Article

ZOOTAXA

Two new species of diminutive leaf-litter skinks (Squamata: Scincidae: *Tytthoscincus*) from Gunung Penrissen, Sarawak, Malaysia (northern Borneo)

BENJAMIN R. KARIN[1], INDRANEIL DAS[2] & AARON M. BAUER[1]

[1]*Department of Biology, Villanova University, 800 Lancaster Avenue, Villanova, PA 19085, USA.*
E-mail: bkarin@villanova.edu, aaron.bauer@villanova.edu
[2]*Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak, 94300 Kota Samarahan, Sarawak, Malaysia. E-mail: idas@ibec.unimas.my*

Abstract

We describe two new species of skinks from Gunung Penrissen, Sarawak, Malaysia, in northern Borneo, *Tytthoscincus batupanggah* **sp. nov.** and *T. leproauricularis* **sp. nov.** Morphological and molecular analyses both corroborate the two new species as unique compared to all other *Tytthoscincus* and additional *Sphenomorphus* that are candidates for taxonomic placement in the genus *Tytthoscincus*. Despite their phenotypic similarity and sympatric distribution, a molecular analysis shows that the new species are not sister taxa and exhibit a deep genetic divergence between each of their respective sister taxa. We discuss how historical climatic and geographic processes may have led to the co-distribution of two relatively distantly related phenotypically similar species. In light of these discoveries, we also emphasize the importance of conserving primary montane tropical rainforest for maintaining species diversity.

Key words: Endemism, co-distribution, *Sphenomorphus*, Sundaland, Sunda Shelf, sympatric

Introduction

Tytthoscincus Linkem, Diesmos & Brown, 2011 is a genus of diminutive, leaf-litter dwelling skinks in Southeast Asia and the Philippines. Only recently described as part of the revision of the large catch-all genus *Sphenomorphus* Fitzinger, 1843 (Linkem *et al.* 2011). *Tytthoscincus* currently contains just five species previously recognized under the genus *Sphenomorphus*: *T. aesculeticolus* (Inger, Tan, Lakim & Yambun); *T. atrigularis* (Stejneger); *T. biparietalis* (Taylor); *T. hallieri* (Lidth de Juede); *T. parvus* (Boulenger).

In the generic revision, Linkem *et al.* (2011) split the polyphyletic genus *Sphenomorphus sensu lato* into multiple new and resurrected genera, including the new genus *Tytthoscincus*, based largely on genetic evidence, but listed three morphological features to diagnose the genus: (1) small size usually less than 45 mm snout–vent length (SVL), (2) temporal scales that were not differentiated from the lateral body scales in size or shape, and (3) small digits. Based on these criteria, it remains clear that many of the species currently recognized in the genus *Sphenomorphus* are members of the genus *Tytthoscincus* but have not yet undergone morphological or genetic analyses to facilitate a taxonomic revision. Despite some evidence for additional species that should be transferred to the genus (phenotypic and genetic similarity; Linkem *et al.* 2011), the lack of detailed morphological descriptions that include diagnostic characters, their wide geographical distribution, and the difficulty of collecting additional specimens has led to a lag in a comprehensive revision of *Tytthoscincus*. We therefore face a difficulty in describing new species of *Tytthoscincus* in choosing with which species to compare them.

Given that many members of *Sphenomorphus* are yet to be formally transferred to *Tytthoscincus*, we choose a conservative approach in these descriptions and diagnose the two new species against all currently recognized *Tytthoscincus,* as well as the candidate species of *Sphenomorphus* listed below (see Table 1). Unpublished genetic evidence in Linkem (2013) show the following species of *Sphenomorphus* to be more closely related to *Tytthoscincus*: *S. bukitensis* Grismer, *S. butleri* (Boulenger), *S. ishaki* Grismer, *S. langkawiensis* Grismer, *S. perhentianensis* Grismer, Wood & Grismer, *S. perhentianensis* Grismer, Wood, Grismer, *S. sanana* (Kopstein), *S.*

sibuensis Grismer, *S. temengorensis* Grismer, Ahmad & Onn, *S. temmincki* (Duméril & Bibron), and *S. textus* (Müller). Additional species currently recognized as *Sphenomorphus* that are phenotypically similar to *Tytthoscincus* include *S. buttikoferi* (Lidth de Jeude), *S. malayanus* (Doria), *S. necopinatus* (Brongersma), *S. schlegeli* (Dunn), *S. senja* Grismer & Quah, and *S. vanheurni* (Brongersma) (Linkem *et al.* 2011). We also include for comparison other *Sphenomorphus* species that (1) are distributed in Sundaland, mainland Southeast Asia, the Philippines, or Sulawesi (geographically proximate to the new species locality on Borneo), (2) have an adult SVL ≤ 50 mm, and (3) are not represented by existing genetic data. These include *S. apalpebratus* Datta-Roy, Das, Bauer, Tron & Karanth, *S. alfredi* (Boulenger), *S. cophias* Boulenger, *S. courcyanum* (Annandale), *S. grandisonae* (Taylor), *S. helenae* Cochran, *S. maculicollus* Bacon, *S. mimicus* Taylor, *S. modigliani* (Boulenger), *S. puncticentralis* Iskandar, *S. sanctus* (Duméril & Bibron), *S. scotophilus* (Boulenger), *S. sheai* Nguyen, Nguyen, Van Devender, Bonkowski & Ziegler, *S. tanahtinggi* Inger, Lian, Lakim & Yambun, *S. tenuiculus* (Mocquard), *S. tetradactylus* (Darevsky & Orlov), *S. tonkinensis* Nguyen, Schmitz, Nguyen, Orlov, Böhme & Ziegler, and *S. tridigitus* (Bourret). Finally, one member of the *Sphenomorphus* group, *S. shelfordi* (Boulenger), is endemic to the same mountain as the new species described in this paper, Gunung Penrissen, and therefore warrants a discussion. No samples were available for direct comparison, however the original description describes a large *Sphenomorphus* (SVL = 67 mm) with relatively long limbs and 29 subdigital lamellae on toe IV (evidence that the toes could be longer than most *Tytthoscincus*) (Boulenger 1900). Though we expect that *S. shelfordi* is a member of the genus *Sphenomorphus sensu stricto*, we conservatively choose to directly diagnose the new species against *S. shelfordi* as well.

Localized endemism is common among this group of small, secretive, leaf-litter specialists. Many species of *Sphenomorphus sensu lato* are restricted to a single mountain or single island and it is likely that their small size and thus lowered vagility has led to this increased endemism (Grismer *et al.* 2009, 2015; Linkem *et al.* 2011). Of the 16 species of *Sphenomorphus sensu lato* on Borneo, 11 are highly restricted in their range with most of these restricted to a single mountain (*T. aesculeticolus*; *S. alfredi*; *S. buettikoferi*; *S. crassus* Inger, Lian, Lakim & Yambun; *S. kinabaluensis* (Bartlett); *S. maculicollus*; *S. murudensis* Smith; *S. shelfordi*; *S. stellatus* (Boulenger); *S. tanahtinggi*; and *S. tenuiculus*). The more widespread species tend to be larger bodied and have been confirmed genetically to be members of *Sphenomorphus sensu stricto* (*S. cyanolaemus* Inger & Hosmer; *S. haasi* Inger & Hosmer; *S. multisquamatus* Inger; *S. sabanus* Inger) (Linkem *et al*. 2011). The exception is *T. hallieri,* which has been collected in Sarawak, Sabah, Brunei, and Kalimantan, though it is by far the largest of the currently recognized *Tytthoscincus* (SVL = 48–52 mm). Given the patterns of endemism in this group, it is not unexpected to continue to find new mountain endemic species of *Tytthoscincus* on Borneo.

Materials and methods

Measurements follow that of Grismer *et al.* (2009) and Linkem *et al.* (2010): snout-vent length (SVL) measured from the tip of the snout to the cloacal opening; tail length (TL) measured from the cloacal opening to the tip of the tail; axilla-groin distance (AGD) measured from the posterior margin of the forelimb insertion to the anterior margin of the hind limb insertion; head length (HL) measured from the anterior margin of the ear opening to the tip of the snout; head width (HW) measured at the widest part of the temporal region; snout-forelimb length (SFL) measured from the anterior margin of the forelimb insertion to the tip of the snout; midbody scale rows (MBSR) counted as the number of longitudinal scale rows encircling the body at a point midway between the limb insertions; paravertebral scale rows (PVSR) counted as the number of scales in a line from the parietal scales to the point on the dorsum opposite the vent; and ventral scale rows (VSR) counted as a row of scales between the postmentals and the cloacal plate. Other standard counts include supraoculars, loreals, supralabials, infralabials, and subdigital lamellae (SDL) beneath the fourth toe. Additional characters examined were the degree of contact between the parietals and supraoculars, enlargement of posterior supraciliary scales, degree of contact between the prefrontal scales, presence or absence of enlarged precloacal scales, and texture of subdigital lamellae. Color pattern characters examined were the degree of dark, dorsolateral striping and the presence or absence of well-defined, white, dorsolateral and/or postorbital stripes.

All measurements were made using Mitutoyo™ digital calipers accurate to the nearest 0.1 mm. Scale were counted by BRK using a dissecting microscope and confirmed on each side of the body (noted when different).

The type specimens are deposited at the California Academy of Sciences (CAS) and the Zoological Reference Collection (ZRC) of the Lee Kong Chian Natural History Museum at The National University of Singapore.

