



Two new *Tytthoscincus* Linkem, Diesmos, & Brown (Squamata; Scincidae) from Peninsular Malaysia and another case of microsyntopy between ecologically specialized, unrelated, leaf-litter species

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Abstract

Two new species of diminutive, sympatric, lowland, leaf-litter skinks of the genus *Tytthoscincus* Linkem, Diesmos & Brown from the Sekayu region of Hulu Terengganu, Terengganu State in northeastern Peninsular Malaysia are described on the basis genetic and morphological data. One of the new species, *T. monticolus* **sp. nov.**, was collected in a hilly riparian area along Sungai (=river) Bubu and is most closely related to an undescribed species from the Tembak Reservoir area. The other, *T. keciktuek* **sp. nov.** collected along Sungai Peres, is most closely related to *T. perhentianensis* Grismer, Wood, & Grismer from Pulau (=island) Perhentian Besar. Sympatry and syntopy of multiple, specialized, unrelated, leaf-litter species of *Tytthoscincus* was previously only known from upland areas and these new species represent the first example of lowland of sympatry. More importantly, however, these endemic species add to a growing body of research and discoveries that continue to underscore the unrealized biodiversity of the riparian systems of Hulu Terengganu and the Sekayu region and their need for protection and continued study.

Key words: *Tytthoscincus*, niche partitioning, sympatry, new species, conservation, Malaysia

Introduction

The ecological associations of the diminutive, specialized, leaf-litter skinks of the Southeast Asian genus *Tytthoscincus* Linkem, Diemos, & Brown are proving more complicated than previously understood. Grismer *et al.* (2017a) reported a remarkable degree of microsyntopy (=multiple species occupying the same restrictive microhabitat) by as many as three species at multiple upland sites along the Titiwangsa Mountain Range of Peninsular Malaysia (Fig. 1). Similarly, Karin *et al.* (2016) reported syntopy between two upland species from Mount Penrissen, Sarawak. Surprisingly, none of the syntopic species were closely related (i.e. they did not form a monophyletic group) indicating that each had an independent origin in these upland refugia (see discussion in Grismer *et al.* 2017a). Additionally, Grismer *et al.* (2017a) demonstrated that Sundaic *Tytthoscincus* have a specialized body plan (i.e. elongate body and tail, reduced limbs and digits, and shorter head) adapted for locomotion through leaf-litter. They went on to demonstrate that some species are even more specialized than others along this ecomorphological trajectory and manifest additional semi-fossorial characteristics (e.g. a reduced to absent ear opening). They posited that differences in ecomorphology between some syntopic species likely contributes to resource partitioning within their restrictive, leaf-litter microhabitat. However, Grismer *et al.* (2017a)

also noted that ecomorphological differences do not explain the microsyntopy between other highly cryptic, unrelated species. Factoring together all these aspects of life history (i.e. multiple combinations of ecomorphological characters, independent refugial origins, non-monophyly, and crypsis) across various combinations of syntopic species at multiple localities is a clear indication that there is still much to learn about leaf-litter ecology.

Adding to this growing body of data, we describe here two new, unrelated, sympatric—and potentially syntopic—populations of *Tytthoscincus* from a lowland drainage system in the Sekayu region of Hulu Terengganu, Terengganu State along the east coast of Peninsular Malaysia (Fig. 2). Molecular evidence based on 1026 base pairs of the mitochondrial gene NADH dehydrogenase subunit 2 gene (ND2) indicate that a specimen (LSUHC 13858) taken from a hilly area near Sungai Bubu represents the sister population of an undescribed species from the Tembat Reservoir area (Grismer *et al.* 2017a). Another specimen (LSUHC 13859) taken from Sungai Peres, 1.3 km to the south, is most closely related to *T. perhentianensis* Grismer, Wood, & Grismer from Pulau (=island) Perhentian Besar. Each specimen is phylogenetically embedded within *Tytthoscincus* and bear the diagnostic characters of small temporal scales that are the same size and shape as the lateral body scales and short digits with toe IV being equal in length to toe III (Linkem *et al.* 2011). However, each manifests a combination of morphological and color pattern characters that separate them from all other *Tytthoscincus* and the molecular phylogeny indicates that neither is nested within any other known species.

Materials and methods

Phylogenetic analysis. A dataset composed of 1,026 bp of the mitochondrial gene NADH dehydrogenase subunit 2 (ND2) and its flanking tRNA regions ND2 was constructed from 66 individuals comprising 23 ingroup species of *Tytthoscincus* as well as two outgroup species *Larutia seribuatensis* and *Scincella melanosticta* were employed as outgroups (Linkem *et al.* 2011; Linkem 2013). Total genomic DNA was isolated from liver or skeletal muscle from specimens stored in 95% ethanol using the Maxwell RSC Tissue DNA kit on the Promega Maxwell RSC extraction robot. The ND2 gene was amplified using a double-stranded Polymerase Chain Reaction (PCR) under the following conditions: 1.0 ml genomic DNA (~10–33 mg), 1.0 ml (10 mM) light strand primer (5'-AAGCAGTTGGGCCCATACC-3': Macey *et al.* 1997), 1.0 l (10 mM) heavy strand primer (Tyttho948R 5'-KCGTCAYTTGTACTTGTGTTTGTGT-3'; Grismer *et al.* 2017) 1.0 ml dinucleotide pairs (1.5 mM), 2.0 ml 5x buffer (1.5 mM), 1.0 ml MgCl 10x buffer (1.5 mM), 0.18 ml Taq polymerase (5u/l), and 7.5 ml H₂O. PCR reactions were run on a Bio-Rad gradient thermocycler under the following conditions: initial denaturation at 95C for 2 min, followed by a second denaturation at 95C for 35 s, annealing at 52C for 35 s, followed by a cycle extension at 72C for 35 s, for 33cycles. All PCR products were visualized on a 1% agarose gel electrophoresis. Successfully amplified PCR products were then submitted to GENEWIZ for PCR purification, cycle sequencing, and sequencing. 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. All new sequences were deposited in GenBank (Table 1).

We applied two model-based methods for the phylogenetic analyses, Maximum Likelihood (ML) and Bayesian Inference (BI). The Bayesian Information Criterion (BIC) implemented in IQ-TREE (Nguyen *et al.*, 2015) calculated TVM+F+I+G4, HKY+F+I+G4, and TPM3+F+G4 to be the best-fit models of evolution for the first, second, and third codon positions, respectively (Kalyaanamoorthy *et al.* 2017). Maximum Likelihood analyses implemented in IQ-TREE employed 1000 bootstrap pseudoreplicates via the ultrafast bootstrap approximation algorithm (Minh *et al.* 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 *et al.*, 2010) using default priors. Models of evolution used were approximated from those calculated for the ML analysis and employed GTR+I+G for codon positions 1 and 3 and HKY+I+G for position 2. Two simultaneous runs were performed with four chains per run (three hot and one cold) using default priors. The simulation ran for 10 million generations, was sampled every 10,000 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 burnin using the sumt function. Convergence of all parameters and stationarity distributions were verified 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; Nguyen *et al.* 2015; Wilcox *et al.*, 2002). After removing outgroup taxa, MEGA7 (Kumar *et al.* 2016) was used to calculate uncorrected pairwise sequence divergence of the ingroup species.

