Tytthoscincus kakikecil* sp. nov. from Pahang, Peninsular Malaysia. A, paratype LSUHC 12754 from Ulu Kali, Genting Highlands. B, holotype LSUHC 11769 from Richmond Road, Fraser's Hill.

on the road to the Gap, Pahang, Peninsular Malaysia (N 03°42.099', E 101°44.090'; 1078 m in elevation) by Evan S. H. Quah, Marta S. Grismer and L. Lee Grismer on 23 March 2016.

Paratypes: LSUHC 12517–18 collected on 3 December 2015 and LSUHC 12749 and 12751 collected on 21 June 2016 from the Awana Road, Genting Highlands, Pahang, Peninsular Malaysia (N 3°24.036', E 101°47.212'; 1052

Table 9. Meristic and ratiometric characters of the type series of *Tytthoscincus kakikecil* sp. nov.

	LSUHC 11769	LSUHC 11770	LSUHC 11772	LSUHC 12754	FMNH 19945	ZRC 2.5944
	Holotype	Paratype	Paratype	Paratype		
	Fraser's Hill	Fraser's Hill	Fraser's Hill	Genting Highlands	Genting Highlands	Cameron Highlands
Supralabials	6	6	6	6	6	6
Infralabials	5	5	5	5	5	5
Supraoculars	4	4	4	4	4	4
Frontoparietal contacting supraoculars 2, 3 and 4	Yes	Yes	Yes	Yes	Yes	Yes
Superciliaries	9`1	9`1	9`1	9`2	9`1	8`1
Prefrontals in contact	Yes	Yes	Yes	Yes	Yes	Yes
Loreals	2	2	2	2	2	1
Tympanum shallow, pigmented	Yes	Yes	Yes	Yes	Yes	/
Midbody scale rows	33	33	33	30	31	33
Dorsal scales striated	No	No	No	No	No	No
Paravertebral scale rows	73	69	67	71	71	68
Ventral scale rows	65	66	69	66	68	68
Enlarged pectoral scales	Yes	Yes	Yes	Yes	No	Yes
Enlarged preloacal scales	Yes	Yes	Yes	Yes	Yes	Yes
3rd finger lamellae	6	6	6	6	6	6
4th toe lamellae	10	10	10	10	10	10
Lamellae texture	Keeled	Keeled	Keeled	Keeled	Keeled	Keeled
HL	6.2	6.7	5.1	5.9	7.1	6.8
TD	0.6	0.8	0.6	0.7	0.8	0.8
TD/HL	0.10	0.11	0.11	0.12	0.12	0.11
HL/SVL	0.2	0.19	0.21	0.18	0.18	0.19
AXG	19.9	21.7	12.6	17.7	21.89	19.3
AXG/SVL	0.65	0.60	0.52	0.54	0.56	0.54
FL	6.9	7.7	5.6	7.7	7.9	6.5
FL/SVL	0.22	0.22	0.23	0.23	0.2	0.18
HDL	9.9	11.0	6.4	11.3	13.1	10.1
HDL/SVL	0.32	0.31	0.3	0.34	0.34	0.3
SVL	30.8	35.9	24.2	33.0	39.2	36.2
Sex	Male	Male	/	Male	Female	Female

(/), data unobtainable. AXG, axilla–groin length; FL, forelimb length; HDL, hind limb length; HL, head length; SVL, snout–vent length; TD, tympanum diameter.

m in elevation) by Evan S. H. Quah and L. Lee Grismer. ZRC 3.6246 is from the same locality as the holotype and was collected by L. Lee Grismer, Perry L. Wood, Jr. and Timothy M. Youmans on 26 August 2006.

Additional specimen examined: LSUHC 12072 from the Awana Road, Genting Highlands, Pahang, Peninsular Malaysia.

Diagnosis: *Tytthoscincus martae* sp. nov. can be differentiated from all other species of *Tytthoscincus* in the montane clade except *T. bukitensis* by having the combination of 8`1, 9`1 or 10`2 superciliaries; a deep, weakly pigmented tympanum; enlarged pectoral scales; 31–35

midbody scales; 70–74 paravertebral scales; 61–72 ventral scales; keeled, subdigital lamellae; seven subdigital lamellae on the third finger; 12 or 13 subdigital lamellae on the fourth toe; TD/HL = 0.12–0.16; HL/SVL = 0.18–0.26; AXG/SVL = 0.47–0.55; FL/SVL = 0.21–0.26; HDL/SVL = 0.33–0.38; and a maximum SVL of 44.0 mm (Table 6). All non-ratiometric characters are scored across all other *Tytthoscincus* and species of *Sphenomorphus* suspected of being *Tytthoscincus* in Grismer *et al.* (2016a: 237) and Karin *et al.* (2016: 416).

Description of holotype: Adult female, SVL 34.9 mm; non-regenerated tail length 48.4 mm; AXG 19.1 mm;

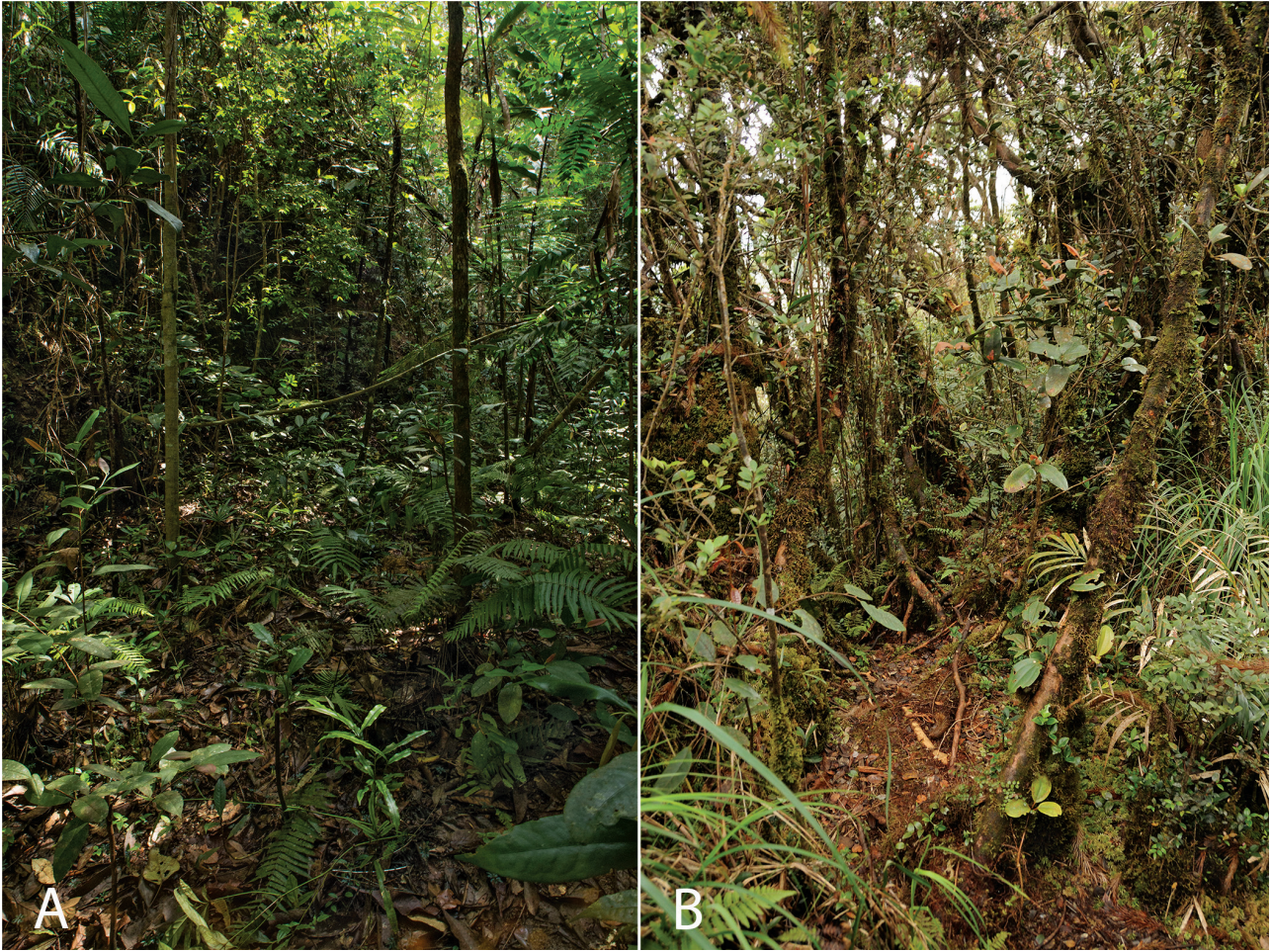


Figure 12. Microhabitat of *Tyttoscincus kakikecil* sp. nov. from Pahang Peninsular Malaysia. A, hill dipterocarp forests at Jeriau, Fraser's Hill (1305 m elevation). B, mossy forest at Ulu Kali, Genting Highlands (1670 m elevation).