Genomic DNA was extracted as described in Aljanabi & Martinez (1997). Polymerase chain reaction (PCR) was performed on a Eppendorf Mastercycler nexus gradient thermal cycler and PCR product was cleaned using a home-made magnetic bead solution (Rohland & Reich 2012). All PCR reactions began with an initial 2 min denaturation at 95°C followed by 95°C for 35 s, annealing for 35 s at 50°C and extension at 72°C for 1 min 35 s for 34 cycles. Cycle sequencing was performed using Big Dye v3.1 chemistry, followed by an additional magnetic bead cleanup and analysis on an ABI3730xl. We sequenced the mitochondrial NADH dehydrogenase subunit 2 (ND2: 1095 bp after trimming to coding region) and the nuclear RNA fingerprint protein 35 (R35: 689 bp). For PCR of the ND2 gene we used the forward primer METF1 (5'-AAGCTTTCGGGCCCATACC-3') of Macey *et al.* (1997) and reverse primer CO1R1 (5'- AGRGTGCCAATGTCTTTGTGRTT-3') of Arevalo *et al.* (1994). For PCR of the R35 gene we used the forward primer R35F (5'-GACTGTGGAYGAYCTGATCAGTGTGGTGCC-3') and reverse primer R35R (5'- GCCAAAATGAGSGAGAARCGCTTCTGAGC-3') both of Leaché (2009). All seven newly generated sequences are available on GenBank (GenBank accession KU587720–KU587726).

DNA reads were manually checked and corrected for errors and aligned by eye to the existing dataset of *Sphenomorphus* group skinks of Linkem *et al.* (2011) downloaded from Dyrad (http://datadryad.org/resource/ doi:10.5061/dryad.30064). The dataset was trimmed to include a single representative of each species outside of *Tytthoscincus*. This led to the inclusion of four additional genes in the dataset that helped in reconstructing the structure of the tree as a whole, but did not aid in the phylogenetic placement of the new species as they were missing these data. These genes included NADH dehydrogenase subunit 4 (ND4: 705 bp), ribosomal 12s (447 bp), ribosomal 16s (518 bp) and nerve growth factor beta polypeptide (NGFB: 567 bp). A Maximum Likelihood analysis were performed in RAxML v8.1.15 (Stamatakis 2006) using the same partitioning scheme as Linkem *et al.* (2011), with each gene and codon position partitioned separately, and 12s and 16s stems and loops with separate partitions (a partition file from Linkem *et al.* (2011) can be downloaded on Dryad), and each partition run under the GTRCAT model of evolution. The analysis was run for 1000 non-parametric rapid bootstrap replicates, which are summarized on the phylogeny (Fig. 5) as a percentage.

For this study, we define a species using the General Lineage Concept (de Queiroz 1998, 1999) as an extension of the Evolutionary Species Concept (Wiley 1978), for which phenotypically divergent populations represent distinct and separately evolving lineages. We diagnose a new species based on the possession of non-overlapping morphological characters when compared to closely related species. We corroborate this morphological evidence using genetic data.

Phylogenetic results

The maximum likelihood analysis produced a well-resolved phylogeny that strongly supported the placement of the two new species within *Tytthoscincus* (Fig. 5). *T. batupanggah* **sp. nov.** is supported as being sister to a clade that includes *T. atrigularis*, *T. hallieri*, and *T. parvus*. *T. leproauricularis* **sp. nov.** is supported as sister to *T. aesculeticola*, and the genetic divergence between the new species and their respective sister lineages is substantial. We did not obtain an ND2 sequence due to a low quality read (only an R35 sequence) for the holotype of *T. leproauricularis* **sp. nov.**, so missing data and not true genetic divergence explains the increased branch length seen in the phylogeny for this specimen. For both *T. batupanggah* **sp. nov.** and *T. leproauricularis* **sp. nov.**, raw mitochondrial pairwise sequence divergence in ND2 was greater than 22% between the new species and any other species of *Tytthoscincus*.

Systematics

***Tytthoscincus batupanggah* sp. nov.**
(Figs. 1–2)

Holotype. A specimen (CAS 259189) from Batu Panggah, 1.120666° N 110.226922° E (WGS84), 1,050 m elevation, on the north face of Gunung Penrissen, Kuching Division, Sarawak, Malaysia collected 4 July 2014 at 20:00 h by Benjamin R. Karin, Pui Yong Min, Samuel Shonleben, and Adi Shabrani.

Paratype. One additional specimen (ZRC 2.7123) was collected at the same locality at the same time as the holotype.

Diagnosis. *Tytthoscincus batupanggah* **sp. nov.** can be identified by the following combination of characters: (1) body size small (SVL = 26.8–33.2 mm); (2) MBSR = 30–31; (3) PVSR = 62–66; (4) VSR = 55–61; (5) four enlarged supraoculars; (6) parietals in contact with the last supraocular; (7) prefrontals in contact with one another; (8) two loreals; (9) six supralabials; (10), five infralabials; (11) nine SDL on Toe IV; (12) smooth texture of the subdigital lamellae; (13) enlarged precloacal scales; (14) a dark dorsolateral stripe; (15) a light postorbital stripe; and (16) a light dorsolateral stripe.

Description of Holotype. All measurements in mm. SVL = 33.2; TL = 28.4 (tail incomplete, used for additional genetic material); AGD = 17.5; HL = 6.9; HW = 4.5; SFL = 12.8; sex unknown; rostral wider than long, in broad contact with frontonasal; frontonasal wider than long; prefrontals large, in broad contact, left prefrontal overlapping right; frontal elongate, triangular in shape, in contact with the first two supraoculars and one preocular; frontoparietals in broad contact, contacting second, third, and fourth supraoculars, parietals, interparietal, and frontal; right frontoparietal overlaps left; interparietal diamond-shaped, large, elongate posteriorly, with parietal eyespot in posterior projection; parietals large, in contact posterior to interparietal, in slight contact with posterior portion of fourth interparietal; left parietal overlaps right; enlarged nuchal scales absent; nasals small, widely separated, completely enclosing the nares, and contacting the rostral anteriorly, frontonasal dorsally, first loreal posteriorly, and first supralabial ventrally; six supralabials; supranasals absent; two similarly sized loreals taller than wide; three similarly sized preoculars in contact with posterior margin of second loreal; nine supraciliaries; posterior supraciliary elongate, projecting medially; temporals not distinctly enlarged in comparison to lateral body scales; lower eyelid transparent, scaly, without central window; mental twice as wide as long; single postmental, contacting first infralabial on each side; two enlarged pairs of genials following postmental, anterior pair in contact medially, posterior pair widely separated by a single ventral scale; genials contacting first, second, and third infralabials; five infralabials; external ear opening two-thirds the diameter of the eye, circular, with an auricular component projecting from the posterior margin; tympanum sunk.

FIGURE 1. Photo in life of the holotype of *Tytthoscincus batupanggah* **sp. nov.** (CAS 259189).
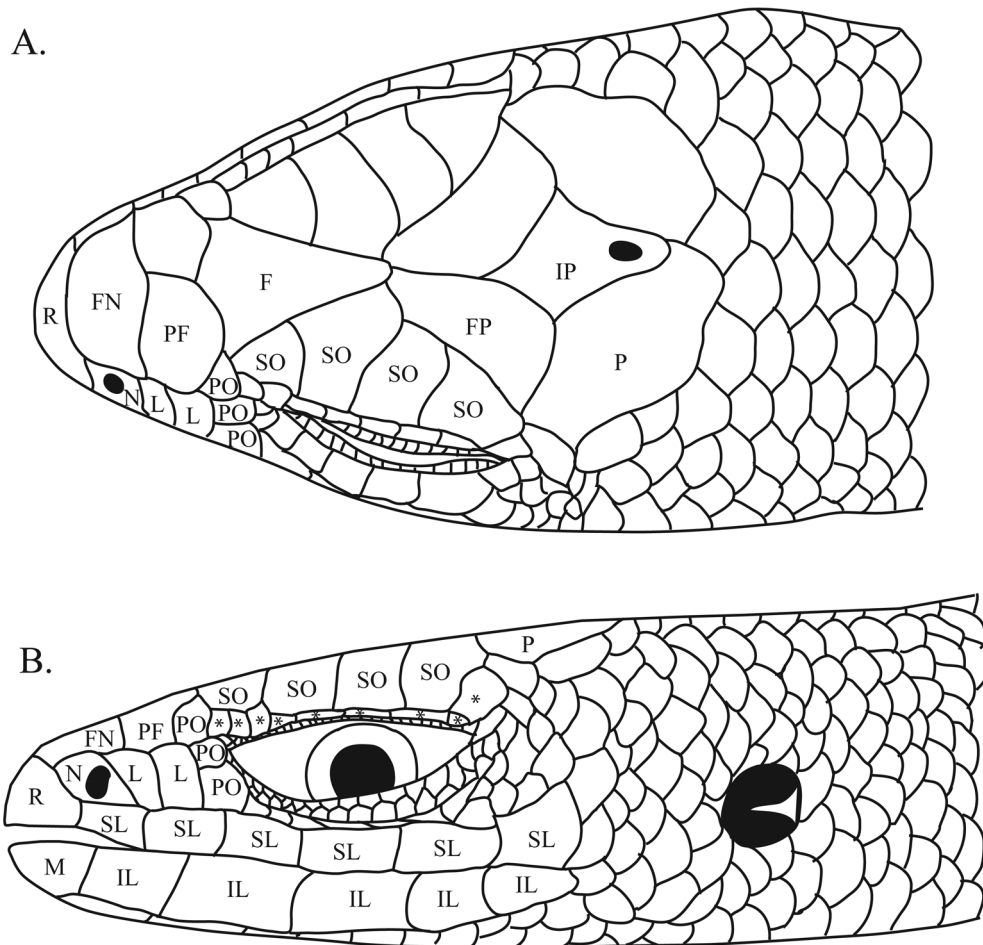
FIGURE 2. Head scalation of the holotype of *Tytthoscincus batupanggah* **sp. nov.** (CAS 259189). Scales are labeled as follows: R = Rostral, N = Nasal, FN = Frontonasal, L = Loreal, PO = Preocular, PF = Prefrontal, F = Frontal, SO = Supraocular, FP = Frontoparietal, IP = Interparietal, P = Parietal, SL = Supralabial, M = Mental, IL = Infralabial, * = Supraciliary.