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>Scincella melanosticta</i>	LSUHC 11575	West Malaysia, Kedah, Pulau Langkawi, Gunung Raya	KU872728
<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. panchoensis</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. sibuenis</i>	LSUHC 5583	West Malaysia, Johor, Pulau Sibiu	KU872743
<i>T. temmincki</i>	BS 10263	Indonesia, Java	KY989396
<i>T. textus</i>	JAM 7497	Indonesia, Sulawesi	KY989397
<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. bukitensis</i>	LSUHC 11655	West Malaysia, Pahang, Fraser’s Hill, Telecom Loop	forthcoming
<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, Air Hitam Dam	KY989408

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TABLE 1. (Continued)

Species	Voucher	Locality	GenBank no.
<i>T. butleri</i>	LSUHC 12071	West Malaysia, Penang, Penang Island, Air Hitam Dam	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> (previous 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 11802	West Malaysia, Penang, Penang Island, Air Hitam Dam	KY989412
<i>T. butleri</i>	LSUHC 9206	West Malaysia, Kedah, Pulau Langkawi, Gunung Raya	KU872732
<i>T. butleri</i>	LSUHC 11552	West Malaysia, Kedah, Pulau Langkawi, Gunung Raya	KU872737
<i>T. butleri</i>	LSUHC 13860	West Malaysia, Penang, Bukit Mertajam	MG907572
<i>T. ishaki</i>	LSUHC 5165	West Malaysia, Pahang, Pulau Tioman, Gunung Kajang	KY989413
<i>T. ishaki</i>	LSUHC 6150	West Malaysia, Pahang, Pulau Tioman, Gunung Kajang	KU872735
<i>T. ishaki</i>	LSUHC 6151	West Malaysia, Pahang, Pulau Tioman, Gunung Kajang	KY989414
<i>T. jaripendek</i> (paratype)	LSUHC 11681	West Malaysia, Pahang, Cameron Highlands, Robinson Falls	KU872745
<i>T. jaripendek</i> (holotype)	LSUHC 11679	West Malaysia, Pahang, Cameron Highlands, Robinson Falls	KU872746
<i>T. jaripendek</i> (paratype)	LSUHC 11680	West Malaysia, Pahang, Cameron Highlands, Robinson Falls	KU872747
<i>T. jaripendek</i> (paratype)	LSUHC 11987	West Malaysia, Pahang, Cameron Highlands, Robinson Falls	KU872748
<i>T. kakikecil</i> (holotype)	LSUHC 11769	West Malaysia, Pahang, Fraser's Hill, Richmond Rd.	KY989415
<i>T. kakikecil</i> (paratype)	LSUHC 11770	West Malaysia, Pahang, Fraser's Hill, Richmond Rd.	KY989416
<i>T. kakikecil</i> (paratype)	LSUHC 11772	West Malaysia, Pahang, Fraser's Hill, Telecom Loop	KY989417
<i>T. kakikecil</i> (paratype)	LSUHC 12754	West Malaysia, Pahang, Genting Highlands, Ulu Kali	KY989418
<i>T. keciktuek</i> sp. nov.	LSUHC 13859	West Malaysia, Terengganu, Sekayu, Sungai Peres	MG970573
<i>T. martae</i> (holotype)	LSUHC 12688	West Malaysia, Pahang, Fraser's Hill, Hindu Temple	KY989419

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TABLE 1. (Continued)

Species	Voucher	Locality	GenBank no.
<i>T. martae</i> (previous paratype of <i>T. bukitensis</i>)	ZRC 3.6246	West Malaysia, Pahang, Fraser's Hill, Bishop's Trail	KY989420
<i>T. martae</i> (paratype)	LSUHC 12749	West Malaysia, Pahang, Genting Highlands, Awana Rd.	KY989421
<i>T. martae</i> (paratype)	LSUHC 12518	West Malaysia, Pahang, Genting Highlands, Awana Rd.	KY989422
<i>T. martae</i> (paratype)	LSUHC 12751	West Malaysia, Pahang, Genting Highlands, Awana Rd.	KY989423
<i>T. martae</i> (paratype)	LSUHC 12517	West Malaysia, Pahang, Genting Highlands, Awana Rd.	KY989424
<i>T. monticolus</i> sp. nov.	LSUHC 13858	West Malaysia, Terengganu, Sekayu, Sungai Bubu	MG970574
<i>T. perhentianensis</i> (holotype)	LSUHC 9206	West Malaysia, Terengganu, Pulau Perhentian Besar	KU872742
<i>T. temasekensis</i> (holotype)	ZRC 2.6490	Pasir Laba Road, Singapore	KY9893945
<i>T. temengorensis</i> (paratype)	LSUHC 5650	West Malaysia, Perak, Temengor Forest Reserve	KU872744
<i>Tythoscincus</i> sp. nov.	LSUHC 12515	West Malaysia, Terengganu, Tembat Forest Reserve	MG182075

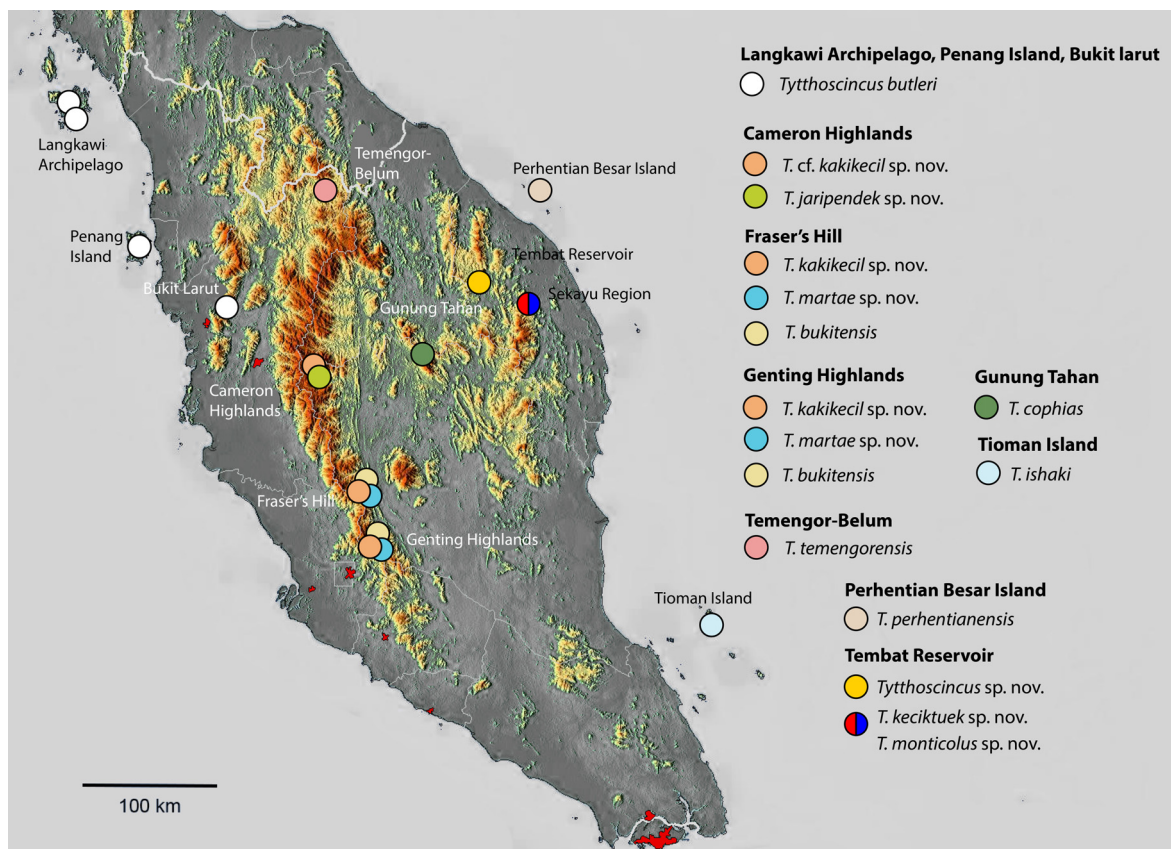


FIGURE 1. Distribution of the species of the montane clade of *Tythoscincus* in Peninsular Malaysia.