HL 7.2 mm; head width 4.5 mm; snout to anterior margin of foreleg 12.4 mm; rostral wider than long, in broad contact with frontonasal; frontonasal wider than long; prefrontals large, in point contact on midline; frontal elongate, diamond-shaped, in contact with first two supraoculars; four supraoculars; frontoparietals in contact posterior to frontal, contacting second, third and fourth supraoculars anterolaterally and parietals and interparietal posteriorly; interparietal diamond-shaped, large, slightly projecting posteriorly, eyespot in posterior projection; parietals large, in medial contact posterior to interparietal, contacting fourth supraocular anteriorly; one slightly enlarged nuchal scale left of midline; nasals small, widely separated, trapezoidal, contacting rostral anteriorly, frontonasal dorsally, first loreal posteriorly, first supralabial ventrally; nostril in centre of nasal; supranasals absent; two loreals, posterior loreal taller than wide; upper and lower preocular present; lower preocular followed by a series of suboculars; eight superciliaries, posterior

superciliary elongate and projecting dorsomedially; seven suboculars; six supralabials, third, fourth and fifth below eye; two postsupralabials; three primary temporals; three secondary temporals, uppermost not contacting parietals; lower eyelid transparent, scaly, no enlarged central window; mental twice as wide as long; single, large postmental, contacting first infralabial on each side; two enlarged pairs of chin shields posterior to postmental, anterior pair contacting medially, posterior pair widely separated posteriorly by a single scale; anterior and posterior chinshield pairs contacting first, second and third infralabials; six infralabials; external ear opening 0.9 mm, subcircular, lacking anterior lobules; and tympanum deeply set, non-pigmented.

Body scales smooth, cycloid, imbricate; ventral scales slightly larger than dorsal scales; 31 longitudinal scale rows around midbody; 73 paravertebral scales; 69 ventral scales; slightly enlarged median preloacal scales overlapping outer preloacal scales; tail slightly compressed



Figure 13. Type specimens of *Tytthoscincus martae* sp. nov. from Pahang, Peninsular Malaysia. A, holotype LSUHC 12688 from the Hindu Temple, Fraser's Hill. B, paratype LSUHC 12749 from Awana Road, Genting Highlands.

laterally; subcaudals slightly larger than dorsal caudals; limbs relatively robust, short (FL/SVL = 0.22; HDL/SVL = 0.33), widely separated when adpressed; scales of dorsal surface slightly larger than those of ventral and posterior surfaces; palmar and plantar scales slightly raised; and digits moderate in length, scales on dorsal surfaces in single row, subdigital lamellae bicarinate, seven on third finger, 12 on fourth toe.

Coloration in life: Overall dorsal ground colour of head, body, limbs and tail dark brown; head speckled with light-coloured markings; supralabials three and four bearing a light central spot; infralabials weakly banded; dorsum, posterior portion of flanks and tail bearing small, light-coloured spots; limbs mottled; anterior of flanks to posterior margin of jaws dull-orange bearing irregularly shaped dark speckles; thick, dark, irregularly margined post-orbital stripe extending from eye to groin, merging

with dorsal ground colour posterior to hind limbs, bordered dorsally above anterior portion of flanks by a thick, immaculate, dull-orange stripe; all ventral surfaces dull-yellow to beige, generally immaculate; distal portions of forelimbs and palmer surfaces dark; planter surface dark; subcaudal region stippled with dark brown.

Variation: The paratypes closely approach the holotype in all aspects of coloration except for their supralabial scales being distinctly barred (Fig. 13). The dorsum of LSUHC 12749 is slightly darker overall and the spotting less bold. The juveniles LSUHC 12072 (SVL 22.4 mm) and 12518 (SVL 26.5 mm) show no difference in colour pattern or pattern boldness, indicating ontogenetic changes in coloration and pattern are absent. LSUHC 12518 has a damaged neck, LSUHC 12749 has a damaged gular region and LSUHC 12751 has an incomplete tail. Meristic variation is presented in Table 10.

Table 10. Meristic and ratiometric characters of the type series of *Tyttthoscincus martae* sp. nov.

	LSUHC 12517	LSUHC 12518	LSUHC 12688	LSUHC 12749	LSUHC 12751	ZRC 3.6246	LSUHC 12072
	Paratype	Paratype	Holotype	Paratype	Paratype	Paratype	
	Awana Road	Awana Road	Fraser's Hill	Awana Road	Awana Road	Fraser's Hill	Awana Road
Supralabials	6	6	6	6	6	6	6
Infralabials	5	5	6	6	6	5	5
Supraoculars	4	4	4	4	4	4	4
Frontoparietal contacting supraoculars 2, 3 and 4	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Superciliaries	9`1	9`1	8`1	9`2	10`2	10`2	8`1
Prefrontals in contact	Point	Yes	Point	Yes	Yes	Yes	Yes
Loreals	2	2	2	2	2	2	2
Tympanum deep, non-pigmented	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Midbody scale rows	34	/	31	35	33	33	34
Dorsal scales striated	No	No	No	No	No	No	No
Paravertebral scale rows	74	/	73	70	73	73	71
Ventral scale rows	70	68	69	69	72	61	70
Enlarged pectoral scales	No	No	Yes	Yes	Yes	Yes	Weak
Enlarged precloacal scales	Yes	Yes	Yes	Yes	Yes	Yes	Yes
3rd finger lamellae	7	7	7	7	7	7	7
4th toe lamellae	12	13	12	13	13	13	13
Lamellae texture	Keeled	Keeled	Keeled	Keeled	Keeled	Keeled	Keeled
HL	6.6	0.12	7.2	7.59	6.9	8.4	5.85
TD	0.81	0.23	0.9	1.21	0.99	1.02	0.8
TD/HL	29.76	6.33	0.12	0.16	0.52	0.12	0.14
HL/SVL	29.76	0.24	0.21	0.18	0.14	0.19	0.26
AXG	22.8	12.8	19.1	22.8	18.5	20.73	11.2
AXG/SVL	0.53	0.48	0.55	0.53	0.52	0.47	0.50
FL	29.76	9.22	7.69	10.93	0.19	9.28	5.88
FL/SVL	29.76	0.35	0.22	0.26	8.08	0.21	0.26
HDL	29.76	26.5	11.43	15.73	0.23	14.34	8.3
HDL/SVL	29.76	0.12	0.33	0.38	13.04	0.33	0.37
SVL	29.76	26.5	34.9	42.78	35.8	44	22.4
Sex	/	/	Female	Female	Male	Male	/

(/), data unobtainable. AXG, axilla–groin length; FL, forelimb length; HDL, hind limb length; HL, head length; SVL, snout–vent length; TD, tympanum diameter.

Distribution: *Tyttthoscincus martae* sp. nov. is known from the type locality at the Hindu temple south of the town of Fraser’s Hill and Awana Road at Genting Highlands, Pahang, Peninsular Malaysia (Fig. 9). However, it is likely to range further north of Fraser’s Hill and south of Genting Highlands.

Natural history: *Tyttthoscincus martae* sp. nov. inhabits leaf-litter in hill dipterocarp forests from at least 991–1239 m in elevation (Fig. 14). Specimens from Awana Road, Genting Highlands were collected by raking leaves that had accumulated at the foot of an earthen bank and by turning logs and rocks buried in leaf-litter. Lizards were most commonly found in areas

where moisture from the hillside had seeped down to the edge of the road. During overcast days, lizards were seen running swiftly through small rocks and root tangles on the forest floor beneath the canopy in the nearby forest. However, we do not know if these specimens were *T. martae* sp. nov. or *T. bukitensis*. At Fraser’s Hill, specimens were found along the edges of seeps or small streams in damp microhabitats. ZRC 3.6246 was found beneath a log and LSUHC 12688 was found buried in the leaf-litter, both near the edges of small drainages.