Body scales smooth, hexagonal; ventral scales not enlarged; 30 longitudinal scale rows around the midbody; 66 paravertebral scale rows; 61 ventral scale rows; two enlarged, semi-transparent precloacal scales, left overlapping right, and both overlapping outer scales; tail robust, cylindrical, incomplete; anterior subcaudals equal in size to dorsal caudals; posterior subcaudals enlarged.

Adpressed limbs widely separated; lamellae texture smooth; manus subdigital lamellae (L/R) in parentheses: I(2/2), II(4/4), III(5/5), IV((incomplete)/6), V(4/4); pes subdigital lamellae (L/R) in parentheses: I(5/4), II((incomplete)/5), III(8/8), IV(9/9), V(6/6);

Color in alcohol. Dorsal and lateral surfaces of holotype mostly brown with tiny cream-yellow spots dotting the entirety of the body; dorsolateral stripe extending from the orbit to midway along the body, cream in color, underlined by a solid-colored, dark-brown lateral stripe, both stripes fading away posterior to the forelimbs; a second lateral stripe extends from the orbit to the ear opening, cream in color; ventral surface of body and ventral surface of base of tail cream in color, posterior ventral surface of tail punctuated with tiny brown dots of pigmentation.

Variation. The paratype (ZRC 2.7123) differs from the holotype in SVL = 26.8, TL = 11.0 (incomplete), AGD = 13.7, HL = 6.1, HW = 3.9, SFL = 10.2, MBSR = 31, and VSR = 55 but is identical to the holotype in all other scale characters reported (four supraoculars, parietals contact supraocular, nine supraciliaries, prefrontals in contact, two loreals, six supralabials, five infralabials, SDL on toe IV = 9, precloacal scales enlarged). The coloration of the paratype is extremely similar to the holotype, but differs in the thickness of the cream-colored dorsolateral stripe, which in the paratype is more distinct nearer to the orbit than the stripe of the holotype. In life, the coloration of both the holotype and paratype is more orange, with a highlight of orange near the axilla (Fig. 1).

Distribution. *Tytthoscincus batupanggah* is known only from the type locality from Batu Panggah on the

North side of Gunung Penrissen, Kuching Division, Sarawak, Malaysia (Fig. 6). We expect that it exists in much of the high-elevation forest on the mountain, though it is possible that it is replaced in other parts of its range by *Tytthoscincus leproauricularis* **sp. nov.**, another similarly-sized, leaf-litter species. Unfortunately, much of the original forest on Gunung Penrissen has been clear-cut to make way for a golf course, substantially limiting the suitable habitat for this species (see Fig. 6).

Natural history. The two known specimens of *Tytthoscincus batupanggah* **sp. nov.** were collected at the same time, date, and location from leaf-litter surrounding Batu Panggah on Gunung Penrissen. The area is primary, highland, mixed-dipterocarp forest. When collected, the forest understory around Batu Panggah had been recently cleared to improve the view of the large sandstone rock, consequently making it easier for herpetologists to inspect the leaf-litter for lizards. This species appears to be a leaf-litter specialist and was seen running and jumping through this microhabitat (BRK, pers. obs.). The specimens were found after dark, at approximately 20:00 h. It is difficult to determine whether this species was actively foraging during this time (as was the initial speculation by BRK) and therefore semi-nocturnal, or if resting individuals were simply disturbed by nearby human footsteps, though we expect the latter to be true.

Etymology. The species epithet *batupanggah* is in reference to the type locality at Batu Panggah on Gunung Penrissen. From Malay, Batu Panggah translates to "Stone of the Head House" or "Cursed Stone" to refer to the large sandstone rock that is believed by local peoples to be cursed. The story goes that a young couple from different longhouses fell in love, but when their respective longhouses found out about their romance they sent out the headhunters to hunt them down. As they fled into the jungle it began to pour rain with thunder and lightning, they found a house in the woods, a head house, where human heads were traditionally kept as a symbol of victory, and ran inside to take shelter. However, women are not traditionally allowed in the head house and when they ran inside the house turned to stone, leaving behind a large rock that is now known as Batu Panggah. Suggested common name: Cursed-stone Diminutive Leaf-Litter Skink.

Comparisons. In order to be conservative in differentiating the new species from all others, we compare *Tytthoscincus batupanggah* **sp. nov.** to all currently recognized *Tytthoscincus* and all candidate species of the genus *Sphenomorphus* that have genetic or phenotypic similarity or which are geographically proximate and have an adult SVL less than or equal to 50 mm (see Introduction; Table 1). Though we cannot be completely sure that other uncollected individuals of *T. batupanggah* **sp. nov.** (SVL = 33.2 mm) may have a maximum SVL > 50 mm, since the Holotype lacks an umbilical scar it is likely that it represents an adult size. Therefore, all *Sphenomorphus* with an adult SVL greater than 50 mm can be differentiated from *T. batupanggah* **sp. nov.** (SVL = 26.8–33.2 mm) by body size, however we do not directly list them here. Though we consider *Sphenomorphus shelfordi* to be too large to be a member of *Tytthoscincus* (see Introduction), nevertheless we conservatively choose to compare directly with it as it was described from the same type locality as the new species.

MBSR = 30–31 in *T. batupanggah* **sp. nov.** distinguishes it from *T. leproauricularis* **sp. nov.** (35–37), *T. hallieri* (33–41), *S. langkawiensis* (34–37), *S. sanana* (28), *S. buttikoferi* (24), *S. schlegeli* (22), *S. apalpebratus* (27–28), *S. alfredi* (26), *S. cophias* (24), *S. courcyanum* (24), *S. grandisonae* (34), *S. macullicolus* (35–36), *S. sheai* (20), *S. tanahtinggi* (40–42), *S. tenuiculus* (26), *S. tetradactylus* (20), and *S. tridigitus* (18). PVSR = 62–66 in *T. batupanggah* **sp. nov.** distinguishes it from *T. leproauricularis* **sp. nov.** (68–74), *S. bukitensis* (73–74), *S. ishaki* (68–73), *S. sibuensis* (58), *S. temengorensis* (68–70), *S. temmincki* (68–80), *S. malayanus* (76–80), *S. senja* (72–73), *S. vanhuerni* (81), *S. cophias* (56), *S. grandisonae* (71), *S. macullicolus* (79), *S. mimicus* (61), *S. sanctus* (71), *S. scotophilus* (67–74), *S. sheai* (53), *S. tanahtinggi* (76–79), *S. tenuiculus* (57), *S. tetradactylus* (48), and *S. tridigitus* (50). VSR = 55–61 in *T. batupanggah* **sp. nov.** distinguishes it from *T. leproauricularis* **sp. nov.** (80–81), *T. hallieri* (63–73), *S. butleri* (62–63), *S. langkawiensis* (70–72), *S. sibuensis* (52), *S. temengorensis* (70,71), *S. temmincki* (62–72), *S. malayanus* (74), *S. senja* (68), *S. macullicolus* (84), *S. sheai* (54), and *S. tenuiculus* (68). The presence of 4 supraoculars distinguishes *T. batupanggah* **sp. nov.** from *S. textus* (5), *S. apalpebratus* (5), *S. macullicolus* (7), *S. puncticentrallis* (5), *S. sanctus* (5), *S. scotophilus* (5), and *S. tanahtinggi* (5). The contact of the parietal with the last supraocular distinguishes T. *batupanggah* **sp. nov.** from *T. hallieri*, and *S. tetradactylus*. The contact of the prefrontals distinguishes *T. batupanggah* **sp. nov.** from all species with prefrontals separated: *T. leproauricularis* **sp. nov.**, *T. aesculeticola*, *T. biparietalis*, *T. parvus*, *S. sanana*, *S. senja*, *S. vanhuerni*, *S. apalpebratus*, *S. alfredi*, *S. cophias*, *S. helenae*, *S. macullicolus*, *S. sheai*, *S. tenuiculus*, *S. tetradactylus*, and *S. tridigitus*. The presence of a paired anterior loreals distinguishes *T. batupanggah* **sp. nov.** from *S. sibuensis*, *S. macullicolus*, *S. tanahtinggi*, *S. tetradactylus*, and *S. tridigitus*. The presence of 6 supralabials distinguishes *T.*

