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Unrealized diversity in an urban rainforest: A new species of *Lygosoma* (Squamata: Scincidae) from western Sarawak, Malaysia (Borneo)

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Abstract

We collected two specimens of an undescribed species of *Lygosoma* from pitfall traps in an urban rainforest in Kuching and from the base of a forested hill in western Sarawak, East Malaysia. The new species is diagnosable from all south-east Asian congeners by morphological characters, and most closely resembles *Lygosoma herberti* from the Thai-Malay Peninsula. The new species shows substantial molecular divergence from its closest relatives in two protein-coding genes, one mitochondrial (ND1) and one nuclear (R35) that we sequenced for several south-east Asian congeners. We describe the new species on the basis of this distinct morphology and genetic divergence. It is the third species of *Lygosoma* known from Borneo, and highlights the continuing rise in lizard species diversity on the island. In addition, the discovery of this species from a small urban rainforest underscores the importance of preserving intact rainforest areas of any size in maintaining species diversity.

Key words: Borneo; Sarawak; Scincidae; *Lygosoma samajaya* new species

Introduction

The island of Borneo, the third-largest island in the world, is one of the most biodiverse regions on earth, yet it suffers from several decades of severe deforestation that has impacted most of the rainforest on the island, and particularly the lowlands (Bryan *et al.* 2013; Gaveau *et al.* 2014). Borneo has been designated as a biodiversity hotspot (Mittermeier *et al.* 1998; Myers *et al.* 2000), defined as a place with exceptional diversity under threat by anthropogenic activity. Understanding the diversity of the region is important for generating local interest and implementing effective conservation strategies (Gadgil *et al.* 1993).

Despite having a long history of zoological (e.g., de Bruyn *et al.* 2014; Inger 1966; Wallace 1869) and especially herpetological research (see Das 2004a), it is clear that the lizard diversity on Borneo remains underestimated, particularly for scincids and gekkonids. This is especially evident when compared to 33 recent species described from the much smaller adjacent Peninsular Malaysia (see Grismer *et al.* 2016). Currently, 36 species of geckos and 51 species of skinks are recognized to occur on Borneo (Uetz & Hošek 2017). In the past year alone (2016–2017), three new skink species including *Tytthoscincus batupanggih* Karin, Das & Bauer 2016, *Tytthoscincus leproauricularis* Karin, Das & Bauer 2016, and *Tropidophorus sebi* Pui, Karin, Bauer & Das, 2017, and one new gecko species, *Cnemaspis leucura* Kurita, Nishikawa, Matsui, & Hikida, 2017, have been described from specimens recently collected from (mostly south-western) Sarawak. This has resulted in an increase of six

percent in the known skink diversity and three percent for known gecko diversity. Over the past two decades, several other gekkonid and scincid species were described including the geckos *Luperosaurus sorok* Das, Lakim & Kandaung, 2008 from Sabah and *Cnemaspis paripari* Grismer & Onn, 2009 from Sarawak, and the skinks *Sphenomorphus aesculeticola* Inger, Tan, Lakim & Yambun, 2001; *Sphenomorphus crassa* Inger, Tan, Lakim & Yambun, 2001; *Sphenomorphus tanahtinggi* Inger, Tan, Lakim & Yambun, 2001, and *Lipinia inexpectata* Das & Austin, 2007 from Sabah. All of these species are relatively localized endemics, suggesting that lizard diversity in Borneo is likely to be underestimated. Additionally, many of these species have type localities in parks and green spaces frequented by tourists (e.g., *C. paripari* from Fairy Cave and Gua Angin, popular tourist destinations near Kuching, Sarawak), indicating the importance of conservation in protecting the island's diversity. Here, we describe a new species of scincid lizard in the genus *Lygosoma* from a small urban forest in Kuching, and another nearby locality, both in western Sarawak.

There are currently 30 recognized species of *Lygosoma* Hardwicke & Gray, 1827 (Geissler *et al.* 2012; Heitz *et al.* 2016) distributed across the Old World tropics in India and south-east Asia, and although five African taxa have not been formally transferred out of *Lygosoma*, it is likely that most or all of these are referable to *Mochlus*. A total of 17 species occur in south-east Asia, ranging from Indochina through the Thai-Malay Peninsula through the Indo-Australian Archipelago and Palawan Island in the Philippines, with one species found in the South Pacific (Geissler *et al.* 2012; Grismer 2011; Heitz *et al.* 2016; Uetz & Hošek 2017; Ziegler *et al.* 2007). South-east Asian species in the genus are terrestrial or semifossorial forest inhabitants and can be found under rotting logs and leaf litter, or in loose soil (Geissler *et al.* 2012). Most of the recognized *Lygosoma* diversity in south-east Asia is found in Indochina, but recent descriptions in Indochina and the Philippines highlight the potential for further species discovery in this group across south-east Asia, including on Borneo (Geissler *et al.* 2013; Heitz *et al.* 2016). Currently, only two species are known from Borneo—*L. bampfyldei* Bartlett, 1895 and *L. bowringii* (Günther, 1864)—but the region's forests and geography make it likely that there remain additional undescribed *Lygosoma* on Borneo.

Materials and methods

Specimen collection. Two pitfall trap arrays were set at two separate localities in the vicinity of Kuching, Malaysia in 2014, one at the Sama Jaya Forest Reserve and the other at the base of Gunung Gumbang (46 km apart). At the former locality, the pitfall arrays were built following the design of Fisher & Rochester (2012:235) and consisted of seven 5-gallon buckets dug into the ground so the rims would be at ground level. One central bucket was placed and arranged with three arms at 120° angles spreading 5 m in length from it, with two buckets each placed at 2.5 m intervals. Galvanized steel sheet metal was dug into the ground between the buckets for a drift fence to direct any organisms that contacted the pitfall trap towards the buckets. At Gumbang, individual buckets were placed into holes dug in the ground alongside a sandy streambed, and drift fencing was not used. Specimens were preserved in formalin and later transferred to ethanol. Liver tissue was stored in 95% EtOH.