Etymology: The specific epithet *martae* is a matronym honouring my (LLG) wife Marta S. Grismer for her long, non-wavering commitment and support of my



Figure 14. Microhabitat of *Tytthoscincus martae* sp. nov. from Pahang Peninsular Malaysia. A, Hindu Temple, Fraser's Hill. B, Awana Road, Genting Highlands.

work for many years, her efforts in the field on many trips across Southeast Asia and Latin America and for generating the morphological data sets for a number of our studies.

Comparisons: *Tytthoscincus martae* sp. nov. can be differentiated from *T. jaripendek* sp. nov. and *T. kakikecil* sp. nov. by having as opposed to lacking a deeply recessed, weakly pigmented tympanic membrane. *Tytthoscincus martae* sp. nov. differs discretely from *T. perhentianensis* and *T. jaripendek* sp. nov. by having 31–35 vs. 28–30 (collectively) midbody scales and 70–74 vs. 63–66 (collectively) paravertebral scales. It is further discretely differentiated from *T. jaripendek* sp. nov., *T. perhentianensis* and *T. kakikecil* sp. nov. by having seven vs. five or six subdigital lamellae on the third toe. It is further discretely differentiated from *T. jaripendek* sp. nov., *T. perhentianensis*, *T. kakikecil* sp. nov., *T. temengorensis* and *T. ishaki* by having 12 or 13 vs. 9–11 (collectively) subdigital lamellae on the fourth

toes. *Tytthoscincus martae* sp. nov. also bears statistically significant mean differences of all ten characters in varying combinations across all other species (Table 6). Numeric trends of these characters among species in the montane clade are presented in Figures 4 and 5.

Although the molecular phylogeny suggests that *Tytthoscincus martae* sp. nov. is a separate species being that it is not nested within any other species, it cannot be discretely nor statistically ($P < 0.05$) differentiated morphologically from *T. bukitensis* and both are sympatric at Fraser's Hill and syntopic at Awana Road, Genting Highlands. The genetic data infer that the monophyly (exclusivity) of each species is strongly supported (1.00/100 and 1.00/96, respectively; Fig. 2) and they share a modest 5.4–7.4% uncorrected pairwise sequence divergence between them. More importantly, both the BI and ML analyses infer *T. martae* sp. nov. and *T. bukitensis* are not sister species – although support for this is moderate (0.89/77) – so this conundrum cannot

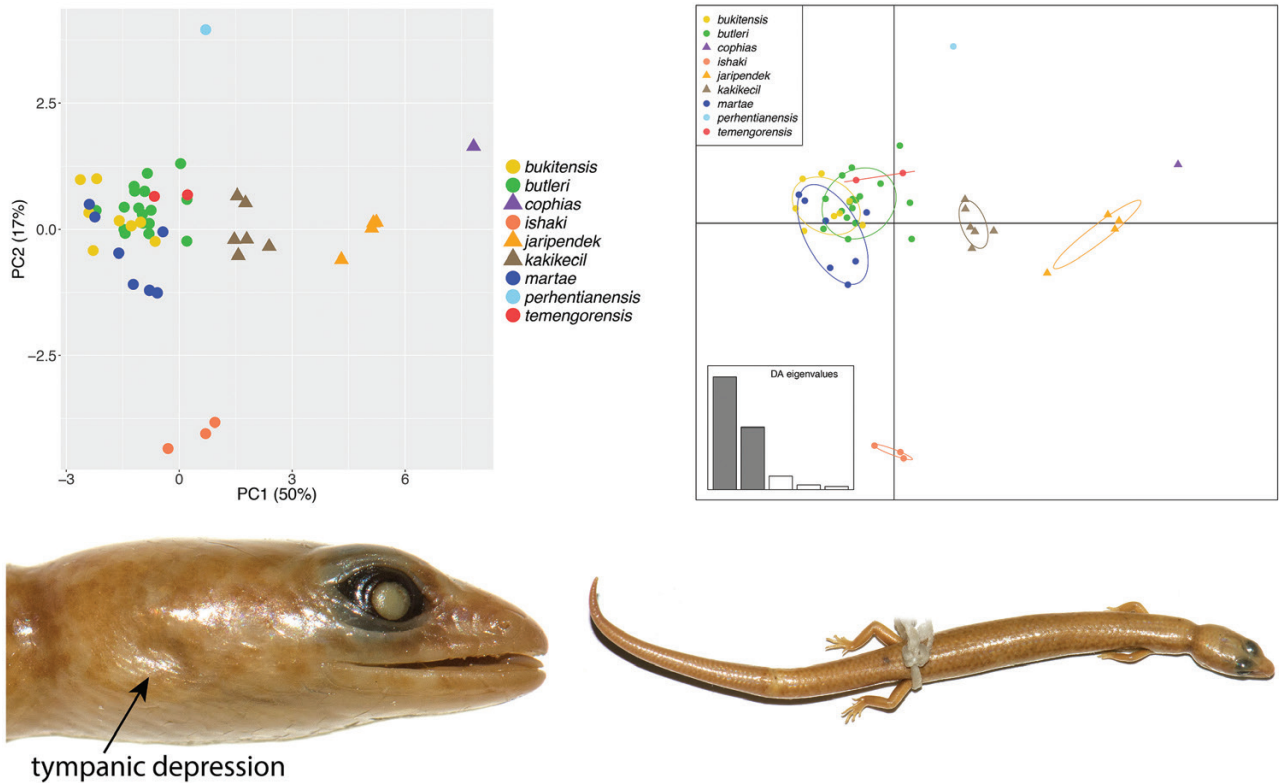


Figure 15. Concatenated PCA analysis showing the placement of *Tytthoscincus cophias*, its tympanic depression, and overall body stature.

be solved by considering them conspecific because it would render *T. bukitensis* paraphyletic. Most notably, however, is that certain individuals from each species are more closely related to conspecifics from the other locality than they are to individuals of the other species found only meters apart at the same locality. For example, *T. martae* sp. nov. LSUHC 12749 from Awana Road is more closely related to *T. martae* sp. nov. LSUHC 12688 from Fraser’s Hill, 38 km to the north than it is to *T. bukitensis* LSUHC 12750 collected within 15 min of *T. martae* sp. nov. LSUHC 12749 on the same day less than 5 m away in the same pile of leaf-litter (Fig. 2). Complicating this issue is that the molecular evidence demonstrates that the current paratype of *T. bukitensis* from Fraser’s Hill (ZRC 3.6246) must be considered part of *T. martae* sp. nov. and is not closely related to the holotype of *T. bukitensis* from Fraser’s Hill (ZRC 2.6245). Thus, the type series of *T. bukitensis* is composed of two different species that are not each other’s closest relatives. Therefore, ZRC 3.6246 is removed here from the type series of *T. bukitensis* and transferred to the species *T. martae* sp. nov.

If *T. bukitensis* and *T. martae* sp. nov. were reciprocally monophyletic and occurred exclusively at different localities (i.e. they were not sympatric), we would not recognize them as separate species and posit that their

genetic distinction represents isolation by distance and individuals from the intervening regions would need to be examined and sequenced. Such is the case with the allopatric sister species *Hemiphyllodactylus titiwangsaensis* and *H. cf. titiwangsaensis* – from the same mountain range as *T. bukitensis* and *T. martae* sp. nov. – that are morphologically indistinguishable yet have an uncorrected pairwise sequence divergence between them of 12.8% (Cobos et al., 2016). However, *T. bukitensis* and *T. martae* sp. nov. are not sister species and individuals of each occur at both localities and are even syntopic at one – strongly suggesting they are separate, highly convergent, genetically exclusive lineages.