batupanggah **sp. nov.** from *S. sanana* (5), *S. malayanus* (7), *S. senja* (7), *S. cophias* (7), *S. mimicus* (7), *S. puncticentrallis* (7), *S. sanctus* (7), *S. scotophilus* (7), *S. tanahtinggi* (8–9), *S. tenuiculus* (7), and *S. tonkinensis* (7). The presence of 5 infralabials distinguishes *T. batupanggah* **sp. nov.** from *T. biparietalis* (6), *S. perhentianensis* (6), *S. malayanus* (7–8), *S. senja* (6), *S. cophias* (7), *S. macullicolus* (6), *S. puncticentrallis* (7), *S. sanctus* (6), *S. scotophilus* (6), *S. tanahtinggi* (7), *S. tenuiculus* (6), *S. tetradactylus* (7), and *S. tonkinensis* (6). SDL on Toe IV = 9 in *T. batupanggah* **sp. nov.** distinguishes it from *T. leproauricularis* **sp. nov.** (10), *T. atrigularis* (10), *T. biparietalis* (10), *T. hallieri* (10–15), *T. parvus* (10), *S. bukitensis* (12–13), *S. butleri* (12–13), *S. ishaki* (11), *S. langkawiensis* (11,12), *S. perhentianensis* (10), *S. temengorensis* (10,11), *S. textus* (15), *S. buttikoferi* (21–23), *S. malayanus* (12–13), *S. necopinatus* (11–15), *S. schlegeli* (10), *S. senja* (13–17), *S. vanhuerni* (14–15), *S. alfredi* (12), *S. courcyanum* (11), *S. grandisonae* (12), *S. helenae* (17), *S. macullicolus* (18–23), *S. mimicus* (16), *S. modigliani* (15), *S. puncticentrallis* (25), *S. sanctus* (26–27), *S. scotophilus* (22–23), *S. sheai* (6), *S. shelfordi* (28–29), *S. tanahtinggi* (16–17), *S. tenuiculus* (21–24), *S. tetradactylus* (10), *S. tonkinensis* (15–19), and *S. tridigitus* (7–8). The presence of smooth SDL distinguishes *T. batupanggah* **sp. nov.** from all species with keeled SDL: *S. bukitensis*, *S. ishaki*, *S. langkawiensis*, *S. sibuensis*, *S. temengorensis*, *S. malayanus*, *S. apalpebratus*, and *S. tanahtinggi*. The presence of enlarged precloacal scales distinguishes *T. batupanggah* **sp. nov.** from *T. aesculeticola*, *T. biparietalis*, *T. hallieri*, *S. bukitensis*, *S. temmincki*, *S. apalpebratus*, and *S. alfredi*. The presence of a dark dorsolateral stripe distinguishes *T. batupanggah* **sp. nov.** from *T. leproauricularis* **sp. nov.**, *T. aesculeticola*, *T. parvus*, *S. perhentianensis*, *S. sanana*, *S. senja*, *S. vanhuerni*, *S. macullicolus*, *S. modigliani*, and *S. sanctus*. The presence of a light postorbital stripe distinguishes *T. batupanggah* **sp. nov.** from *T. leproauricularis* **sp. nov.**, *T. aesculeticola*, *T. atrigularis*, *T. hallieri*, *T. parvus*, *S. bukitensis*, *S. butleri*, *S. perhentianensis*, *S. sanana*, *S. sibuensis*, *S. temmincki*, *S. textus*, *S. necopinatus*, *S. schlegeli*, *S. senja*, *S. vanhuerni*, *S. apalpebratus*, *S. alfredi*, *S. cophias*, *S. courcyanum*, *S. grandisonae*, *S. helenae*, *S. macullicolus*, *S. mimicus*, *S. modigliani*, *S. puncticentrallis*, *S. sanctus*, *S. scotophilus*, *S. sheai*, *S. shelfordi*, *S. tanahtinggi*, *S. tenuiculus*, *S. tetradactylus*, *S. tonkinensis*, and *S. tridigitus*. The presence of a light dorsolateral stripe distinguishes *T. batupanggah* **sp. nov.** from *T. leproauricularis* **sp. nov.**, *T. aesculeticola*, *T. atrigularis*, *T. biparietalis*, *T. hallieri*, *T. parvus*, *S. bukitensis*, *S. butleri*, *S. ishaki*, *S. perhentianensis*, *S. temmincki*, *S. textus*, *S. buttikoferi*, *S. malayanus*, *S. necopinatus*, *S. senja*, *S. vanhuerni*, *S. alfredi*, *S. cophias*, *S. macullicolus*, *S. mimicus*, *S. modigliani*, *S. puncticentrallis*, *S. sanctus*, *S. scotophilus*, *S. shelfordi*, *S. tanahtinggi*, *S. tenuiculus*, *S. tonkinensis*, and *S. tridigitus*.

Tytthoscincus leproauricularis **sp. nov.**
(Figs. 3–4)

Holotype. A specimen (CAS 259190) from the West ridge of Gunung Penrissen, 1.115302° N 110.218629° E (WGS84), 1,100 m elevation, Kuching Division, Sarawak, Malaysia collected 14 August 2014 at approximately 13:00 h by Benjamin R. Karin, Pui Yong Min, Samuel Shonleben, and Adi Shabrani.

   Paratype. A juvenile of the same species (ZRC 2.7122) was collected within 100 m of the holotype on 4 July 2014 by Benjamin R. Karin, Pui Yong Min, Samuel Shonleben, and Adi Shabrani.

   Diagnosis. *Tytthoscincus leproauricularis* **sp. nov.** can be identified by the following combination of characters: (1) body size small (SVL = 33.5 mm); (2) MBSR = 35–37; (3) PVSR = 68–74; (4) VSR = 80–81; (5) four enlarged supraoculars; (6) parietals in contact with the last supraocular; (7) prefrontals separated; (8) two loreals; (9) six or seven supralabials; (10), five infralabials; (11) ten SDL on Toe IV; (12) smooth texture of the subdigital lamellae; (13) enlarged precloacal scales; (14) lacking a dark dorsolateral stripe; (15) lacking a light postorbital stripe; and (16) lacking a light dorsolateral stripe.

   Description of Holotype. SVL = 33.5; TL = 5.5 (tail incomplete, used for additional genetic material); AGD = 19.1; HL = 7.3; HW = 4.4; SFL = 12.5; sex unknown; rostral wider than long, in broad contact with frontonasal; frontonasal wider than long; prefrontals large, widely separated; frontal elongate, triangular in shape, in contact with the first two supraoculars and one preocular; frontoparietals in broad contact, contacting second, third, and fourth supraoculars, parietals, interparietal, and frontal; right frontoparietal overlaps left; interparietal diamond-shaped, large, posteriorly elongate, parietal eyespot absent; parietals large, in contact posterior to interparietal, in slight contact with posterior portion of fourth supraocular; left parietal overlaps right; enlarged nuchal scales absent; nasals small, widely separated, completely enclosing the nares, and contacting the rostral anteriorly,

frontonasal dorsally, first loreal posteriorly, and first supralabial ventrally; seven supralabials; supranasals absent; two similarly sized loreals taller than wide; three similarly sized preoculars in contact with posterior margin of second loreal; eight supraciliaries; posterior supraciliary elongate and projecting medially; temporals enlarged relative to lateral body scales; lower eyelid scaly, without central window; mental twice as wide as long, in contact with postmental; single postmental, contacting first infralabial on each side; two enlarged pairs of genials following postmental, anterior pair in contact medially, posterior pair widely separated by a single ventral scale; genials contacting first, second, and third infralabials; five infralabials; ear opening scaly, circular, superficial, without visible tympanum, half the diameter of the eye.

Body scales smooth, hexagonal; ventral scales not enlarged relative to dorsal scales; 35 scale rows around the midbody; 74 paravertebral scale rows; 70 ventral scale rows; three enlarged, semi-transparent precloacal scales, center overlapping outer two; tail robust, cylindrical, incomplete.

Adpressed limbs widely separated; lamellae texture smooth; toe IV slightly longer than toe III; manus subdigital lamellae (L/R) in parentheses: I(2/2), II(3/3), III(4/4), IV(4/,(incomplete)), V(3/3); pes subdigital lamellae (L/R) in parentheses: I(4/4), II(6/6), III(9/9), IV(10/10), V(5/5).

Color in alcohol. Dorsal and lateral surfaces mostly brown with tiny beige spots dotting the entirety of the body; no dorsolateral stripe; ventral surface of body cream in color, chin and neck with small brown flecks of pigmentation.

Variation. The paratype (ZRC 2.7122) differs from the holotype in SVL = 18.2, TL = 9.0 (incomplete), AGD = 8.3, HL = 4.4, HW = 2.9, SFL = 7.8, MBSR =37, PVRS = 68, VSR = 80, six supralabials but is identical to the holotype in all other scale characters reported (four supraoculars, parietals contact supraocular, eight supraciliaries, prefrontals separated, two loreals, five infralabials, SDL on toe IV = 10, precloacal scales enlarged). Coloration of the juvenile paratype extremely similar to the holotype, though the paratype has slightly more intense beige spotting along the body. In life, the coloration of the holotype is nearly identical to the preserved specimen (see Fig. 3).