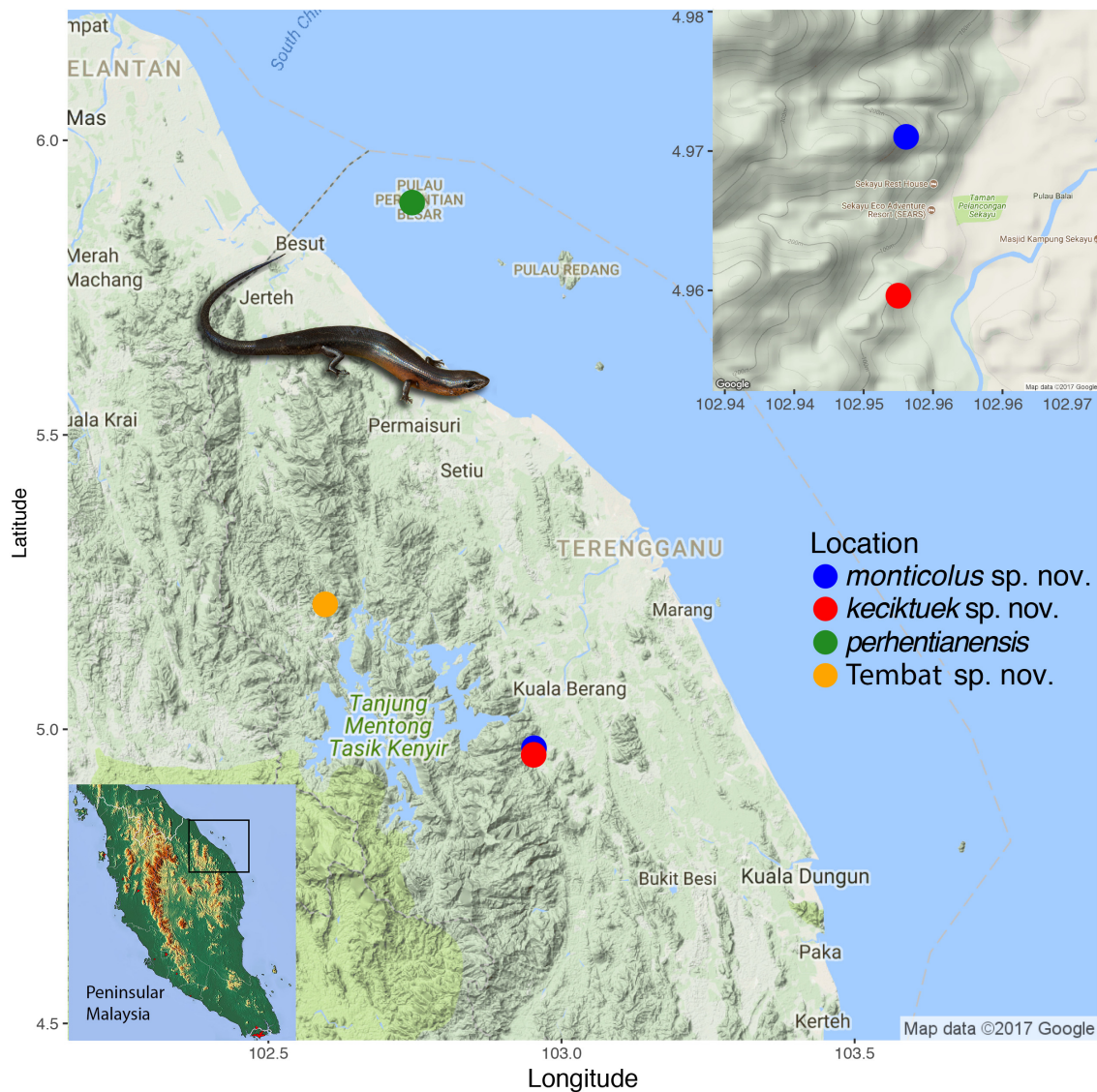


FIGURE 2. Type localities for *Tythoscincus keciktuek* **sp. nov.** and *T. monticolus* **sp. nov.** and their closest relatives *T. perhentianensis* and *Tythoscincus* **sp. nov.**, respectively, in Peninsular Malaysia.

Morphological analysis. All measurements were made with Mitutoyo digital calipers to the nearest 0.1 mm by LLG. Scale counts were taken on the right side of the body when possible using a Nikon SMZ 1500 dissecting microscope. Scale terminology is modified from Grismer *et al.* (2017a) and Taylor (1935) and head scales are illustrated in Figure 3. Measurements and scale counts used are snout-vent length (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; head width (HW) measured at the widest part of the head posterior to the eyes; ear opening diameter (EO) measured from the anterior to the posterior margin of the ear opening; 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 point 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.

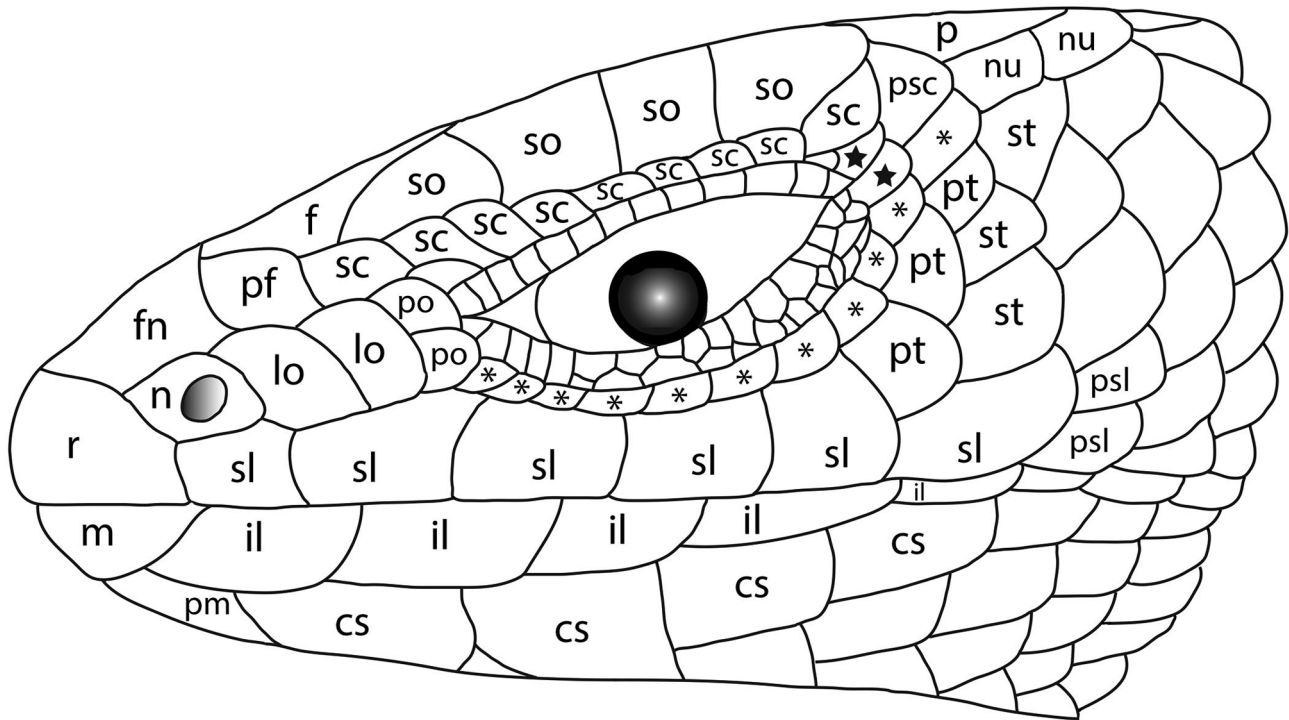


FIGURE 3. Generalized illustration of head scale terminology of *Tytthoscincus* adapted from Grismer *et al.* (2017a) and Taylor (1935). cs = chinshield; fn = frontonasal; il = infralabial; lo = loreal; m = mental; n = nasal; p = parietal; pf = prefrontal; pm = postmental; po = preorbital; psc = postsuperciliary; psl = postsupralabial; pt = primary temporal; r = rostral; sc = superciliary; sl = supralabial; so = supraorbital; st = secondary temporal; asterisk = subocular; and star = postocular.