Tytthoscincus martae sp. nov. and *T. bukitensis* are differentiated in their 50% combined upper and lower quartile ranges of midbody scales that only narrowly approach one another at 32.9 (Fig. 5). Although the mean values of their respective counts are not statistically significantly different, this is due to a high outlying value of 35 for midbody scales in *T. bukitensis* (LSUHC 12750). Given that these two species are syntopic in at least one part of their range and the only way to unequivocally separate them is with a molecular analysis, we consider them cryptic species (see below). We are well aware of the potential pitfalls using a single

mitochondrial marker in cases such as these and that the use of nuclear markers might resolve the issue of potential conspecificity. However, genomic data would be the best way to test these hypotheses and plans are in progress to do so.

Specimens conferre: We were unsuccessful in obtaining DNA sequences from ZRC 2.5944 from Telom Valley, Cameron Highlands considered by Grismer (2011) to be *T. bukitchensis* and LSUHC 12072 from the Awana Road, Genting Highlands that is newly reported here. Based on retained posteriors from a separate concatenated DAPC analyses, ZRC 2.5944 from Telom Valley clustered with *T. kakikecil* sp. nov. with only a 43% probability and was closest in morphospace to individuals from Fraser's Hill. Unfortunately, due to its state of preservation, we could not confirm the presence of reduced tympanae. The left tympanum looks as though it may be deeply inset but the right tympanum did not. We are also concerned with the accuracy of the mensural data. ZRC 2.5944 was collected in 1935 and the specimen is quite limp and in overall poor condition so we cannot conclude that the measurements taken from this specimen are congruous with those from freshly preserved specimens. Some scale counts (MB, PV and VS), however, are outside the range of those of *T. jaripendek* sp. nov. (the new species from Cameron Highlands) but consistent with those of *T. kakikecil* sp. nov. (Tables 6 and 9). We consider this specimen as *T. cf. kakikecil* sp. nov. but do not include it as part of the type series.

The retained DAPC posteriors indicate that LSUHC 12072 from the Awana Road, Genting Highlands clusters with *T. martae* sp. nov. with only a 59% probability which is consistent with its meristic and mensural data (Table 10). Furthermore, it plots within *T. martae* and outside of *T. bukitchensis* in the concatenated PCA and the DAPC. We consider this specimen as *T. cf. martae* sp. nov. but do not include it as part of the type series.

Sphenomorphus cophias: Boulenger (1908) described *Sphenomorphus cophias* from a single specimen (BMNH 1946.8.3.15) collected on Gunong (=Gunung) Tahan in the Banjaran Timur at ~1000 m in elevation and Smith (1922) reported a second specimen (which can no longer be located) from the same mountain at ~1100 m in elevation. Both specimens are small (36 mm and 29 mm SVL, respectively) and Boulenger (1908) reported that the ear of BMNH 1946.8.3.15 was hidden and replaced by a depression (Fig. 15). Lim (1998) and Grismer (2011) re-examined the holotype and found that along with it being less than 45 mm SVL, it had small temporal scales that were the same size and shape as the lateral body scales; and it had short digits with toe IV being equal in length to toe

III – characters Linkem *et al.* (2011) used to diagnose the genus. However, based on aspects of head scalation and lower eyelid morphology, Shea (in literature, 2016) believes it may be an undescribed species of *Lipina*. Nonetheless, data from the holotype are presented in Table 6. If it belongs in the genus *Tytthoscincus* on the basis of Linkem *et al.* (2011), its low numbers of digital lamellae (3FL = 5; 4TL = 10), very short limbs (FL/SVL = 0.17; HDL/SVL = 0.28), elongate body (AXG/SVL = 0.58) and lack of a tympanum further extend the trends of these characters shown for *T. jaripendek* sp. nov. and *T. kakikecil* sp. nov. and indicate this species has a semi-fossorial ecomorphology as demonstrated by its placement in the PCA and DAPC analyses (Fig. 15). This, coupled with its upland locality in hill dipterocarp forests, suggests it may belong to the montane clade allied to the semi-fossorial lineage. However, given that there are at least two clades of distantly related species of *Tytthoscincus* in Peninsular Malaysia and the propensity for convergence of semi-fossorial ecomorphology in skinks in general (see below), we do not propose a formal placement in either clade in the absence of molecular data.

DISCUSSION

ECOMORPHOLOGY

Within tropical ecosystems, leaf-litter is one of the most ubiquitous microhabitats in which a number of amphibians and reptiles have become adapted (Fauth, Crother & Slowinski, 1989; Vitt & Caldwell, 1994; Vonesh, 2001; Whitfield *et al.*, 2007). In Peninsular Malaysia, this is particularly true for lizards where at least 35 species are considered leaf-litter inhabitants (Grismer, 2011; Grismer *et al.*, 2011; Grismer & Quah, 2015). As more species are described from montane regions in Peninsular Malaysia, it is becoming clear that the ecological relationships among them is far more complex than previously considered (Grismer, 2007; Grismer & Quah, 2015) and this is especially true for closely related, syntopic, leaf-litter species (Grismer & Quah, 2015). The fact that multiple lineages of closely related, highly specialized species such as *Tytthoscincus* occur in close sympatry and syntopy in such a restrictive microhabitat indicates that resource partitioning must be highly regulated (Schoener, 1974; Walter, 1991; Goodman, 2007). This may also be the case for *T. leproauriculatus* and *T. batupanggah* that occur within 100 m of one another in the uplands of Borneo at Gunung Penrissen, Sarawak (Karin *et al.*, 2016). Knowing little about *Tytthoscincus* life history makes it difficult to test hypotheses as to how these species partition resources. However, because correlations between morphology and microhabitat structure underscore the link between a phenotype and an

environment (e.g. Herrel, Meyers & Vanhooydonck, 2001; Goodman, Miles & Schwarzkopf, 2008; Losos, 2009; Gomes, Carretero & Kaliontzopoulou, 2016), inferences can be made based on quantifiable differences in ecomorphology (Vitt *et al.*, 1997; Vanhooydonck, Van Damme & Aerts, 2000; Herrel *et al.*, 2001; Losos, 2009; Lee, Skinner & Camacho, 2013).

It has been demonstrated that body elongation, limb and digital reduction, shortening of the head and closure of the ear opening are correlated phenomena that have occurred multiple times during the evolution of fossorial and semi-fossorial skinks (Greer, 1989; Schmitz *et al.*, 2005; Brandley, Huelsenbeck & Wiens, 2008; Siler & Brown, 2011; Lee *et al.*, 2013; Wu *et al.*, 2015). For small skinks (SVL < 50 mm), these characteristics have been shown or suggested to be adaptive for locomoting within or beneath the surface of leaf-litter or through other types of restrictive vegetation (Van Damme *et al.*, 1998; Melville & Swain, 2000; Kohlsdorf *et al.*, 2001; Herrel *et al.*, 2002; Siler & Brown, 2011) and that various species have differing combinations of these characters in varying degrees of development (Pianka, 1969; Melville & Swain, 2000; Brandley *et al.*, 2008). *Tyttthoscincus*, in general, aligns well with this ecomorphological paradigm in that all species have relatively elongate bodies, short limbs and digits, and reside in leaf-litter and two species, *T. jaripendek* sp. nov. and *T. kakikecil* sp. nov., extend these trends further by having relatively shorter limbs and digits (i.e., fewer lamellae), longer bodies, shorter heads and vestigial tympanae (Tables 6, 67; Figs 4, 5, 7). The concatenated PCA, DAPC and Tukey HSD test indicate that *T. jaripendek* sp. nov. and *T. kakikecil* sp. nov. – who have varying combinations of these characters – cluster separately from all other species (Fig. 6) and differ statistically (Table 7) from various combinations of species in many characters including those associated with digit and limb reduction (3TL, 4FL, FL, HDL), elongation of the body (AXG) and shortening of the head (HL).