FIGURE 3. Photo in life of the holotype of *Tytthoscincus leproauricularis* **sp. nov.** (CAS 259190).
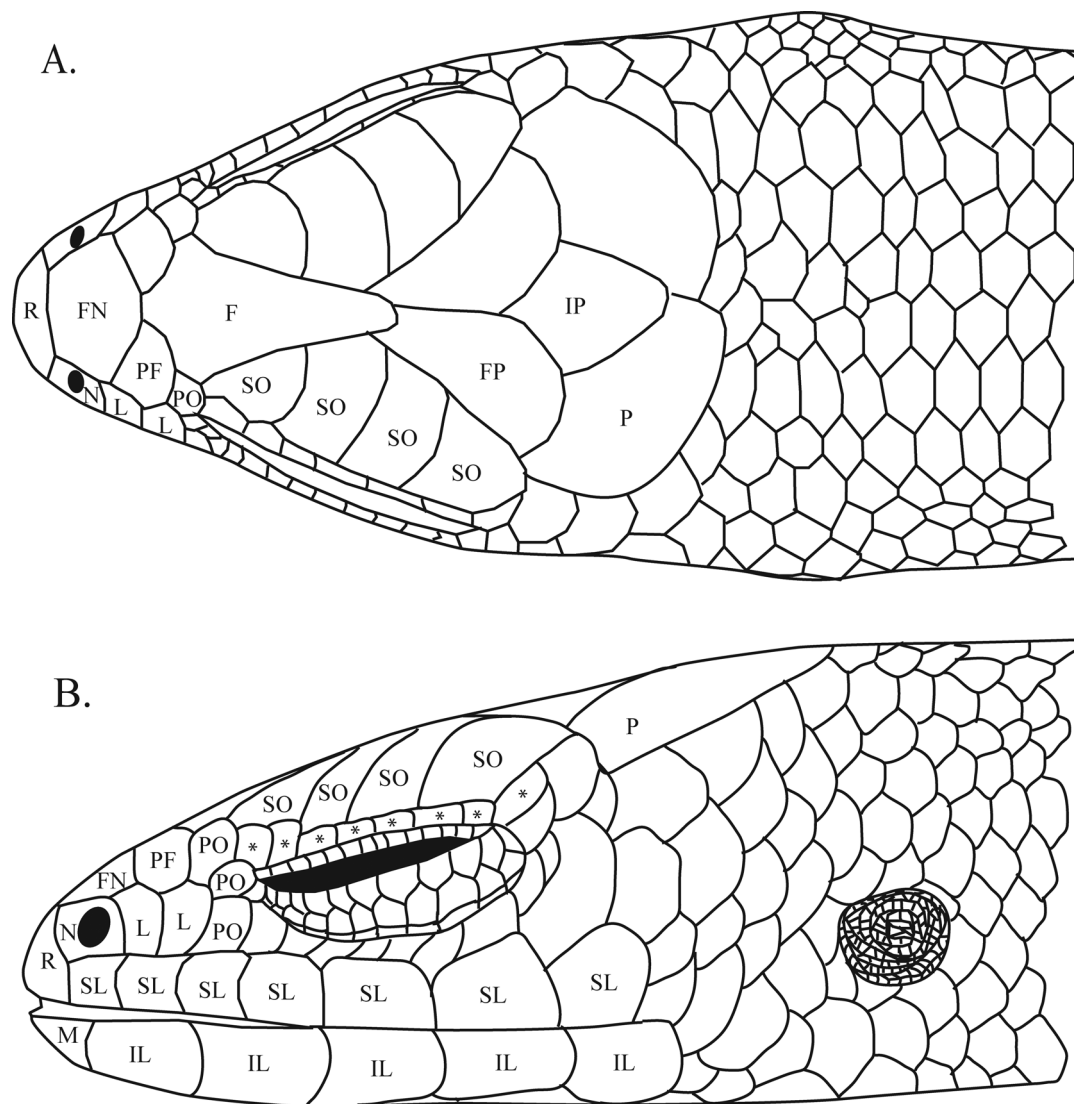
FIGURE 4. Head scalation of the holotype of *Tytthoscincus leproauricularis* **sp. nov.** (CAS 259190). Scales are labeled as follows: R = Rostral, N = Nasal, FN = Frontonasal, L = Loreal, PO = Preocular, PF = Prefrontal, F = Frontal, SO = Supraocular, FP = Frontoparietal, IP = Interparietal, P = Parietal, SL = Supralabial, M = Mental, IL = Infralabial, * = Supraciliary.

Distribution. *Tytthoscincus leproauricularis* **sp. nov.** is only known from the type locality on the Western side of Gunung Penrissen, Kuching Division, Sarawak, Malaysia (Fig. 6). We expect that it exists over much of the high-elevation forests on these mountains, though it is possible that it is replaced in other parts of its range by *Tytthoscincus batupanggah* **sp. nov.**, another similarly-sized, leaf-litter species. Unfortunately, much of the original forest on Gunung Penrissen has been clearcut to make way for a golf course, substantially limiting the suitable habitat for this species (see Fig. 6).

Natural history. The holotype and paratype of *Tytthoscincus leproauricularis* **sp. nov.** were collected within 100 m of each other while walking on the summit trail up to the ridge on the west face of Gunung Penrissen. The collection location is composed of primary, highland, mixed-dipterocarp forest. Only 100–150 m elevation above the collection location the forest transitions to a localized area of tropical cloud forest with substantially shorter trees. The paratype was collected on 4 July 2014 and the holotype over a month later, on 14 August 2014. Both were encountered around midday, active in the leaf litter along the edge of the trail. Nothing more is known about this species, besides that it is likely a leaf-litter specialist.

Etymology. From the Greek *lepros* (scaly) and latin *auricularis* (pertaining to the ear) in reference to the scaly, superficial ear that is a distinctive character in the new species. Suggested common name: Scaly-eared Diminutive Leaf-Litter Skink.

TABLE 1. Summary of diagnostic characters (+ present; 0 absent; — missing) among species in the genus *Tytthoscincus* as well as phenotypically or genetically similar species of the genus *Sphenomorphus*. Organized by type of evidence used for inclusion as a comparison. Column headings are listed under the following numbers: (1) adult SVL (mm), (2) MBSR, (3) PVSR, (4) VSR, (5) number of supraoculars, (6) parietal in contact with supraocular, (7) prefrontals in contact, (8) number of loreals, (9) number of supralabials, (10) number of infralabials, (11) SDL on toe IV, (12) lamellae texture (k = keeled, s = smooth), (13) enlarged precloacal scales, (14) dark dorsolateral scales, (15) light post-orbital stripe, and (16) light dorsolateral stripe. Data taken from the literature is cited from: (A) (Grismer *et al.* 2009a); (B) (Stejneger 1908); (C) (Taylor 1918); (D) (Boulenger 1897); (E) (Kopstein 1926); (F) (Müller 1895); (G) (Dunn 1927); (H) (Grismer & Quah 2015); (I) (Brongersma 1942); (J) (Datta-Roy *et al.* 2013); (K) (Boulenger 1898); (L) (Annandale 1912); (M) (Taylor 1962); (N) (Cochran 1927); (O) (Boulenger 1894); (P) (Darevsky & Orlov 2005); (Q) (Quang Nguyen *et al.* 2011); and (R) (Greer *et al.* 2006).

	Locality	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	ref.
Recognized as Tytthoscincus																		
T. batupanggah sp. nov.	Borneo	**26.8–33.2**	**30–31**	**62–66**	**55–61**	**4**	**+**	**+**	**2**	**6**	**5**	**9**	**s**	**+**	**+**	**+**	**+**	
T. leproauricularis sp. nov.	Borneo	**33.5**	**35–37**	**68–74**	**80–81**	**4**	**+**	**0**	**2**	**6,7**	**5**	**10**	**s**	**+**	**0**	**0**	**0**	
T. aesculeticola	Borneo	40–43	26–32	—	60–68	4	+	0	2	6	5	6–10	—	0	0	0	0	A
T. atrigularis	Philippines	31	30	—	—	4	+	+	2	6	5	10	s	+	+	0	0	B
T. biparietalis	Philippines	35	32	—	—	4	+	0	—	6	6	10	s	0	+	+	0	C
T. hallieri	Borneo	48–52	33–41	—	63–73	4	0	+	2	—	—	10–15	—	0	+	0	0	A
T. parvus	Sulawesi	36	30	—	—	4	—	0	—	—	—	10	s	+	0	0	0	D
Genetic evidence supports placement in Tytthoscincus (Linkem 2013), but not formally recognized																		
S. bukitensis	W Malaysia	40.5–44	31–33	73–74	61–74	4	+	+	2	6	5	12–13	k	0	faint	0	0	A
S. butleri	W Malaysia	34–44	31–33	66–67	62–63	4	+	+	1,2	6	5–6	12–13	s	+	+	0	0	A
S. ishaki	W Malaysia	38–41	30–32	68–73	60–70	4	+	+	2	6	5	11	k	+	faint	+	0	A
S. langkawiensis	W Malaysia	37.2	34–37	60–72	70–72	4	+	+	2	6	5,6	11,12	k	+	+	+	+	A
S. perhentianensis	W Malaysia	30	29	65	61	4	+	+	2	6	6	10	s	+	0	0	0	A
S. sanana	Sanana	32	28	—	—	4	—	0	—	5	—	9	s	+	0	0	+	E
S. sibuensis	W Malaysia	juv	29	58	52	4	+	+	1	6	5	9	k	+	+	0	+	A
S. temengorensis	W Malaysia	35.5	30–35	68–70	70,71	4	+	+	2	6	5	10,11	k	+	+	+	+	A
S. temmincki	Java	56	30–37	68–80	62–72	4	+	0,+	2	6	4–5	9–11	s	0	+	0	0	A
S. textus	Sulawesi	38	30	—	—	5	+	+	—	—	—	15	—	+	+	0	0	F
Morphologically similar to Tytthoscincus																		
S. buttikoferi	Borneo	35	24	—	—	4	+	+	—	—	—	21–23	s	+	+	—	0	A
S. malayanus	Sumatra	52–60	32–33	76–80	74	4	0,+	+	2	7	7–8	12–13	k	+	0,+	0,+	0	A
S. necopinatus	Java	39	28–32	63–75	—	4	+	0,+	2	—	—	11–15	—	+	+	0	0	A
S. schlegeli	Komodo	32	22	—	—	4	—	+	—	—	—	10	s	+	+	0	+	G

TABLE 1. (Continued)

	Locality	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	ref.
S. senja	W Malaysia	60–65	32	72–73	68	4	+	0	2	7	6	13–17	s	+	0	0	0	H
S. vanhuerni	Java	20	31	81	—	4	+	0	2	6	5	14–15	s	+	0	0	0	I
Other *Sphenomorphus* with adult SVL ≤ 50 mm																		
S. apalpebratus[1]	NE India	42	27–28	62–64	60	5	+	0	2	5–6	4–5	8–9	k	0	+	0	+	J
S. alfredi	Borneo	33	26	—	—	4	—	0	—	6	—	12	s	0	+	0	0	K
S. cophias	W Malaysia	37	24	56	—	4	+	0	2	7	7	9	—	+	+	0	0	A
S. courcyanum	NE India	35	24	—	—	4	+	+	—	—	—	11	s	—	+	0	+	L
S. grandisonae	Thailand	30	34	71	—	4	—	+	2	6	5	12	—	—	+	0	+	M
S. helenae	Thailand	28	30	—	—	4	—	0	1	—	—	17	s	+	+	0	+	N
S. macullicolus	Borneo	47	35–36	79	84	7	+	0	1	6	6	18–23	s	+	0	0	0	A
S. mimicus	Vietnam	36	30	61	—	4	—	+	2	7	6	16	—	+	+	0	0	M
S. modigliani	Sumatra	41	32	—	—	4	—	+	—	—	—	15	s	+	0	0	0	O
S. puncticentrallis	Java	45	29	64	—	5	+	+	2	7	7	25	s	+	+	0	0	A
S. sanctus	Java	40–45	32–34	71	—	5	+	+	2	7	6	26–27	—	+	0	0	0	A
S. scotophilus	W Malaysia	50	28–31	67–74	—	5	+	0,+	2	7	6	22–23	—	+	+	0	+	A
S. sheai	Vietnam	35.2	20	53	54	4	+	0	2	6	5	6	s	—	+	0	0	A
S. shelfordi[2]	Borneo	67	23–34	—	—	4	+	+	—	—	—	28–29	s	+	+	0	0	A
S. tanahtinggi	Borneo	48–64	40–42	76–79	—	5	+	0,+	4	8–9	7	16–17	k	+	+	0	0	A
S. tenuiculus	Borneo	46	26	57	68	4	+	0	—	7	6	21–24	s	+	+	0	0	A
S. tetradactylus	Vietnam	35	20	48	—	4	0	0	1	6	7	10	s	+	+	0	+	P
S. tonkinensis	Vietnam	37.5–48.8	32–34	65–72	61–67	4	+	+	2	7	6	15–19	s	+	+	0	0	Q
S. tridigitus	Vietnam	36.5	18	50	—	4	+	0	1	6	5	7–8	—	—	+	0	0	R

[1] Some genetic data exists, but phylogenetic placement is not supported.
[2] Despite a SVL > 50 mm, this species is included because it has the same type locality as the new species.