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 the notation of a ` [e.g. 8`1]), supraoculars, loreals, supralabials, infralabials, nuchals, postoculars, 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 precloacal and pectoral scales, texture of subdigital lamellae, and the depth and degree of development of the tympanum. Color pattern characters examined were the degree of light speckling on the dorsum, the presence of dorsolateral striping, and overall ground color.

The sample size of each new population ($n=1$) was too small to test for significant mean differences in the morphological data however Principal Component Analysis (PCA) and Discriminant Analysis of Principal Components (DAPC) were used to determine the degree to which the morphospacial variation among the populations coincided with putative species boundaries delimited by the molecular phylogenetic analyses. Three PCAs and corresponding DAPCs were run on each category of data (meristic, mensural and concatenated) and compared. PCA, implemented by the `prcomp` command in R v 3.2.1 (R Core Team, 2015), searches for the best overall low-dimensional representation of significant morphological variation in the data. Characters used in the PCAs and DAPCs were discrete meristic data from the scale counts MB, PV, VS, 3FL, and 4TL and continuous mensural data from EO, HL, HW, AXG, FL, and HDL. To reduce the effects of body size in the latter, only adults ($SVL \geq 30$ mm determined by the possession eggs or through dissection) were used and mensural data were converted to ratiometric data by dividing EO by HL and dividing HL, AXG, FL, and HDL by SVL. These data were then natural log-transformed and scaled to their standard deviation prior to the PCA analysis in order to normalize their distribution so as to ensure characters with very large and very low values did not over-leverage the results owing to intervariable nonlinearity and to transform meristic and mensural data into comparable units for the concatenated analysis.

To characterize clustering and separation in morphospace, DAPC analyses were performed to search for linear combinations of morphological variables having the greatest between-group variance and the smallest within-group variance (Jombart *et al.* 2010). DAPC relies on log transformed data from the PCA as a prior step to ensure that variables analyzed are not correlated and number fewer than the sample size. Principal components with eigenvalues greater than one were retained for the DAPC according to the criterion of Kaiser (1960). All statistical analyses were performed using the platform R v 3.2.1 (R Core Team 2015).

Specimens examined are listed in the Appendix. Museum acronyms follow Sabaj (2016) except for the following non-standard acronyms for the Sabah Parks (SP), Sabah, East Malaysia; La Sierra University Herpetological Collection (LSUHC), La Sierra University, Riverside, California, USA; Rafe M. Brown field series (RMB), University of Kansas, Lawrence, Kansas, USA; and Jimmy A. McGuire field series (JAM), University of California, Berkeley, California, USA.

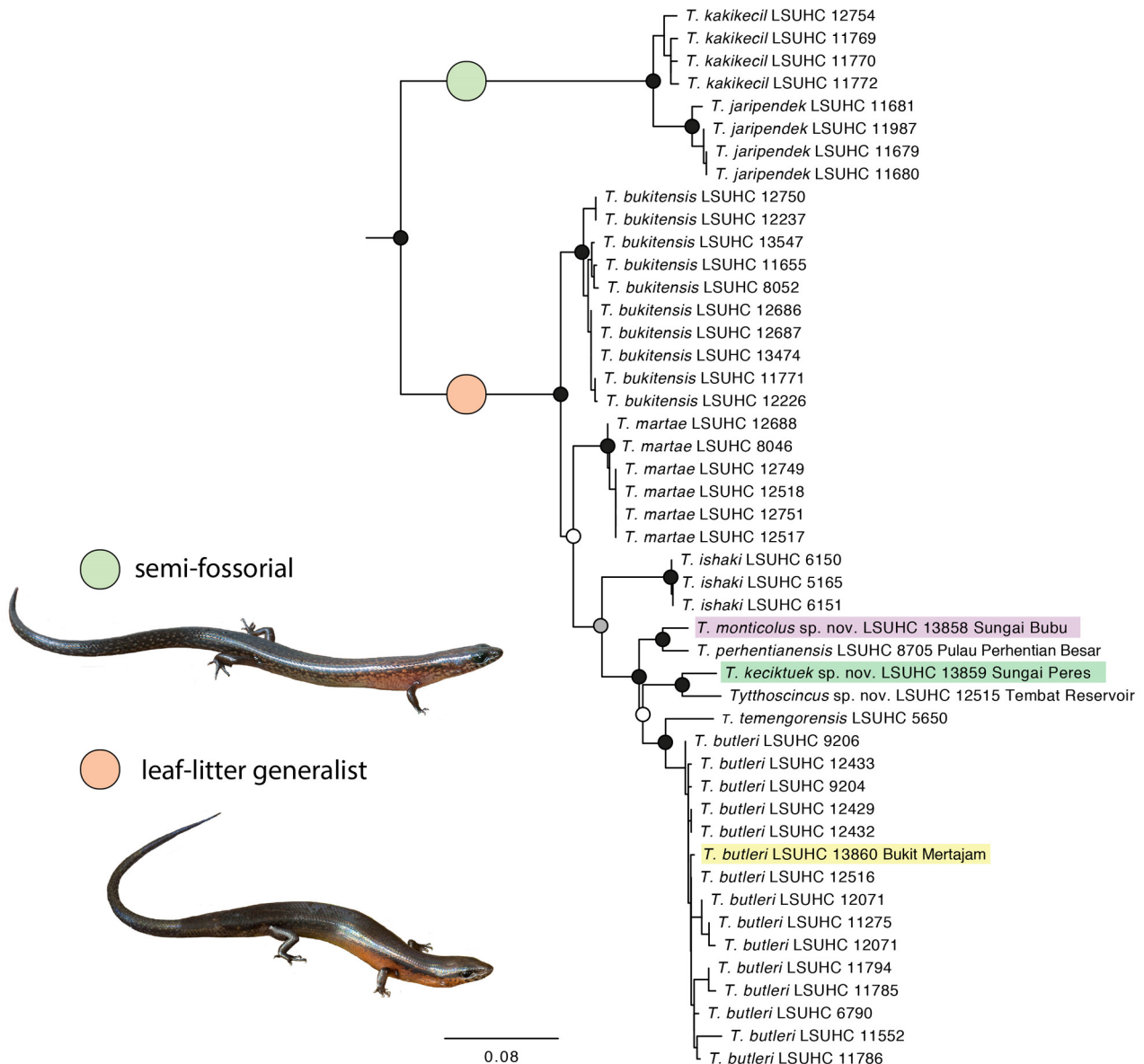


FIGURE 4. Maximum Likelihood phylogram depicting the relationships of species within the montane clade of *Tythoscincus* and the delimitation of the semi-fossorial and leaf-litter generalist lineages. Black circles denote nodal Bayesian support ≥ 0.95 and ultrafast bootstrap support ≥ 95 , grey circle denotes nodal Bayesian support ≥ 0.95 only, and the white circle denotes poor Bayesian and ultrafast bootstrap support.

Results

Both phylogenetic analyses recover the new populations from the Sekayu region to be deeply nested within the montane clade (*sec. Grismer et al. 2017a*) of *Tytlhoscincus* from Peninsular Malaysia and not members of the lowland swamp clade (*sec. Grismer et al. 2016, 2017b*) nor are they each other's closest relatives despite their occurrence in the same area (Fig. 4). The Sungai Peres specimen represents the well-supported (1.00/100) sister population of *Tytlhoscincus* **sp. nov.** from the Tembat Reservoir area 46 km to the northeast (Fig. 2) and the Sungai Bubu specimen represents the well-supported (1.00/100) sister population of *T. perhentianensis* from Pulau Perhentian Besar 102 km to the north off the east coast of Terengganu. Collectively these four populations are part of a well-supported clade (1.00/100) of montane species that also contains *T. temengorensis* Grismer, Ahmad, & Chan and *T. butleri* (Boulenger). The analyses also recovered a new lowland population of the latter at Bukit Mertajam, Penang (Fig. 1).