As to how the ecomorphological differences of the semi-fossorial species *T. kakikecil* sp. nov. may allow it to function differently in leaf-litter at Fraser's Hill where it is sympatric and probably syntopic with the leaf-litter generalists *T. bukitensis* is speculative. Melville & Swain (2000), Bergmann & Irschick (2010) and Lee *et al.* (2013) noted that shorter-bodied skinks were faster and spent more time on the surface, whereas elongate, limb-reduced species spent more time below the surface and were possibly more cryptic and substrate-specific. Although *T. kakikecil* sp. nov. and *T. bukitensis* can be 'raked up' from the same pile of leaves, we hypothesize that they may be spending different amounts of time foraging at different levels in the leaf-litter mass which can be densely packed and as thick as 0.5 m. At both Fraser's Hill and

Awana Road, we often see *T. bukitensis* or *T. martae* sp. nov. (or both) above ground moving through and across the surface of the leaf-litter but have never observed *T. kakikecil* sp. nov. (nor have we seen *T. jaripendek* sp. nov.) above ground. It is tempting to posit that these ecomorphological differences evolved as a result of competition, forcing these species into different microhabitats (e.g. Vitt *et al.*, 1997; Herrel *et al.*, 2001) and may have even been the initial driving force behind the speciation of the two major ecomorphological lineages within *Tyttthoscincus* (Fig. 2). If competition was or is the driving force for the evolution of these two ecomorphologies, then we hypothesize we should find a yet undiscovered, leaf-litter generalist co-occurring with *T. jaripendek* sp. nov. at Cameron Highlands.

CRYPTIC SPECIES

Ironically, many studies employing integrative taxonomic analyses that purport to reveal 'cryptic species' go on to provide traditional, discrete, morphological diagnoses for those 'cryptic species' using taxon-specific characters that have traditionally been used to diagnose other species within those groups – diagnoses that stand alone from the molecular evidence and were generated retrospectively following prudent morphological analyses (e.g. Wood *et al.*, 2009; Grismer *et al.*, 2013a, b; Loredó *et al.*, 2013). So are these species truly 'cryptic'? The definition of cryptic species ranges broadly from two different species erroneously classified under the same name (Bickford *et al.*, 2006) to species that are morphologically indistinguishable but well delineated on the basis of genetic markers (Jöger & Schroll, 2013). Most herpetologists would probably consider *Tyttthoscincus* species to be 'cryptic' in that they are small, elongate, little brown skinks that move rapidly in and out of the leaf-litter and are hard to tell apart. However, as demonstrated here and elsewhere (Grismer, 2006b, 2007; Grismer *et al.*, 2009a; Linkem *et al.*, 2011; Karin *et al.*, 2016), with judicious examination, many of these species are easily differentiated from one another solely on the basis of morphological characters that have been useful in skink taxonomy for over a century (e.g. Boulenger, 1887, 1912). However, this is not the case with *T. bukitensis* and *T. martae* sp. nov., that live in the same piles of leaves and are not unequivocally distinguishable morphologically but are genetically exclusive and not sister species (Fig. 2). We lean toward the view of Jöger & Schroll (2013) and consider cryptic species to be genetically exclusive lineages that are not discretely or statistically diagnosable from one another on the basis of morphology and thus consider *T. bukitensis* and *T. martae* sp. nov. to be cryptic species with respect to one another. They are not cryptic with respect to other species of *Tyttthoscincus* in that they are discretely

and/or statistically diagnosable from them (Tables 6, 7). As noted above, differences in ecomorphology can be used to entertain hypotheses as to how the syntopic semi-fossorial and leaf-litter generalists may be partitioning resources. However, this simplistic explanation does not account for the morphological and ecological similarity between these syntopic, cryptic species. Understanding the ecological relationships between *T. bukitensis* and *T. martae* sp. nov. will contribute a great deal to a general understanding of the complex nature of leaf-litter ecology. Ecological studies of these species are currently being designed.

BIOGEOGRAPHY IN A SKY-ISLAND ARCHIPELAGO

Understanding the phylogenetic relationships among unrelated, co-distributed species across a common landscape and the phylogeographic structure within other species across those same landscapes provides a relative, temporal framework necessary to interpret how those lineages evolved. Time-calibrating those relationships allows researchers to distinguish between old (pre-Pleistocene) and recent cladogenic events among sympatric populations (Bell *et al.*, 2012; Grismer *et al.*, 2015a). Time-calibrated phylogeographic and phylogenetic studies have demonstrated that speciation in tropical, montane forests is not solely the result of oscillating, climatic events of the Late Pleistocene as posited by many (Morley, 2000, 2012; Bird, Taylor & Hunt, 2005; Outlaw & Voelker, 2008; Reddy, 2008; Cannon, Morley & Bush, 2009; Cannon, 2012) but have emerged along a significantly longer time continuum and that some upland species have existed in isolated refugia as paleoendemics since the Miocene (Vences *et al.*, 2009; Tolley *et al.*, 2011; Bell *et al.*, 2012; Grismer *et al.*, 2015a). In comparison, other species distributed across the same landscapes may remain essentially morphologically and genetically identical (Loredo *et al.*, 2013; Grismer *et al.*, 2014a, 2015b). In the sky-island archipelago of Peninsular Malaysia, Grismer *et al.* (2013b, 2016c) noted that the deep genetic divergences within co-distributed clades of Slender Geckos *Hemiphyllodactylus* and Stream Toads *Ansonia*, respectively, dated from the Late Eocene to the Late Pliocene (~35.5–2.7 Mya). These deep divergences stand in contrast to those of co-distributed species of snakes (*Asthenodipsas vertebralis*, *A. lasgalenensis* and *Lycodon butleri*) whose allopatric populations bear less than 1.0% mtDNA sequence divergence among them across distances as great as 210 km (Loredo *et al.*, 2013; Grismer *et al.*, 2014a). Loredo *et al.* (2013) and Grismer *et al.* (2014a, 2015b) hypothesized that being vagile and not microhabitat-restricted enabled allopatric populations to migrate downslope with advancing montane forests

during cyclical, glacial maxima (Cannon *et al.*, 2009; Woodruff, 2010; Cannon, 2012) and establish repeated episodes of secondary contact. Whereas small, non-vagile (*Hemiphyllodactylus*) and microhabitat-restricted (*Ansonia*) species remained in place and diverged along their own genetic trajectories.

Node age estimates from a time-calibrated BEAST analysis plotted on the ML topology (Fig. 2) illustrate that within the upland clade of *Tytthoscincus*, both relatively old and recent cladogenic events have contributed to the diversity within this lineage. The separation between the semi-fossorial and leaf-litter generalist clades occurred during the Upper Pliocene (mean of 4.8 Mya; 6.8–2.8 HPD [highest posterior density]) and speciation within the leaf-litter generalists began much more recently in the Upper Pleistocene (mean of 1.7 Mya; 2.1–1.0 HPD). Separation between the three allopatric, phylogeographically discordant populations of *T. butleri* – that have an uncorrected pairwise sequence divergence of less than 1.0% across 203 km of insular and continental mountain tops – was a very recent Pleistocene event (mean of 0.60 Mya; 0.65–0.22 HPD), reminiscent of the snakes noted above. In the semi-fossorial lineage, the separation between *T. jaripendek* sp. nov. and *T. kakikecil* sp. nov., which share a 3.6% sequence divergence between them, was also a recent Pleistocene event (mean of 0.90 Mya; 1.14–0.23 HPD). Thus, unlike other co-distributed lineages, the cladogenic history of *Tytthoscincus* extends across the Plio-Pleistocene boundary. The deep split during the Upper Pliocene resulting in the evolution of the different ecomorphologies is in contrast to the younger, Pleistocene cladogenic events that happened in rapid succession (*T. bukitensis*, (*T. martae* sp. nov., (*T. ishaki*, (*T. perhentianensis*, (*Tytthoscincus* sp. nov., (*T. temengorensis*, (*T. butleri*)))))) from approximately a mean of 1.7–0.06 Mya. The latter events were most probably the result of cyclical ecological changes generated by rapid, ongoing glacier-driven, climate oscillations (Cannon *et al.*, 2009; Woodruff, 2010; Cannon, 2012). The phylogenetic and phylogeographic structure of 21 additional co-distributed species (Grismer *et al.*, in preparation) support the hypothesis of Grismer *et al.* (2015b) in that evolution and diversification of sky-island archipelago lineages in Peninsular Malaysia happened along a continuum from the Upper Eocene well into the Pleistocene and that speciation or lack thereof has been influenced by life history and dispersal capabilities (Loredo *et al.*, 2013; Grismer *et al.*, 2014a, 2015b).