Comparisons. Refer to the Introduction and previous Comparisons for background on the choice of species for which to compare to.

MBSR = 35–37 in *T. leproauricularis* **sp. nov.** distinguishes it from *T. batupanggah* **sp. nov.** (30–31), *T. aesculeticola* (26–32), *T. atrigularis* (30), *T. biparietalis* (32), *T. parvus* (30), *S. bukitensis* (31–33), *S. butleri* (31–33), *S. ishaki* (30–32), *S. perhentianensis* (29), *S. sanana* (28), *S. sibuensis* (29), *S. textus* (30), *S. buttikoferi* (24), *S. malayanus* (32–33), *S. necopinatus* (28–32), *S. schlegeli* (22), *S. senja* (32), *S. vanhuerni* (31), *S. apalpebratus* (27–28), *S. alfredi* (26), *S. cophias* (24), *S. courcyanum* (24), *S. grandisonae* (34), *S. helenae* (30), *S. mimicus* (30), *S. modigliani* (32), *S. puncticentrallis* (29), *S. sanctus* (32–34), *S. scotophilus* (28–31), *S. sheai* (20), *S. shelfordi* (23–34), *S. tanahtinggi* (40–42), *S. tenuiculus* (26), *S. tetradactylus* (20), *S. tonkinensis* (32–34), and *S. tridigitus* (18). PVSR = 68–74 in *T. leproauricularis* **sp. nov.** distinguishes it from *T. batupanggah* **sp. nov.** (62–66), *S. perhentianensis* (65), *S. sibuensis* (58), *S. vanhuerni* (81), *S. apalpebratus* (62–64), *S. cophias* (56), *S. macullicolus* (79), *S. mimicus* (61), *S. puncticentrallis* (64), *S. sheai* (53), *S. tanahtinggi* (76–79), *S. tenuiculus* (57), *S. tetradactylus* (48), and *S. tridigitus* (50). VSR = 80–81 in *T. leproauricularis* **sp. nov.** distinguishes it from *T. batupanggah* **sp. nov.** (55–61), *T. aesculeticola* (60–68), *T. hallieri* (63–73), *S. bukitensis* (61–74), *S. butleri* (62–63), *S. ishaki* (60–70), *S. langkawiensis* (70–72), *S. perhentianensis* (61), *S. sibuensis* (52), *S. temengorensis* (70,71), *S. temmincki* (62–72), *S. malayanus* (74), *S. senja* (68), *S. apalpebratus* (60), *S. macullicolus* (84), *S. sheai* (54), *S. tenuiculus* (68), and *S. tonkinensis* (61–67). The presence of 4 supraoculars distinguishes *T. leproauricularis* **sp. nov.** from *S. textus* (5), *S. apalpebratus* (5), *S. macullicolus* (7), *S. puncticentrallis* (5), *S. sanctus* (5), *S. scotophilus* (5), and *S. tanahtinggi* (5). The contact of the parietal with the last supraocular distinguishes *T. leproauricularis* **sp. nov.** from *T. hallieri*, and *S. tetradactylus*. The separation of the prefrontals distinguishes *T. leproauricularis* **sp. nov.** from all species with prefrontals in contact: *T. batupanggah* **sp. nov.**, *T. atrigularis*, *T. hallieri*, *S. bukitensis*, *S. butleri*, *S. ishaki*, *S. langkawiensis*, *S. perhentianensis*, *S. sibuensis*, *S. temengorensis*, *S. textus*, *S. buttikoferi*, *S. malayanus*, *S. schlegeli*, *S. courcyanum*, *S. grandisonae*, *S. mimicus*, *S. modigliani*, *S. puncticentrallis*, *S. sanctus*, *S. shelfordi*, and *S. tonkinensis*. The presence of paired anterior loreals distinguishes *T. leproauricularis* **sp. nov.** from *S. sibuensis*, *S. macullicolus*, *S. tanahtinggi*, *S. tetradactylus*, and *S. tridigitus*. The presence of 6 or 7 supralabials distinguishes *T. leproauricularis* **sp. nov.** from *S. sanana* (5), and *S. tanahtinggi* (8–9). The presence of 5 infralabials distinguishes *T. leproauricularis* **sp. nov.** from *T. biparietalis* (6), *S. perhentianensis* (6), *S. malayanus* (7–8), *S. senja* (6), *S. cophias* (7), *S. macullicolus* (6), *S. puncticentrallis* (7), *S. sanctus* (6), *S. scotophilus* (6), *S. tanahtinggi* (7), *S. tenuiculus* (6), *S. tetradactylus* (7), and *S. tonkinensis* (6). SDL on Toe IV = 10 in *T. leproauricularis* **sp. nov.** distinguishes it from *T. batupanggah* **sp. nov.** (9), *S. bukitensis* (12–13), *S. butleri* (12–13), *S. ishaki* (11), *S. langkawiensis* (11,12), *S. sanana* (9), *S. sibuensis* (9), *S. textus* (15), *S. buttikoferi* (21–23), *S. malayanus* (12–13), *S. necopinatus* (11–15), *S. senja* (13–17), *S. vanhuerni* (14–15), *S. apalpebratus* (8–9), *S. alfredi* (12), *S. cophias* (9), *S. courcyanum* (11), *S. grandisonae* (12), *S. helenae* (17), *S. macullicolus* (18–23), *S. mimicus* (16), *S. modigliani* (15), *S. puncticentrallis* (25), *S. sanctus* (26–27), *S. scotophilus* (22–23), *S. sheai* (6), *S. shelfordi* (28–29), *S. tanahtinggi* (16–17), *S. tenuiculus* (21–24), *S. tonkinensis* (15–19), and *S. tridigitus* (7–8). The presence of smooth SDL distinguishes *T. leproauricularis* **sp. nov.** from all species with keeled SDL: *S. bukitensis*, *S. ishaki*, *S. langkawiensis*, *S. sibuensis*, *S. temengorensis*, *S. malayanus*, *S. apalpebratus*, and *S. tanahtinggi*. The presence of enlarged precloacal scales distinguishes *T. leproauricularis* **sp. nov.** from *T. aesculeticola*, *T. biparietalis*, *T. hallieri*, *S. bukitensis*, *S. temmincki*, *S. apalpebratus*, and *S. alfredi*. The absence of a dark dorsolateral stripe distinguishes *T. leproauricularis* **sp. nov.** from *T. batupanggah* **sp. nov.**, *T. atrigularis*, *T. biparietalis*, *T. hallieri*, *S. butleri*, *S. langkawiensis*, *S. sibuensis*, *S. temengorensis*, *S. temmincki*, *S. textus*, *S. buttikoferi*, *S. necopinatus*, *S. schlegeli*, *S. apalpebratus*, *S. alfredi*, *S. cophias*, *S. courcyanum*, *S. grandisonae*, *S. helenae*, *S. mimicus*, *S. puncticentrallis*, *S. scotophilus*, *S. sheai*, *S. shelfordi*, *S. tanahtinggi*, *S. tenuiculus*, *S. tetradactylus*, *S. tonkinensis*, and *S. tridigitus*. The absence of a light postorbital stripe distinguishes *T. leproauricularis* **sp. nov.** from *T. batupanggah* **sp. nov.**, *T. biparietalis*, *S. ishaki*, *S. langkawiensis*, and *S. temengorensis*. The absence of a light dorsolateral stripe distinguishes *T. leproauricularis* **sp. nov.** from *T. batupanggah* **sp. nov.**, *S. langkawiensis*, *S. sanana*, *S. sibuensis*, *S. temengorensis*, *S. schlegeli*, *S. apalpebratus*, *S. courcyanum*, *S. grandisonae*, *S. helenae*, *S. sheai*, and *S. tetradactylus*.
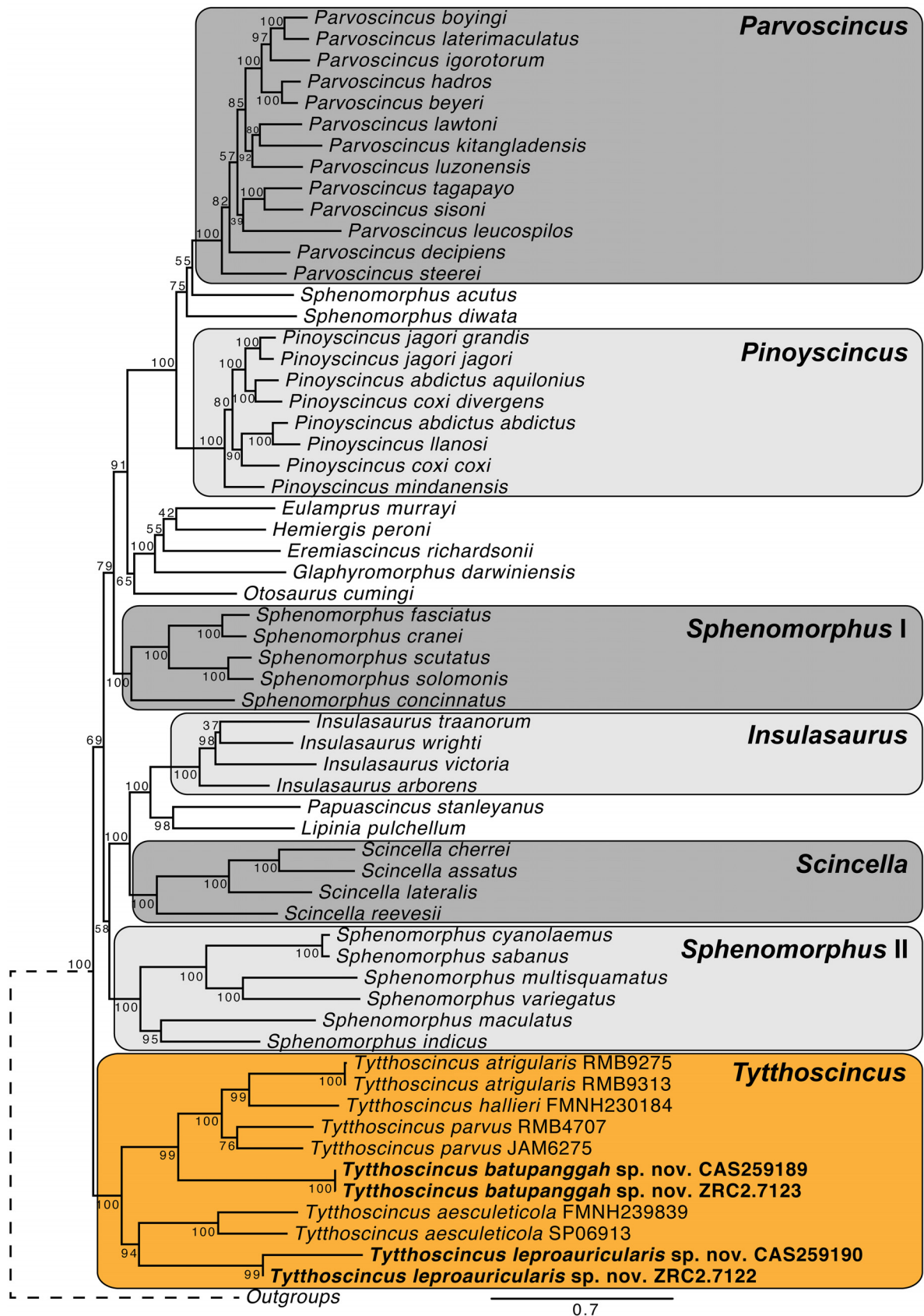
FIGURE 5. Concatenated maximum likelihood phylogram of *Sphenomorphus* group of skinks with bootstrap replicates (percentage of 1000 replicates) shown at the nodes. The two new species are indicated in bold, and the genus *Tytthoscincus* is indicated by a orange rectangle.
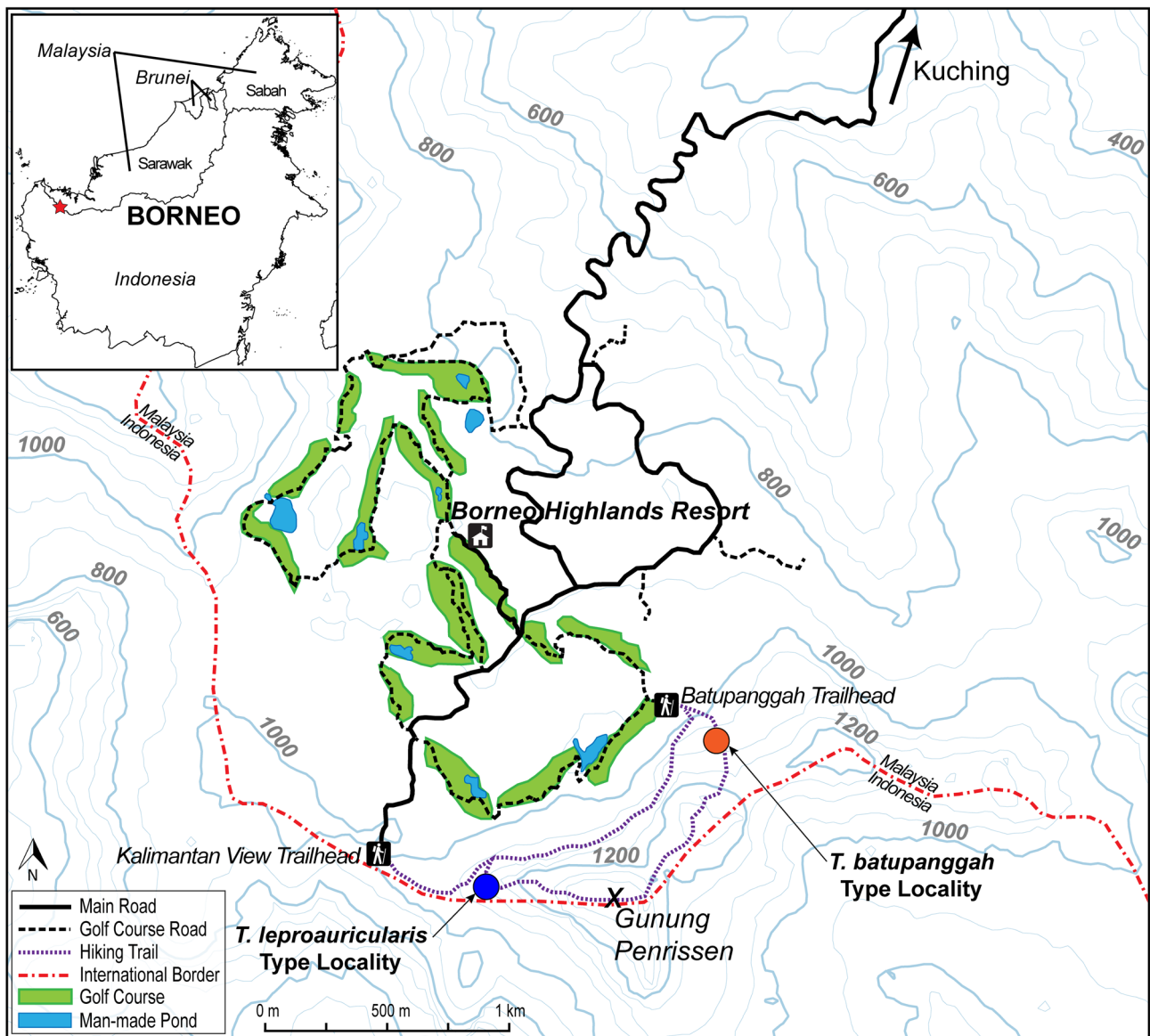
FIGURE 6. Map indicating the type localities of *T. leproauricularis* **sp. nov.** (blue circle) and *T. batupanggah* **sp. nov.** (orange circle). The large forest clear-cut to build the Borneo Highland Resort's golf course (green) likely depleted a large amount of the habitat formerly available to the new species. The detail map region is denoted by a red star in the overview map of Borneo (top left). Spatial data for contour intervals were obtained from the NASA Shuttle Radar Topography Mission (available from https://lpdaac.usgs.gov) and interpolated using the open source program QGIS (http://www.qgis.org/). Other features were drawn by hand based on available satellite imagery (Google, Digital Globe, 2012).