All three PCA analyses agree with the molecular analyses in showing wide morphological separation between the new populations. The analyses indicate that the overall morphology of the new populations aligns itself within that of the leaf-litter generalist lineage and not the semi-fossorial lineage (Fig. 5). Seventy-six percent of the total meristic variation occurs along principal components 1 and 2 (PC1 and PC2) with PC1 loading most heavily for finger and toe lamellae (3FT and 4TL) and PC2 loading most heavily for midbody scale rows (MB; Table 2). Sixty-nine percent of the total mensural variation occurs along PC1 and PC2 with PC1 loading most heavily for limb length (FL and HDL) and PC2 loading most heavily for axilla-groin length (AXG; Table 3). In the concatenated data set, 56% of the total morphological variation occurs along PC1 and PC2 with PC1 loading most heavily for finger and toe lamellae (3FT and 4TL) and limb length (FL and HDL) and PC2 loading most heavily for head length (HL; Table 4). The DAPC analyses also show wide separation between the new populations, especially in

TABLE 2. Summary statistics and principal component scores for the meristic characters. Abbreviations are in the Materials and methods.

	PC1	PC2	PC3	PC4	PC5
Standard deviation	1.726706425	0.896550623	0.787758724	0.629099753	0.445366811
Proportion of Variance	0.5963	0.16076	0.12411	0.07915	0.03967
Cumulative Proportion	0.5963	0.75706	0.88118	0.96033	1
Eigenvalue	2.981515078	0.80380302	0.620563807	0.395766499	0.198351596
MB	-0.390946311	0.646046341	-0.419007374	0.500462163	-0.061282549
PV	-0.449464801	-0.5262483	0.185742696	0.538087082	0.443853651
VS	-0.394633579	0.370751392	0.817363502	-0.121503728	-0.154795004
3FL	-0.494899904	0.07485671	-0.27619696	-0.653771502	0.495750563
4TL	-0.494449996	-0.403270048	-0.213458697	-0.13349001	-0.727673191

TABLE 3. Summary statistics and principal component scores for the mensural characters. Abbreviations are in the Materials and methods.

	PC1	PC2	PC3	PC4	PC5
Standard deviation	1.563007138	0.988917268	0.958416951	0.721841766	0.373406933
Proportion of Variance	0.4886	0.19559	0.18371	0.10421	0.02789
Cumulative Proportion	0.4886	0.68419	0.8679	0.97211	1
Eigenvalue	2.442991312	0.977957363	0.918563052	0.521055536	0.139432737
AXG	-0.299207765	0.791038936	-0.251257488	0.459149893	0.103842026
TD	0.388602453	0.010405098	0.688921209	0.611769467	0.002357048
HL	0.357957318	-0.392023296	-0.655364453	0.516736287	0.147191498
FL	0.562426421	0.340275846	-0.180584044	-0.156935541	-0.714597445
HDL	0.561253888	0.323541682	-0.012003344	-0.351104459	0.675941146

TABLE 4. Summary statistics and principal component scores for the concatenated data set. Abbreviations are in the Materials and methods.

	PC1	PC2	PC3	PC4	PC5	PC6
Standard deviation	2.105105781	1.322073966	1.061288981	1.012899467	0.873712645	0.746026258
Proportion of Variance	0.40286	0.1589	0.10239	0.09327	0.0694	0.0506
Cumulative Proportion	0.40286	0.56176	0.66415	0.75742	0.82682	0.87742
Eigenvalue	4.431470349	1.747879572	1.1263343	1.025965331	0.763373786	0.556555177
SVL	-0.026529229	0.689638636	-0.176371675	0.046690547	-0.028332713	0.163066275
AXG	-0.198579833	0.333844617	0.443026445	0.428466935	0.212720141	-0.283791852
TD	0.261589839	0.11739183	-0.55232448	0.032436936	-0.2288248	-0.588904913
HL	0.213502288	-0.559624293	0.180488925	0.176646158	-0.109778765	-0.029736787
FL	0.365144326	-0.051067716	-0.027862412	0.539321221	0.173380751	0.050478462
HDL	0.37298243	0.031069936	-0.119941742	0.411671928	0.293118013	0.009286205
MB	0.288289404	0.18594748	0.29188893	0.122046504	-0.572902352	0.434805923
PV	0.315226577	0.126260577	0.218411482	-0.369376177	0.566893053	0.085292408
VS	0.258455009	0.120564321	0.524423997	-0.225196637	-0.207993839	-0.570619611
3FL	0.403311267	0.131570211	-0.016899316	-0.091452296	-0.20978747	0.102970769
4TL	0.401828274	0.006943052	-0.091597509	-0.333508239	0.191570144	0.100016441

	PC7	PC8	PC9	PC10	PC11
Standard deviation	0.710894229	0.61277858	0.439301445	0.398613439	0.340110068
Proportion of Variance	0.04594	0.03414	0.01754	0.01444	0.01052
Cumulative Proportion	0.92336	0.9575	0.97504	0.98948	1
Eigenvalue	0.505370604	0.375497588	0.19298576	0.158892674	0.115674858
SVL	-0.100492297	0.385854267	-0.439713573	0.202711469	-0.263803414
AXG	0.493198233	0.111895436	0.209947426	0.10496361	0.180580831
TD	0.380722069	-0.186406674	-0.107263995	-0.132549303	-0.02265565
HL	0.290075787	0.458096392	-0.492616496	0.138146372	-0.093648035
FL	-0.161354463	-0.072786682	0.292973317	-0.087575226	-0.644184063
HDL	-0.349591691	-0.135311906	-0.253859267	0.106594207	0.61132974
MB	0.244842413	-0.435701548	-0.108420298	-0.008113426	0.057797294
PV	0.25613488	-0.147088693	-0.280364373	-0.441439395	-0.105794741
VS	-0.439937838	-0.031818369	-0.068764178	0.114491171	-0.108021158
3FL	-0.011152321	0.598250116	0.415576803	-0.390470234	0.271233796
4TL	0.223811019	-0.001548737	0.300545919	0.729174478	-0.006966654

Continued.

regard to body shape (mensural data) where the Sungai Bubu specimen has a notably larger ear opening, shorter head, and shorter limbs than the Sungai Peres specimen (Table 5). Given the corroboration between the molecular and morphological data, these species are described below.