CONSERVATION

Globally, upland ecosystems in tropical rainforests are renowned for their high levels of endemism (Blackburn & Measey, 2009; Bell *et al.*, 2010, 2012; Grismer *et al.*,

2010a, b; Grismer, 2011; Tolley *et al.*, 2011) and the sky-island archipelago of Peninsular Malaysia is no exception. It has been noted that the montane regions of Sundaland have served as refuges for upland, range-restricted species during drier interglacial periods since at least the early Miocene (23 Mya; de Bruyn *et al.*, 2013; Grismer *et al.*, 2016c) and thus, the foundations for these species' complex ecological relationships have probably been developing over considerable periods of time. We posit that understanding the current ecological relationships of microhabitat-specific, range-restricted, refugial species will contribute greatly to a general understanding of rainforest ecosystems and that such knowledge should underlie the platform upon which effective and efficient forest management and conservation programs are conceived.

ACKNOWLEDGEMENTS

We wish to thank many La Sierra University students for assistance in the field. We thank Chan Kin Onn for providing R script for the analyses and hours of his time helping trouble shoot. We thank Kelvin P. K. Lim for being a gracious host while examining specimens under his care. Funding for LLG came from grants from the College of Arts and Sciences at La Sierra University and from a National Geographic Society Explorers Grant (9277-15). SA was supported by Universiti Sains Malaysia (USM) and Ministry of Higher Education Research Grants. Field work for PLW was supported in part by an NSF grant EF-1241885 issued to Jack W. Sites Jr. Fieldwork for AMIN and AN in the Tembat Forest Reserve, Hulu Terengganu, was fully funded by Tenaga Nasional Berhad Research Grant TNBR BG-R-STAP001-00-0000000-B21101.

REFERENCES

- Bell RC, MacKenzie JB, Hickerson MJ, Chavarria KL, Cunningham M, Williams S, Moritz 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.
- Bergmann PJ, Irschick DJ. 2010. Alternate pathways of body shape evolution translate into common patterns of locomotion in two clades of lizards. *Evolution* **64**: 1569–1582.
- Bickford D, Lohman DJ, Sodhi NS, Ng PKL, Meier R, Winker K, Ingram KK, Das I. 2006. Cryptic species as a window on diversity and conservation. *Trends in Ecology and Evolution* **22**: 148–155.
- 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**: 2228–2242.
- Blackburn DC, Measey GJ. 2009. Dispersal to or from an African biodiversity hotspot? *Molecular Ecology* **18**: 1904–1915.
- Boulenger GA. 1887. *Catalogue of the lizards in the British Museum (natural history). III. Lacertidae, Gerrhosauridae, Scincidae, Anelytropidae, Dibamidae, Chamaeleontidae*. London: Taylor & Francis.
- Boulenger GA. 1908. Report on the Gunong Tahan expedition, May–Sept. 1905. III. Fishes, batrachians, and reptiles. *Journal of the Federated Malaya States Museum* **3**: 61–69.
- Boulenger GA. 1912. *Vertebrate fauna of the Malay Peninsula from the Isthmus of Kra to Singapore including adjacent islands*. London: Taylor and Francis.
- Brandley MC, Huelsenbeck JP, Wiens JJ. 2008. Rates and patterns in the evolution of snake-like body form in squamate reptiles: evidence for repeated re-evolution of lost digits and long-term persistence of intermediate body forms. *Evolution* **62**: 2042–2064.
- 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, Vol. 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* **106**: 11188–11193.
- 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, Norhayati A, Belabut D. 2009. A new species of *Gastrophrynoidea* (Anura: Microhylidae): an addition to a previously monotypic genus and a new genus for Peninsular Malaysia. *Zootaxa* **2124**: 63–68.
- Chan KO, Wood PL Jr., Anuar S, Muin MA, Quah ESH, Sumarli AX, Grismer LL. 2014. A new species of upland stream toad of the genus *Ansonia* Stoliczka (Anura: Bufonidae) from northeastern Peninsular Malaysia. *Zootaxa* **3764**: 427–440.
- Chapple DG, Alish B, Miller KA, Daugherty CH, Gleeson DM. 2012. Phylogeography of the endangered Otago skink, *Oligosoma ottagense*: population structure, hybridization and genetic diversity in captive populations. *PLoS ONE* **7**: 1–11.
- Cobos A, Grismer LL, Wood PL Jr., Quah ESH, Anuar S, Muin MA. 2016. Phylogenetic relationships of geckos of the *Hemiphyllodactylus harterti* group, a new species from Penang Island, Peninsular Malaysia, and a likely case of true cryptic speciation within *H. titiwangsaensis*. *Zootaxa* **4107**: 367–380.
- Davis HR, Grismer LL, Wood PL Jr., Muin MA, Anuar S, Klabacka R. 2016. The phylogenetic relationships of a new stream toad of the genus *Ansonia* Stoliczka, 1870 (Anura:

- Bufoidea) from a montane region in Peninsular Malaysia. *Zootaxa* **4103**: 137–153.
- de Bruyn M, Rüber L, Nylinder S, Stelbrink B, Lovejoy NR, Lavoué S, Tan HH, Nugroho E, Wowor D, Ng PKL, Siti Azizah MN, von Rintelen T, Hall R, Carvalho GR. 2013.** Paleo-drainage basin connectivity predicts evolutionary relationships across three Southeast Asian biodiversity hotspots. *Systematic Biology* **62**: 398–410.
- Drummond AJ, Ashton B, Buxton S, Cheung M, Cooper A, Duran C. 2011.** Geneious, Version 5.4. Available at: <http://www.geneious.com/>.
- Drummond AJ, Suchard MA, Xie D, Rambaut A. 2012.** Bayesian phylogenetics with BEAUti and BEAST 1.7. *Molecular Biology and Evolution* **29**: 1969–1973.
- Fauth JE, Crother BI, Slowinski JB. 1989.** Elevational patterns of species richness, evenness, and abundance of the Costa Rican leaf-litter herpetofauna. *Biotropica* **21**: 178–185.
- Gomes V, Carretero MA, Kaliontzopoulou A. 2016.** The relevance of morphology for habitat use and locomotion in two species of wall lizards. *Acta Oecologica* **70**: 87–95.
- Goodman BA. 2007.** Microhabitat separation and niche overlap among five assemblages of tropical skinks. *Australian Journal of Zoology* **55**: 15–27.
- Goodman BA, Miles DB, Schwarzkopf L. 2008.** Life on the rocks: habitat use drives morphological and performance evolution in lizards. *Ecology* **89**: 3462–3471.
- Greer AE. 1989.** *The biology and evolution of Australian lizards*. Chipping Norton: Survey Beatty and Sons Pty. Ltd.
- 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 Peninsula. *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.** *Lizard of Peninsular Malaysia, Singapore, and their adjacent archipelagos*. Frankfurt am Main: Edition Chimira, 1–728.
- Grismer LL, Anuar S, Muin MA, Quah ESH, Wood PL Jr. 2013a.** Phylogenetic relationships and description of a new upland species of bent-toed gecko (*Cyrtodactylus* Gray, 1827) of the *C. sworderi* complex from northeastern Peninsular Malaysia. *Zootaxa* **3616**: 239–252.
- 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. 2010a.** A checklist of the herpetofauna of the Banjaran Bintang, Peninsular Malaysia. *Russian Journal of Herpetology* **17**: 147–160.
- Grismer LL, Chan KO, Quah E, Muin MA, Savage AE, Grismer JL, Norhayati A, Greer LF III, Remegio A-C. 2010b.** Another new, diminutive rock gecko (*Cnemaspis* Strauch) from Peninsular Malaysia and a discussion of resource partitioning in sympatric species pairs. *Zootaxa* **2569**: 55–66.
- Grismer LL, Grismer JL, Wood PL Jr., 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, Grismer JL, Youmans TM. 2004.** A new species of *Leptolalax* (Anura: Megophryidae) from Pulau Tioman, West Malaysia. *Asiatic Herpetological Research* **10**: 8–11.
- Grismer LL, Muin MA, Wood PL, Anuar S, Linkem CW. 2016a.** The transfer of two clades of Malaysian *Sphenomorphus* Fitzinger (Squamata: Scincidae) into the genus *Tythoscincus* Linkem, Diesmos, & Brown and the description of a new Malaysian swamp-dwelling species. *Zootaxa* **4092**: 231–242.
- 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, Quah ESH. 2015.** The rediscovery of *Sphenomorphus malayanus* Doria, 1888 (Squamata: Scincidae) from the Titiwangsa Mountain Range of Peninsular Malaysia and its re-description as *S. senja* sp. nov. *Zootaxa* **3931**: 63–70.
- Grismer LL, Quah ESH, Anuar S, Muin MA, Wood PL Jr., Nor SAM. 2014a.** A diminutive new species of cave-dwelling wolf snake (Colubridae: *Lycodon* Boie, 1826) from Peninsular Malaysia. *Zootaxa* **3815**: 51–67.
- Grismer LL, Quah ESH, Siler CD, Chan KO, Wood PL Jr., Grismer JL, Anuar S, Norhayati A. 2011.** Peninsular Malaysia's first limbless lizard: a new species of the genus *Larutia* (Böhme) from Pulau Pinang with a phylogeny of the genus. *Zootaxa* **2799**: 29–40.
- Grismer LL, Quah ESH, Wood PL Jr., Grismer JL, Anuar S, Muin A, Davis HR, Murdoch ML, Grismer JL, Cota M, Cobos AJ. 2016b.** Dragons in the mist: three new species of *Pseudocalotes* Fitzinger (Squamata: Agamidae) from the sky island archipelago of Peninsular Malaysia. *Zootaxa* **4136**: 461–490.
- Grismer LL, Wood PL Jr., Anuar S, Muin MA, Quah ESH, McGuire JA, Brown RM, Ngo VT, Pham H. 2013b.** 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, Mohamed M, Chan KO, Sumarli AX, Loredó 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* **3786**: 359–381.
- Grismer LL, Wood PL Jr., Anuar S, Quah ESH, Muin MA, Chan KO, Sumarli AX, Loredó AL. 2015a.** Repeated evolution of sympatric, paleoendemic species in closely related, co-distributed lineages of *Hemiphyllodactylus* Bleeker, 1860 (Squamata: Gekkonidae) across a sky-island archipelago in Peninsular Malaysia. *Zoological Journal of the Linnean Society* **174**: 859–876.
- Grismer LL, Wood PL Jr., Anuar S, Riyanto A, Norhayati A, Muin MA, Sumontha M, Grismer JL, Chan KO, Quah ESH, Pauwels OSG. 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., Aowphol A, Cota M, Grismer MS, Murdoch ML, Aguilar C, Grismer JL. 2016c.** Out of Borneo again and again: biogeography of the stream toad genus *Ansonia* Stoliczka (Anura: Bufonidae) and the discovery of the first limestone cave dwelling species. *Biological Journal of the Linnean Society* **120**: 371–395.
- Grismer LL, Wood PL Jr., Grismer JL. 2009b.** A new insular species of skink of the genus *Sphenomorphus* Strauch 1887 (Squamata: Scincidae) from Pulau Perhentian Besar, Terengganu, Peninsular Malaysia. *Tropical Life Sciences Research* **20**: 51–69.
- Grismer LL, Wood PL Jr., Lee CH, Quah ESH, Anuar S, Ngadi E, Sites JW Jr. 2015b.** An integrative taxonomic review of the agamid genus *Bronchocela* (Kuhl, 1820) from Peninsular Malaysia with descriptions of new montane and insular endemics. *Zootaxa* **3948**: 1–23.
- Grismer LL, Wood PL Jr., Quah ESH, Anuar S, 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.
- Grummer JA, Bryson RW Jr., Reeder TW. 2014.** Species delimitation using Bayes factors: simulations and application to the *Sceloporus scalaris* species group (Squamata: Phrynosomatidae). *Systematic Biology* **63**: 119–133.
- 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.
- Herrel A, Meyers JJ, Vanhooydonck B. 2001.** Correlations between habitat use and body shape in a phrynosomatid lizard (*Urosaurus ornatus*): a population-level analysis. *Biological Journal of the Linnean Society* **74**: 305–314.
- Herrel A, Meyers JJ, Vanhooydonck B. 2002.** Relations between microhabitat use and limb shape in phrynosomatid lizards. *Biological Journal of the Linnean Society* **77**: 149–163.
- Huelsenbeck J, Ronquist F. 2001.** MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* **17**: 754–755.
- Huelsenbeck JP, Ronquist F, Nielsen R, Bollback JP. 2001.** Bayesian inference of phylogeny and its impact on evolutionary biology. *Science* **294**: 2310–2314.
- Jöger KM, Schrödl M. 2013.** How to describe a cryptic species? Practical challenges of molecular taxonomy. *Frontiers in Zoology* **10**: 59–86.
- Jombart T, Devillard S, Balloux F. 2010.** Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. *BMC Genetics* **11**: 94.
- Kaiser HF. 1960.** The application of electronic computers to factor analysis. *Education and Psychological Measurement* **20**: 141–151.
- Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermiin LS. 2017.** ModelFinder: fast model selection for accurate phylogenetic estimates. *Natural Methods* **14**: 587–589.
- Karin BR, Das I, Bauer AA. 2016.** Two new species of diminutive leaf-litter skinks (Squamata: Scincidae: *Tytthoscincus*) from Gunung Penrissen, Sarawak, Malaysia (northern Borneo). *Zootaxa* **4093**: 407–423.
- Kohlsdorf T, Garland T Jr., Navas CA. 2001.** Limb and tail lengths in relation to substrate usage in *Tropidurus* lizards. *Journal of Morphology* **248**: 151–164.
- Lee MSY, Skinner A, Camacho A. 2013.** The relationship between limb reduction, body elongation and geographical range in lizards (*Lerista*, Scincidae). *Journal of Biogeography* **2013**: 1–8.
- Leonart J, Salat J, Torres GJ. 2000.** Removing allometric effects of body size in morphological analysis. *Journal of Theoretical Biology* **205**: 85–93.
- Lim LJ. 1998.** *The taxonomy of West Malaysian and Singapore Scincidae (Reptilia: Sauria)*. Unpublished M.S. thesis, National University of Singapore, Kent Ridge.
- Linkem CW. 2013.** *Molecular phylogenetics and biogeography of Sphenomorphini (Squamata: Scincidae)*. Unpublished PhD thesis, Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence.
- Linkem CW, Diesmos AC, Brown RM. 2011.** Molecular systematics of the Philippine forest skinks (Squamata: Scincidae: *Sphenomorphus*): testing morphological hypotheses of interspecific relationships. *Zoological Journal of the Linnean Society* **163**: 1217–1243.
- Loredó AI, Wood PL Jr., Quah ESH, Anuar S, Greer LF, Grismer LL. 2013.** A phylogenetic based taxonomy of *Asthenodipsas vertebralis* (Boulenger, 1900), the description of a new species from Peninsular Malaysia, and the resurrection of a species from Sumatra. *Zootaxa* **3664**: 505–524.
- Losos JB. 2009.** *Lizards in an evolutionary tree: ecology and adaptive radiation of anoles*. Harvard: University of California Press.
- Macey JR, Schulte JA, Larson A, Tuniyev BS, Orlov N, Papenfuss TJ. 1997.** Molecular phylogenetics, tRNA evolution, and historical biogeography in anguillid lizards and related taxonomic families. *Molecular Phylogenetics and Evolution* **12**: 250–272.
- Maddison WP, Maddison DR. 2015.** *Mesquite: a modular system for evolutionary analysis, Version 3.04*. Available at: <http://mesquiteproject.org>