Discussion

What stands out in the description of these two diminutive skink species is their extreme proximity and phenotypic similarity to one another, coupled with their genetic distinctiveness. *Tytthoscincus batupanggah* **sp. nov.** and *Tytthoscincus leproauricularis* **sp. nov.** were found only a kilometer apart at a similar elevation on the same mountain and genetic results support separate evolutionary origins (i.e., non-sister lineages) of each species. What historical processes could cause such a pattern? One possibility (Grismer *et al.* 2015) is that co-distribution of genetically and morphologically distinct, non-sister species could be due to delayed back-migration after allopatric speciation due to climate fluctuations. In Peninsular Malaysia, Grismer *et al.* (2015) found co-distribution of many species on mountaintops whose divergence dates back to before the Pleistocene, with more recent divergences of sister species on geographically distant mountains. It is therefore possible that old divergences occurred on these

distant mountains, and more recent climatic fluctuations allowed for cross-dispersal and later allopatric speciation. Paleoclimatic models predict that during glacial maxima, montane rainforests on the Sunda Shelf expanded and spread downhill to the lowlands (Cannon *et al.* 2009), potentially allowing for this migration of divergent montane populations to other mountains during the Pleistocene. During glacial minima, these montane forest corridors would have allowed for dispersal of montane-adapted species between mountaintops. This hypothesis could explain the co-distribution of the two genetically divergent new species (26.3% raw mitochondrial divergence), *Tytthoscincus batupanggah* **sp. nov.** and *Tytthoscincus leproauricularis* **sp. nov.**, on Gunung Penrissen. Increased sampling from additional montane regions in Borneo is essential in validating this hypothesis.

In recent years, the Sunda Shelf has been host to a number of species descriptions within the *Sphenomorphus* group (Grismer & Quah 2015; Grismer 2006, 2007, 2008, 2009; Grismer *et al.* 2009a; b; Inger *et al.* 2001). These recent descriptions (mostly from Peninsular Malaysia) highlight the probability that there is significant undescribed species diversity on Borneo. Given that many of the species in the *Sphenomorphus* and *Tytthoscincus* group are localized endemics, if we extrapolate the possibility of discovering two new species on the same mountain to the rest of Borneo, the number of potential new species in Borneo is staggering. However, given the difficulty of properly diagnosing the new species against the multitude of *Sphenomorphus* species that have yet to be taxonomically revised and placed into the recently erected genera (Linkem *et al.* 2011), a comprehensive taxonomic study is critical in facilitating new descriptions and discoveries.