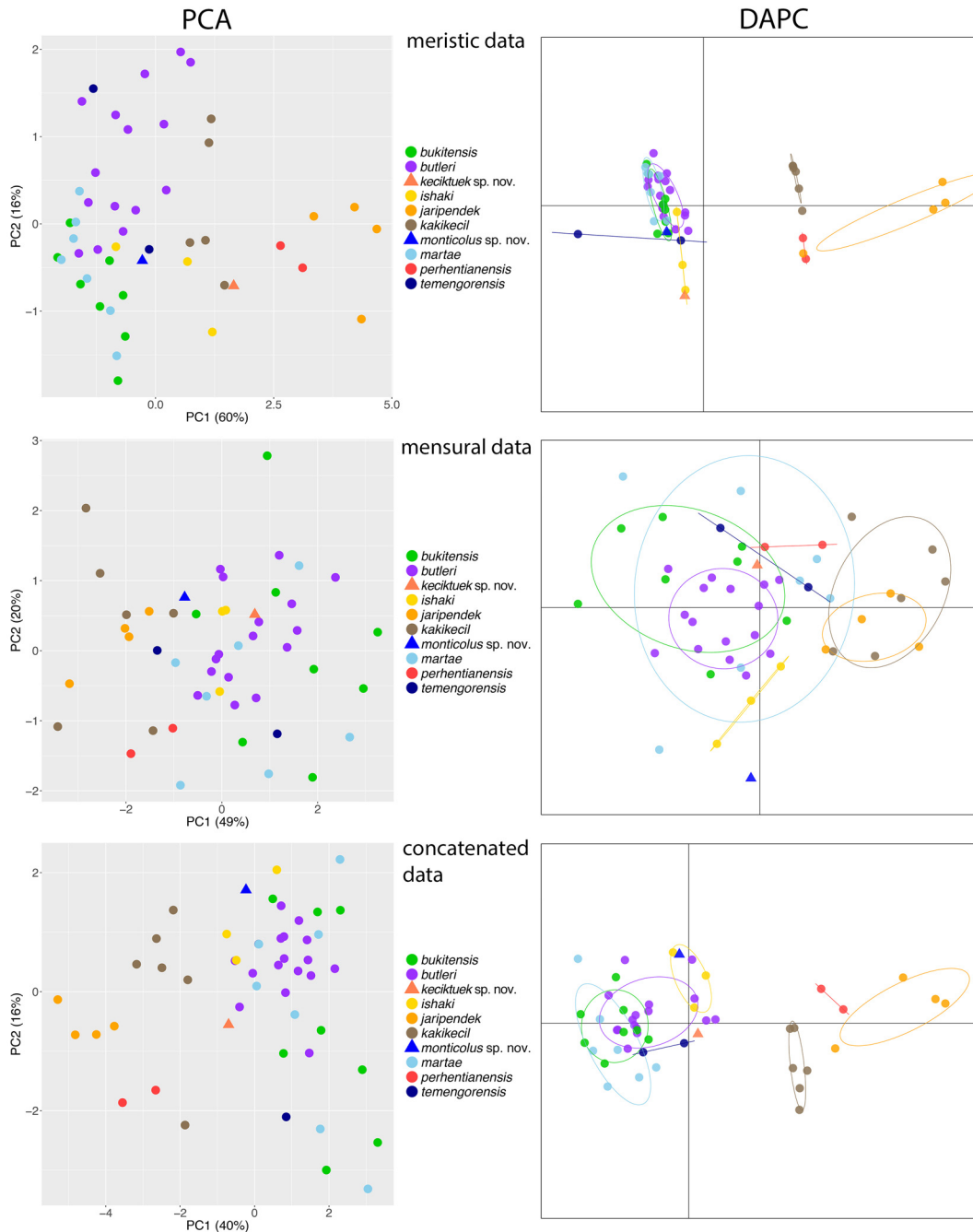


FIGURE 5. Plots of the principal component analyses (PCA) and discriminant analyses of principal components (DAPC) for the meristic, mensural, and concatenated data sets illustrating the morphological separation of *Tythoscincus monticolus* sp. nov. and *T. keckituek* sp. nov.

TABLE 5. Meristic and mensural characters of the type specimens.

	LSUHC 13859 <i>keciktuek</i> sp. nov.	LSUHC 13858 <i>monticolus</i> sp. nov.
Supralabials	6	6
Infralabials	5	5
Supraoculars	4	4
Frontoparietal contacting supraoculars 2,3,4	yes	yes
Superciliaries	8`1	7`1
Prefrontals in contact	yes	yes
Loreals	1	2
Tympanum shallow, pigmented	no	no
Midbody scale rows	31	30
Dorsal scales striated	no	no
Paravertebral scale rows	69	66
Ventral scale rows	68	60
Enlarged pectoral scales	yes	yes
Enlarged precloacal scales	yes	yes
3rd finger lamellae	7	7
4th toe lamellae	12	11
Lamellae texture	keeled	keeled
HL	6.4	7.5
HW	3.8	4.4
EO	1.0	0.9
AXG	20.0	19.7
FL	8.0	9.0
HDL	12.1	13.4
SVL	36.6	36.2
HL/SVL	0.17	0.21
HW/SVL	0.10	0.12
EO/HL	0.16	0.12
AXG/SVL	0.55	0.54
FL/SVL	0.22	0.25
HDL/SVL	0.33	0.37
Sex	male	female

Systematics

Tythoscincus monticolus sp. nov.

Suggested common names: Sungai Bubu Forest Skink and Mengkarung Hutan Sungai Bubu (Fig. 6)

Holotype. Adult male (LSUHC 13858) collected from a hilly area near Sungai Bubu, Sekayu, Hulu Terengganu, Terengganu State, Peninsular Malaysia (4.9710° N, 102.9531° E; 174 m in elevation) by M. Afiq-Shuhaimi and Baizul-Hafsyam B. S. on 5 August 2017.

Diagnosis *Tythoscincus monticolus* sp. nov. can be differentiated from all other species of *Tythoscincus* in the upland clade by having the combination of 8`1, superciliaries; a deeply set, unpigmented tympanum; enlarged

pectoral scales; 31 midbody scale rows; 69 paravertebral scales; 68 ventral scales; keeled, subdigital lamellae; seven subdigital lamellae on the third finger; 12 subdigital lamellae on the fourth toe; EO/HL = 0.16; HL/SVL = 0.17; AXG/SVL = 0.55; FL/SVL = 0.22; HDL/SVL = 0.33; and a maximum SVL of 36.6 mm (Tables 5,6). All 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).



FIGURE 6. Upper: type specimen (LSUHC 13858) of *Tytthoscincus monticolus* **sp. nov.** collected from a hilly area near Sungai Bubu, Sekayu, Hulu Terengganu, Terengganu State, Peninsular Malaysia. Photograph by A. B. Ahmad. Middle: type specimen (LSUHC 13859) of *Tytthoscincus keciktuek* **sp. nov.** collected along a small tributary of the Sungai Peres, Sekayu, Hulu Terengganu, Terengganu State, Peninsular Malaysia. Photograph by A. B. Ahmad. Lower: *Tytthoscincus butleri* (LUSHC 13860) from a new lowland locality at Bukit Mertajam, Penang, Peninsular Malaysia. Photograph by E.S.H. Quah.

Description of holotype. Adult male, SVL 36.6 mm; regenerated tail length 29.4 mm; axilla-groin length 20.0 mm; head length 6.4 mm; head width 3.8 mm; rostral wider than long, in broad contact with frontonasal; frontonasal wider than long; prefrontals large, in broad contact on midline; frontal elongate, triangular, 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; six nuchal scales; nasals small, widely separated, trapezoidal, contacting rostral anteriorly, frontonasal dorsally, loreal posteriorly, first supralabial ventrally; nostril in center of nasal; supranasals absent; loreal single; upper and lower preocular present; lower preocular followed

by a series of seven suboculars; eight superciliaries, posterior superciliary elongate and projecting dorsomedially; two postoculars; one postsuperciliary; six supralabials, third, fourth, and fifth below eye; two postsupralabials; two primary temporals; four secondary temporals, uppermost contacting parietal; 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 1.0 mm, circular, 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; 69 paravertebral scale rows; 68 ventral scale rows; slightly enlarged median precloacal scales overlapping outer precloacal scales; tail slightly compressed 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 surfaces slightly larger than those of ventral and posterior surfaces; palmar and plantar scales raised; and digits moderate in length, scales on dorsal surfaces in single row, subdigital lamellae keeled, seven on third finger, 12 on fourth toe.

Coloration in life (Fig. 6). Overall dorsal ground color of head, body, limbs, and tail dark-brown; hind limbs darker than forelimbs, both limbs mottled; top of head and body speckled with light-colored markings, those above the shoulder tending to coalesce to form a diffuse dull-orange stripe; supralabials and infralabials alternately banded with light and dark bars; dorsal portion of flanks dark, highlighting the light-colored dorsal spots; all ventral surfaces dull-yellow to beige, generally immaculate; distal portions of forelimbs and palmar surfaces dark; planter surface dark; and subcaudal region stippled with dark-brown.