- Matsui M, Belabut DM, Ahmad N. 2014.** Two new species of fanged frogs from Peninsular Malaysia (Anura: Dicroglossidae). *Zootaxa* **3881**: 75–93.
- Matsui M, Belabut DM, Ahmad N, Yong HS. 2009.** A new species of *Leptotalax* (Amphibia, Anura, Megophryidae) from Peninsular Malaysia. *Zoological Science* **26**: 243–247.
- Melville J, Swain R. 2000.** Evolutionary relationships between morphology, performance and habitat openness in the lizard genus *Niveoscincus* (Scinidae: Lygosominae). *Biological Journal of the Linnean Society* **70**: 667–683.
- Miller MA, Pfeiffer W, Schwartz T. 2010.** Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE), New Orleans, 14 November 2010.
- Minh Q, Nguyen MAT, von Haeseler A. 2013.** Ultrafast approximation for phylogenetic bootstrap. *Molecular Biology and Evolution* **30**: 1188–1195.
- Morley RJ. 2000.** *Origin and evolution of tropical rain forests*. Chichester: John Wiley & Sons.
- 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.
- Nguyen L-T, Schmidt HA, von Haeseler A, Minh BQ. 2015.** IQ-TREE: a fast and effective stochastic algorithm for estimating maximum likelihood phylogenies. *Molecular Biology and Evolution* **32**: 268–274.
- 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.
- Pianka ER. 1969.** Sympatry of desert lizards (*Ctenotus*) in Western Australia. *Ecology* **50**: 1012–1030.
- Rambaut A, Drummond AJ. 2013.** TreeAnnotator, Version 1.8.0: MCMC output analysis. Available at: <http://beast.bio.ed.ac.uk/TreeAnnotator>
- Rambaut A, Suchard MA, Xie D, Drummond AJ. 2014.** Tracer, Version 1.6. Available at: <http://beast.bio.ed.ac.uk/Tracer>
- 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.
- Ronquist F, Huelsenbeck JP. 2003.** MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**: 1572–1574.
- Sabaj-Pérez MH (ed.). 2010.** Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an Online Reference, Version 2.0. Washington: American Society of Ichthyologists and Herpetologists. Available at: <http://www.asih.org>
- Schmitz A, Brandley MC, Mausfeld P, Vences M, Glaw F, Nussbaum RA, Reeder TW. 2005.** Opening the box: phylogenetics and morphological evolution of the Malagasy fossorial lizards of the subfamily “Scincinae”. *Molecular Phylogenetics and Evolution* **34**: 118–133.
- Schoener TW. 1974.** Resource partitioning in ecological communities. *Science* **185**: 27–39.
- Siler CD, Brown RM. 2011.** Evidence for repeated acquisition and loss of complex body-form characters in an insular clade of Southeast Asian semi-fossorial skinks. *Evolution* **65**: 2641–2663.
- Sly GR. 1976.** New locality records for some Peninsular Amphibia, Reptilia, and Mammalia. *Malayan Nature Journal* **29**: 155–157.
- Smith M. 1922.** On a collection of reptiles and batrachians from the mountains of Pahang, Malay Peninsula. *Journal of the Federated Malay States Museum* **10**: 263–282.
- Taylor EH. 1935.** A taxonomic study of the cosmopolitan lizards of the genus *Eumeces* with an account of the distribution and relationships of its species. *University of Kansas Science Bulletin* **23**: 1–643.
- Thorpe RS. 1975.** Quantitative handling of characters useful in snake systematics with particular reference to interspecific variation in the Ringed Snake *Natrix natrix* (L.). *Biological Journal of the Linnean Society* **7**: 27–43.
- Thorpe RS. 1983.** A review of the numerical methods for recognized and analysing racial differentiation. In: Felsenstein J, ed. *Numerical taxonomy*. Berlin Heidelberg: Springer, 404–423.
- 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.
- Turan C. 1999.** A note on the examination of morphometric differentiation among fish populations: the Truss system. *Turkish Journal of Zoology* **23**: 259–263.
- Van Damme R, Aerts P, Vanhooydonck B. 1998.** Variation in morphology, gait characteristics and speed of locomotion in two populations of lizards. *Biological Journal of the Linnean Society* **63**: 409–427.
- Van Damme R, Aerts P, Vanhooydonck B. 2002.** Speed versus manoeuvrability: association between vertebral number and habitat structure in lacertid lizards. *Journal of Zoology London* **258**: 327–334.
- Vanhooydonck B, Van Damme R, Aerts P. 2000.** Ecomorphological correlates of habitat partitioning in Corsican lacertid lizards. *Functional Ecology* **14**: 358–368.
- 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.
- Vitt LJ, Caldwell JL. 1994.** Resource utilization and guild structure of small vertebrates in the Amazon forest leaf litter. *Journal of Zoology* **234**: 463–476.
- Vitt LJ, Caldwell JP, Zani PA, Titus TA. 1997.** The role of habitat shift in the evolution of lizard morphology: evidence from tropical *Tropidurus*. *Proceedings of the National Academy of Sciences* **94**: 3828–3832.
- Vonesh JR. 2001.** Patterns of richness and abundance in a tropical African leaf-litter herpetofauna. *Biotropica* **33**: 502–510.
- Walter GH. 1991.** What is resource partitioning? *Journal of Theoretical Ecology* **150**: 137–143.

- Whitfield SM, Bell KE, Philippi T, Sasa M, Bolaños F, Chaves G, Savage JM, Donnelly MA. 2007.** Amphibian and reptile declines over 35 years at La Selva, Costa Rica. *Proceedings of the National Academy of Sciences* **104**: 8352–8356.
- Wilcox TP, Zwickl DJ, Heath TA, Hillis DM. 2002.** Phylogenetic relationships of the dwarf boas and a comparison of Bayesian and bootstrap measures of phylogenetic support. *Molecular Phylogenetics and Evolution* **25**: 361–371.
- Wood PL Jr., Grismer JL, 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, Senawi J. 2008.** Two new species of torrent-dwelling toads *Ansonia* Stoliczka, 1870 (Anura: Bufonidae) from Peninsular Malaysia. *Herpetologica* **64**: 321–340.
- Woodruff DS. 2010.** Biogeography and conservation in Southeast Asia: how 2.7 million years of repeated environmental fluctuations affect today's patterns and the future of the remaining refugial-phase biodiversity. *Biodiversity Conservation* **19**: 919–941.
- Wu NC, Alton LA, Clemente CJ, Kearney MR, White CR. 2015.** Morphology and burrowing energetics of semi-fossorial skinks (*Liopholis* spp.). *Journal of Experimental Biology* **218**: 2416–2426.
- 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.

APPENDIX

The following specimens were examined.

Tytthoscincus bukitchensis: West Malaysia, Pahang, Fraser's Hill, Telecom Loop (LSUHC 11655, 11771), Jeriau (LSUHC 12226, 12686–87), Bishops's Trail [ZRC 2.6245 (holotype)]. West Malaysia, Pahang, Genting Highlands, Awana Road (LSUHC 12237, 12750).

Tytthoscincus butleri: West Malaysia: Kedah, Pulau Langkawi, Gunung Raya; LSUHC 6790, 11152, 11784–87, 11840–41, LRCUKM 143, 148. West Malaysia: Kedah, Pulau Singa Besar; DWNP 3032. West Malaysia: Perak, Bukit Larut; LSUHC 9043, 9204–06, 12429, 12432–33. West Malaysia: Penang, Penang Island, Air Hitam Dam (LSUHC 11275, 11802) and Penang Hill (LSUHC 12071).

Tytthoscincus ishaki: West Malaysia: Pahang, Pulau Tioman, Gunung Kajang LSUHC 4429, 12582, ZRC 2.6157 (holotype), 2.6158–59 (paratypes).

Tytthoscincus jaripendek sp. nov.: West Malaysia: Pahang, Cameron Highlands, Robinson Falls LSUHC 11679, 11681, 11987 (paratypes), 11680 (holotype).

Tytthoscincus kakikecil sp. nov.: West Malaysia: Pahang, Fraser's Hill, Richmond Road [LSUHC 11769 (holotype)], Telecom Loop (LSUHC 11770, 11772). West Malaysia: Pahang, Genting Highlands, Ulu Kali LSUHC 12754, FMNH 19945. West Malaysia: Pahang, Cameron Highlands, Telom Valley ZRC 2.5944.

Tytthoscincus martae sp. nov.: West Malaysia: Pahang, Fraser's Hill, Hindu Temple LSUHC 12688 (holotype), ZRC 3.6246 (paratype). West Malaysia, Pahang, Genting Highlands, Awana Road LSUHC 12517–18, 12749, 12751 (paratypes), 12072.

Tytthoscincus perhentianensis: West Malaysia: Terengganu, Pulau Perhentian Besar LSUHC 8075 (holotype).

Tytthoscincus temengorensis: West Malaysia: Perak, Royal Belum Park DWNP 5018 (holotype). West Malaysia: Perak, Temengor Forest Reserve, Gibbon Trail LSUHC 5650 (paratype).