The discovery of these two new species of skinks from Gunung Penrissen highlights the evolutionary importance montane rainforests have had in shaping the species diversity in tropical regions. Even the small area of primary forest that remains on Gunung Penrissen after the bulldozing of a large swath for a golf course hosts a variety of endemic species including the two newly described species in this paper. Particularly on Malaysian Borneo, where logging is destroying rainforests at an alarming rate (Bryan *et al.* 2013), we must consider the irreversible impacts of these practices on species diversity and the potential extinction of species before they are described.

Acknowledgements

References

Aljanabi, S.M. & Martinez, I. (1997) Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. *Nucleic Acids Research*, 25, 4692–4693.
http://dx.doi.org/10.1093/nar/25.22.4692
Annandale, N. (1912) Zoological results of the Abor expedition, 1911–1912. *Records of the Indian Museum*, 8, 7–59.
http://dx.doi.org/10.5962/bhl.part.1186
Arévalo, E., Davis, S.K. & Sites, J.W. (1994) Mitochondrial DNA sequence divergence and phylogenetic relationships among eight chromosome races of the *Sceloporus grammicus* complex (Phrynosomatidae) in central Mexico. *Systematic Biology*, 43, 387–418.
http://dx.doi.org/10.1093/sysbio/43.3.387
Boulenger, G.A. (1894) A list of the reptiles and batrachians collected by Dr. E. Modigliani on Sereinu (Sipora), Mentawei Islands. *Annali del Museo Civico di Storia Naturale di Genova,* Series 2, 34, 613–618.

Boulenger, G.A. (1897) A catalogue of the reptiles and batrachians of Celebes, with special reference to the collections made by Drs. P. & F. Sarasin in 1893–1896. *Proceedings of the Zoological Society of London*, 65, 193–237.

Boulenger, G.A. (1898) Third report on additions to the lizard collection in the Natural History Museum. *Proceedings of the Zoological Society of London*, 66, 912–923.
http://dx.doi.org/10.1111/j.1096-3642.1898.tb03194.x

Boulenger, G.A. (1900) Descriptions of new reptiles and Batrachians from Borneo. *Proceedings of the Zoological Society of London*, 69, 182–187.
http://dx.doi.org/10.1111/j.1096-3642.1890.tb01716.x

Brongersma, L.D. (1942) Notes on scincid lizards. *Zoologische Mededelingen*, 24, 125–152.

Bryan, J.E., Shearman, P.L., Asner, G.P., Knapp, D.E., Aoro, G. & Lokes, B. (2013) Extreme differences in forest degradation in Borneo: comparing practices in Sarawak, Sabah, and Brunei. *PLoS ONE*, 8, e69679.
http://dx.doi.org/10.1371/journal.pone.0069679

Cannon, C.H., Morley, R.J. & Bush, A.B.G. (2009) The current refugial rainforests of Sundaland are unrepresentative of their biogeographic past and highly vulnerable to disturbance. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 11188–11193.
http://dx.doi.org/10.1073/pnas.0809865106

Cochran, D.M. (1927) New reptiles and batrachians collected by Dr. Hugh M. Smith in Siam. *Proceedings of the Biological Society of Washington*, 40, 179–192.

Darevsky, I.S. & Orlov, N.L. (2005) New species of limb-reduced lygosomine skink genus *Leptoseps* Greer, 1997 (Sauria, Scincidae) from Vietnam. *Russian Journal of Herpetology*, 12, 65–68.

Datta-Roy, A., Das, I., Bauer, A.M., Tron, R.K.L. & Karanth, P. (2013) Lizard wears shades. A spectacled *Sphenomorphus* (Squamata: Scincidae), from the sacred forests of Mawphlang, Meghalaya, north-east India. *Zootaxa*, 3701 (2), 257–276.
http://dx.doi.org/10.11646/zootaxa.3701.2.7

de Queiroz, K. (1998) The general lineage concept of species. Species criteria, and the process of speciation. *In*: Howard, D.J. & Berlocher, S.H. (Eds.), *Endless forms: Species and Speciation*. Oxford University Press, New York, USA, pp. 57–75.

de Queiroz, K. (1999) The general lineage concept of species and the defining properties of the species category. *In*: Wilson, R.A. (Ed.), *Species: New Interdisciplinary Essays*. Massachusetts Institute of Technology Press, Cambridge, Massachusetts, pp. 49–89.

Dunn, E.R. (1927) Results of the Douglas Burden Expedition to the island of Komodo. III.—Lizards from the East Indies. *American Museum Novitates*, 288, 1–13.

Greer, A.E., David, P. & Teynié, A. (2006) The southeast Asian Scincid lizard *Siaphos tridigitus* Bourret, 1939 (Reptilia, Scincidae): a second specimen. *Zoosystema*, 28, 785–790.

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

Grismer, L.L. (2007) A new species of small montane forest floor skink (Genus *Sphenomorphus* Fitzinger 1843) from southern peninsular Malaysia. *Herpetologica*, 63, 544–551.
http://dx.doi.org/10.1655/0018-0831(2007)63%5B544:ANSOSM%5D2.0.CO;2

Grismer, L.L. (2008) A new species of insular skink (Genus *Sphenomorphus* Fitzinger 1843) from the Langkawi Archipelago, Kedah, west Malaysia with the first report of the her- petofauna of Pulau Singa Besar and an updated checklist of the herpetofauna of Pulau Langkawi. *Zootaxa*, 1691, 53–26.

Grismer, L.L. (2015) *Paleoendemism and genetic uniformity across 17 different clades in the sky island archipelago of Malaysia. Oral Presentation*. Annual Meeting of the Society for the Study of Reptiles and Amphibians, University of Kansas, Lawrence, Kansas.

Grismer, L.L., Ahmad, N. & Onn, C.K. (2009a) A new, diminutive, upland *Sphenomorphus* Fitzinger 1843 (Squamata: Scincidae) from the Belum-Temengor Forest Complex, Peninsular Malaysia. *Zootaxa*, 2312, 27–38.

Grismer, L.L., Wood, P.L. & Grismer, J.L. (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, L.L. & Quah, E.S.H. (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 (1), 63–70.
http://dx.doi.org/10.11646/zootaxa.3931.1.4

Inger, R.F., Lian, T.F., Lakim, M. & Yambun, P. (2001) New species of the lizard genus *Sphenomorphus*, (Lacertilia : Scincidae), with notes on ecological and geographic distribution of species in Sabah, Malaysia. *The Raffles Bulletin of Zoology*, 49, 181–189.

Kopstein, F. (1926) Reptilien von den Molukken und den benachbarten Inseln. *Zoologische Mededelingen*, 9, 71–112.

Leaché, A.D. (2009) Species tree discordance traces to phylogeographic clade boundaries in North American fence lizards (*Sceloporus*). *Systematic Biology*, 58, 547–559.
http://dx.doi.org/10.1093/sysbio/syp057

Linkem, C.W. (2013) *Molecular Phylogenetics and Biogeography of Sphenomorphini (Squamata: Scincidae)*. PhD Thesis, Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, Kansas. 250 pp.

Linkem, C.W., Diesmos, A.C. & Brown, R.M. (2010) A new species of scincid lizard (genus *Sphenomorphus*) from Palawan Island, Philippines. *Herpetologica*, 66, 67–79.
http://dx.doi.org/10.1655/08-074.1

Linkem, C.W., Diesmos, A.C. & Brown, R.M. (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.
http://dx.doi.org/10.1111/j.1096-3642.2011.00747.x

Macey, J.R., Larson, A., Ananjeva, N.B., Fang, Z. & Papenfuss, T.J. (1997) Two novel gene orders and the role of light-strand replication in rearrangement of the vertebrate mitochondrial genome. *Molecular Biology and Evolution*, 14, 91–104.
http://dx.doi.org/10.1093/oxfordjournals.molbev.a025706

Müller, F. (1895) Reptilien und amphibien aus Celebes. *Verhandlungen der Naturforschenden Gesellschaft in Basel*, 10, 825–843.

Nguyen, T.,Q., Schmitz, A., Nguyen, T.T., Orlov, N.L., Böhme, W. & Ziegler, T. (2011) Review of the genus *Sphenomorphus* Fitzinger, 1843 (Squamata: Sauria: Scincidae) in Vietnam, with description of a new species from northern Vietnam and southern China and the first record of *Sphenomorphus mimicus* Taylor, 1962 from Vietnam. *Journal of Herpetology*, 45, 145–154.
http://dx.doi.org/10.1670/09-068.1

Rohland, N. & Reich, D. (2012) Cost-effective, high-throughput DNA sequencing libraries for multiplexed target capture. *Genome Research*, 22, 939–946.
http://dx.doi.org/10.1101/gr.128124.111

Stamatakis, A. (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22, 2688–2690.
http://dx.doi.org/10.1093/bioinformatics/btl446

Stejneger, L. (1908) Three new species of lizards from the Philippine Islands. *Proceedings of the United States National Museum*, 34, 199–204.
http://dx.doi.org/10.5479/si.00963801.34-1606.199

Taylor, E.H. (1918) Reptiles of Sulu Archipelago. *Philippine Journal of Science*, 13, 233–265.

Taylor, E.H. (1962) New Oriental reptiles. *University of Kansas Science Bulletin*, 43, 209–263.
http://dx.doi.org/10.5962/bhl.part.13346

Wiley, E.O. (1978) The evolutionary species concept reconsidered. *Systematic Biology*, 27, 17–26.
http://dx.doi.org/10.2307/2412809