Distribution. *Tytthoscincus monticolus* sp. nov. is known only from the type locality near the Sungai Bubu, Terengganu, Peninsular Malaysia (Fig. 2), however, it is likely to range throughout the entire lowland system of the Sekayu region.

Natural history. The holotype of *Tytthoscincus monticolus* sp. nov. (LSUHC 13858) is a leaf-litter species inhabiting hilly areas along riparian systems in lowland dipterocarp forest (Fig. 7) and was captured in a pitfall trap.

Etymology. The specific epithet *monticolus*, comes from the Latin *monti* meaning mountain and *colus* meaning dweller of or within and refers to this species inhabiting hilly areas.

Comparisons. *Tytthoscincus monticolus* sp. nov. is most closely related to *T. perhentianensis* (Fig. 4) and differs from it by an uncorrected pairwise sequence divergence of 3.5%. It is differentiated from *T. perhentianensis* morphologically by having one vs. two loreal scales; 69 vs. 65 or 66 paravertebral scales; 68 vs. 61 or 62 ventral scales; seven vs. six subdigital lamellae on the third finger; and 12 vs. 10 subdigital lamellae on the fourth toe. It differs further by having a larger ear opening (0.16 vs 0.13–0.14 EO/HL); a shorter head (0.17 vs. 0.22–0.23 HL/SVL); longer hind limbs (0.33 vs. 0.29–0.30 HDL/SVL); and a larger maximum SVL (36.2 mm vs. 30.0 mm: Table 6). It differs from *T. keciktuek* (see description below) with which it is likely syntopic by an uncorrected pairwise sequence divergence of 9.8% and having one vs. two loreals; 68 vs 60 ventral scale rows; a larger ear opening (0.16 vs 0.12 EO/HL); a shorter head (0.17 vs. 0.21 HL/SVL); shorter forelimbs (0.22 vs. 0.25 FL/SVL); shorter hind limbs (0.33 vs. 0.37 HDL/SVL); and a dorsal pattern bearing white speckling vs. being nearly unicolor (Table 5; Fig. 6). Differences between *T. monticolus* sp. nov. and all other species of the upland clade are presented in Table 6.

***Tytthoscincus keciktuek* sp. nov.**

Suggested common names: Sungai Peres Forest Skink and Mengkarung Hutan Sungai Peres (Fig. 6)

Holotype. Adult female (LSUHC 13859) collected along a small tributary of the Sungai Peres, Sekayu, Hulu Terengganu, Terengganu State, Peninsular Malaysia (4.9596° N, 102.9596° E; 74 m in elevation) by Murni-Azima, Amirrudin B. Ahmad, and M. Afiq-Shuhaimi. on 17 September 2017.

Diagnosis. *Tytthoscincus keciktuek* sp. nov. can be differentiated from all other species of *Tytthoscincus* in the upland clade by having the combination of 7⁺1, superciliaries; a deeply set, unpigmented tympanum; enlarged

pectoral scales; 30 midbody scale rows; 66 paravertebral scales; 60 ventral scales; keeled, subdigital lamellae; seven subdigital lamellae on the third finger; 11 subdigital lamellae on the fourth toe; EO/HL = 0.12; HL/SVL = 0.21; AXG/SVL = 0.54; FL/SVL = 0.25; HDL/SVL = 0.37; and a maximum SVL of 36.2 mm (Tables 5,6). 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 36.2 mm; broken tail length 31.1 mm; axilla-groin length 19.7 mm; head length 7.5 mm; head width 4.4 mm; rostral wider than long, in broad contact with frontonasal; frontonasal wider than long; prefrontals large, in broad contact on midline; frontal elongate, triangular, 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; six nuchal scales; nasals small, widely separated, trapezoidal, contacting rostral anteriorly, frontonasal dorsally, first loreal posteriorly, first supralabial ventrally; nostril in center of nasal; supranasals absent; two loreals; upper and lower preocular present; lower preocular followed by a series of six suboculars; seven superciliaries, posterior superciliary elongate and projecting dorsomedially; one postsuperciliary; two postoculars; six supralabials, third, fourth, and fifth below eye; two postsupralabials; two primary temporals; four secondary temporals, uppermost contacting parietal; 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 0.9 mm, circular, lacking anterior lobules; and tympanum deeply set, non-pigmented.

Body scales smooth, cycloid, imbricate; ventral scales slightly larger than dorsal scales; 30 longitudinal scale rows around midbody; 66 paravertebral scale rows; 60 ventral scale rows; slightly enlarged median preloacal scales overlapping outer preloacal scales; tail round in cross-section; subcaudals slightly larger than dorsal caudals anteriorly; limbs relatively robust, short (FL/SVL = 0.25; HDL/SVL = 0.37), widely separated when adpressed; scales of dorsal surfaces slightly larger than those of ventral and posterior surfaces; palmar and plantar scales raised; and digits moderate in length, scales on dorsal surfaces in single row, subdigital lamellae keeled, seven on third finger, 11 on fourth toe.

Coloration in life (Fig. 6). Overall dorsal ground color of head, body, limbs, and tail brown, generally patternless and lacking light-colored speckles; top of head weakly speckled with dark-colored markings; rostrum light-colored; diffuse, immaculate, dull-orange, dorsolateral stripe extends from parietal region to anterior margin of flank before fading; supralabials and infralabials alternately banded with light and dark bars; dorsal portion of flanks slightly lighter than dorsum; all ventral surfaces dull-yellow to beige, generally immaculate; distal portions of forelimbs and palmer surfaces dark; planter surface dark; and wide, dark, diffuse lateral strip on tail.

Distribution. *Tytthoscincus keciktuek* **sp. nov.** is known only from the type locality along the Sungai Peres, Terengganu, Peninsular Malaysia (Fig. 2), however, it is likely to range throughout the entire riparian system of the Sekayu region.

Natural history. *Tytthoscincus keciktuek* **sp. nov.** (LSUHC 13859) is a leaf-litter species inhabiting riparian systems in lowland dipterocarp forest (Fig. 7). The holotype (captured in a pitfall trap) is a gravid female indicating that September falls within the reproductive season of this species.

Etymology. The name "*keciktuek*", is a colloquial word in the local dialect of rural Terengganu that means "small, small things" and refers to all small animals. It is used here in reference to the small size of all the species of the upland clade of *Tytthoscincus*.

Comparisons. *Tytthoscincus keciktuek* **sp. nov.** is most closely related to the undescribed species from the Tembak Reservoir area from which it differs by an uncorrected pairwise sequence divergence of 5.3%. Unfortunately, the Tembat specimen was so badly damaged by insects in a pitfall trap that no morphological data were unobtainable. Differences between *T. keciktuek* **sp. nov.** and *T. monticolus* **sp. nov.** are presented above. Differences between *T. keciktuek* **sp. nov.** and all other species of the upland clade are presented in Table 6.

TABLE 6. Scale counts, summary statistics and morphometric ratios of selected characters of the montane clade of *Typhlosincus* from Peninsular Malaysia. DNP = tympanum deep and non-pigmented; SP = tympanum shallow and pigmented

	<i>butleri</i>	<i>buktensis</i>	<i>jarpendek</i>	<i>temengorenensis</i>	<i>perhentianensis</i>	<i>keckituek</i> sp. nov.	<i>monticolus</i> sp. nov.	<i>ishaki</i>	<i>kakkecil</i>	<i>martae</i>	<i>cophias</i>
Supralabials	6	6	6	6	6	6	6	6	6	6	6
Infralabials	5, 6	5	5	5	5, 6	5	5, 6	5, 6	5, 6	5, 6	6
Superciliaries	9'1	8'1, 9'1, 9'2, 10'2	8'1	7'1	9'1	7'1	8'1	9'1	8'1, 9'1, 9'2, 10'2	8'1, 9'1, 10'2	8'1
Loreals	1, 2	2	1, 2	2	2	2	1	1, 2	1, 2	2	2
Tympanum	DNP	DNP	SP	DNP	DNP	DNP	DNP	DNP	SP	DNP	SP
Pectoral scales enlarged	yes(10), no(11)	yes(9), no(1)	no	yes	yes	yes	yes	no	yes	yes	yes
Lamellae texture	keeled	keeled	keeled	keeled	smooth	keeled	keeled	keeled	keeled	keeled	keeled
Midbody scales	32–38	31–35	28–30	30–35	29, 30	30	31	30–32	30–33	31–35	23
Mean	34.2	32.5	29.3	32.5	29.5	/	/	30.7	32.2	33.3	23.0
SD	±1.8	±1.3	±1.0	±3.6	±0.7	/	/	±1.1	±1.3	±1.3	±0.0
n	20	8	4	2	2	1	1	3	6	7	1
Paravertebral scales	60–75	71–74	63–65	68–70	65, 66	66	69	68–73	67–73	70–74	56
Mean	68.9	72.9	64.3	69.0	65.5	/	/	70.0	69.8	72.3	56.0
SD	±3.4	±1.2	±1.0	±1.4	±0.7	/	/	±2.6	±2.2	±1.4	±0.0
n	20	8	4	2	2	1	1	3	6	7	1
Ventral scales	62–73	64–74	60–62	70, 71	61, 62	60	68	60–70	65–69	61–72	56
Mean	67.6	68.3	60.6	70.5	61.5	/	/	65.3	67.0	68.4	56.0
SD	±3.1	±3.5	±1.0	±0.7	±0.7	/	/	±5.0	±1.5	±3.5	±0.0
n	20	8	4	2	2	1	1	3	6	7	1
3rd finger lamellae	6–8	7	5 or 6	7, 8	6	7	7	7	6	7	5
Mean	7	7	5.1	7.5	6	/	/	7.0	6	7	5.0
SD	±0.4	±0.0	±0.5	±0.7	±0.0	/	/	±0.0	±0.0	±0.0	±0.0
n	20	8	4	2	1	1	1	3	6	7	1
4th toe lamellae	10–13	12 or 13	9 or 10	11	10	11	12	11	10	12 or 13	10
Mean	11.6	12.4	9.5	11	10	/	/	11.0	10	12.7	10.0
SD	±0.8	±0.5	±0.6	±0.0	±0.0	/	/	±0.0	±0.0	±0.5	±0.0
n	20	8	4	2	1	1	1	3	6	7	1

.....continued on the next page

TABLE 6. (Continued)

	<i>butleri</i>	<i>bukitensis</i>	<i>jaripendek</i>	<i>temngorensis</i>	<i>perhantianensis</i>	<i>keckituek</i> sp. nov.	<i>monticolus</i> sp. nov.	<i>ishaki</i>	<i>kakikecil</i>	<i>mariae</i>	<i>cophias</i>
TD/HL	0.13–0.16	0.12–0.16	0.11–0.13	0.13	0.13–0.14	0.12	0.16	0.13–0.16	0.10–0.12	0.12–0.16	0.15
Mean	0.14	0.14	0.12	0.13	0.14	/	/	0.14	0.11	0.13	0.15
SD	±0.01	±0.01	±0.01	±0.0	±0.01	/	/	±0.2	±0.01	±0.02	±0.0
n	18	8	4	2	2	1	1	3	6	7	1
HL/SVL	0.19–0.21	0.19–0.24	0.18–0.19	0.21–0.23	0.22–0.23	0.21	0.17	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
n	18	8	4	2	2	1	1	3	6	7	1
AXG/SVL	0.50–0.57	0.48–0.63	0.55–0.57	0.50–0.57	0.54–0.55	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
n	16	8	4	2	2	1	1	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	0.25	0.22	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
n	18	8	4	2	2	1	1	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	0.37	0.33	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
n	18	8	4	2	2	1	1	3	6	7	1
Maximum SVL	40.9	42.6	33.9	35.5	30.0	36.2	36.6	41.0	36.2	44.0	35.9



FIGURE 7. Left: General habitat of *Tythoscincus monticolus* **sp. nov.** and *T. keciktuek* **sp. nov.** from the Sekayu region of Hulu Terengganu. Photograph by L. L. Grismer. Upper right: microhabitat at the type locality of *T. monticolus* **sp. nov.** near Sungai Bubu, Sekayu, Hulu Terengganu, Terengganu State, Peninsular Malaysia. Photograph by M. Afiq-Shuhaimi. Lower right: microhabitat at the type locality of *T. keciktuek* **sp. nov.** from Sungai Peres, Sekayu, Hulu Terengganu, Terengganu State, Peninsular Malaysia. Photograph by M. Aqmal-Naser.

Discussion

Grismer *et al.* (2017a) demonstrated that the montane clade of *Tythoscincus* in Peninsular Malaysia contained a lineage of semi-fossorial species and a lineage of leaf-litter generalists. Species of both lineages possess all the ecomorphological specializations common to leaf-litter skinks (Greer 1989; Schmitz *et al.* 2005; Brandley *et al.* 2008; Siler & Brown 2011; Lee *et al.* 2013; Wu *et al.* 2015) but that species in the semi-fossorial lineage have evolved further along this trajectory. The molecular data recover *T. monticolus* **sp. nov.** and *T. keciktuek* **sp. nov.** as being nested within the leaf-litter generalist lineage and the PCA and DAPC analyses indicate they align themselves morphologically with this lineage as well (Fig. 5). Grismer *et al.* (2017a) noted that ecomorphological differences between syntopic, semi-fossorial and leaf-litter species may contribute to resource partitioning, allowing them to co-exist in their restrictive leaf-litter microhabitat. Although the two new species are nested within the leaf-litter lineage of the montane clade, *T. monticolus* **sp. nov.** has a notably more semi-fossorial body shape (shorter head and limbs) than *T. keciktuek* **sp. nov.** (Table 5). Collectively, these data underscore our lack of knowledge regarding the life history of these small, secretive skinks or the microhabitat complexity within a pile of leaf-litter. The data presented herein expand this gap in our knowledge by demonstrating that this phenomenon also occurs among lowland populations.

The riparian systems in which these species are found are part of a network of drainages that eventually flow

into Sungai Terengganu—the major river of Hulu Terengganu. Hulu Terengganu and its drainage systems are rapidly emerging to be extremely important areas of site-specific biodiversity in that new species are continually being discovered. Grismer *et al.* (2014, 2016b) described the skink *Lipinia sekayuensis* Grismer, Ismail, Awang, Rizal, & Ahmad and Sumarli *et al.* (2016) described the skink *Sphenomorphus sungaicolus* Sumarli, Grismer, Wood, Ahmad, Rizal, Ismail, Izam, Ahmad, & Linkem from Hutan Lipur Sekayu. Additionally, Ng & Ahmad (2016) described a new genus and species of decopod (*Gempala bilobata*) from this drainage system. This clearly highlights the need for additional field surveys and protection of the Hulu Terengganu region.

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APPENDIX

The following specimens were examined.

Tytthoscincus bukitensis. 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, 12516) and Penang Hill (LSUHC 12071).

Tytthoscincus ishaki. West Malaysia: Pahang, Pulau Tioman, Gunung Kajang LSUHC 4429, 5165, 6150, 6161, 12582, ZRC 2.6157 (holotype), 2.6158–59 (paratypes).

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

Tytthoscincus kakikecil. West Malaysia: Pahang, Fraser's Hill, Richmond Road (LSUHC 11769 [holotype], 11770), 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 martaë. 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, 9206 (holotype).

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