Measurements. Measurements were taken with Mitutoyo digital calipers accurate to 0.1 mm. Measurements were taken as follows: head width at front of ears and at center of eyes; inter-eye width from a line drawn on the top of the head between the center of the eyes; neck width at narrowest point; head height at center of eyes with calipers placed on the dorsal and ventral surfaces of head; head length from tip of snout to line drawn between the front of ears; nostril–snout length from anterior margin of nostril to tip of snout; nostril–eye length from posterior margin of nostril to anterior margin of eyeball; internarial distance between the nostrils; interocular distance at anterior margins of eyes; forelimb and hindlimb length from claw tip of fourth digit to insertion on the body.

Scale counts were taken as follows: midbody scale rows are the number of longitudinal rows of scales around the midbody; paravertebral scale rows are the number of dorsal scales from behind parietals to base of tail opposite vent, including nuchals; ventral scale rows are the number of scales from behind first pair of chin shields to in front of cloacal shields; supralabials are the number of enlarged scales along one side of upper margin of mouth; infralabials are the number of enlarged scales along one side of lower margin of mouth; supranasals in contact if they form a medial suture or are separated if the rostral forms a suture with frontonasal. Scale counts were taken using a dissecting scope or from images taken with a Canon EF 100 mm f/2.8 macro lens.

Comparative material. Sources of data on character states and distribution include material in Appendix I as

well as the following works: Bourret (2009); Brown & Alcalá (1980); Das (2004b, 2010); de Rooij (1915); Geissler *et al.* (2011); Greer (1977); Grismer (2011); Heitz *et al.* (2016); Malkmus *et al.* (2002); Manthey & Grossmann (1997); Smith (1935); and Taylor (1963).

Museum abbreviations. Museum abbreviations follow Sabaj Pérez (2016), except for the Lee Kong Chian Museum of Natural History (formerly, the Raffles Museum of Biodiversity Research, National University of Singapore, Singapore) for which we use the acronym ZRC, following widespread usage; BM = Brunei Museum, Bandar Seri Begawan, Brunei Darussalam; BMNH = The Natural History Museum London; CAS = California Academy of Science, San Francisco, USA; FMNH = Field Museum of Natural History, Chicago, U.S.A.; MNHN = Musée National d'Histoire Naturelle, Paris, France; NMW = Naturhistorisches Museum, Vienna, Austria; SBC = Sarawak Biodiversity Centre Museum, Jalan Semenggoh, Sarawak, Malaysia; SM = Sarawak Museum, Kuching, Sarawak, Malaysia; SP = Sabah Park Zoological Museum, Gunung Kinabalu National Park Headquarters, Sabah, Malaysia; SSM = Sabah State Museum, Kota Kinabalu, Sabah, Malaysia; UBD = Museum of Brunei Darussalam, Bandar Seri Begawan, Brunei Darussalam; UKMS = Museum of Zoology, Universiti Kebangsaan Malaysia, Sabah Campus, Kota Kinabalu, Sabah, Malaysia; UMS = “Borneensis” Collection, Universiti Malaysia Sabah, Kota Kinabalu, Sabah, Malaysia (also incorporates the erstwhile UKMS collection); UNIMAS = Universiti Malaysia Sarawak, Kota Samarahan, Sarawak, Malaysia; USNM = National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.; and ZSI = Zoological Survey of India, National Zoological Collection, Kolkata (formerly Calcutta), India.

Molecular methods. We extracted genomic DNA from tissue samples using Qiagen DNeasy blood & tissue kits (QIAGEN). We amplified the nuclear gene RNA fingerprint protein 35 (R35) using the primers R35.F: 5′-GACTGTGGAYGAYCTGATCAGTGTGG-3′ and R35.R: 5′-GCCAAAATGAGSGAGAARCGCTTCTG-3′ (Fry *et al.* 2006) and the mitochondrial gene NADH dehydrogenase subunit 1 (ND1) using the primers 16dr: 5′-CTACGTGATCTGAGTTCAGACCGGAG-3′ and tMet: 5′-ACCAACATTTTCGGGGTATGGG-3′ (Leaché & Reeder 2002) for three species (the new species, *Lygosoma herberti*, and *Lygosoma lineolatum*) following established protocols (Siler *et al.* 2011). We also sequenced mitochondrial 16s ribosomal RNA for a different set of samples (the new species, two specimens of *Lygosoma herberti*, and *Lygosoma bowringii*) using the primers 16Sbr-L: 5′-CGCCTGTTTATCAAAAACAT-3′ and 16Sbr-H 5′-CCGGTCTGAACTCAGATCACGT-3′ (Palumbi *et al.* 1991) for inclusion in a separate phylogenetic analysis with increased taxon sampling incorporated from GenBank. PCR products were visualized on a 1% agarose gel, cleaned using ExoSap-IT (Thermo Fisher Scientific) and sequenced in forward and reverse directions using BigDye® Terminator v3.1 sequencing kit (Thermo Fisher Scientific). Sequences were purified using ethanol precipitation and were sent to Eurofins Genomics for visualization. All sequences are deposited on GenBank (see Table S1 for accession numbers).

Phylogenetic analysis and pairwise distances.—We used Geneious v10.0.9 (Biomatters Ltd.) to check the quality of our sequences and examine them for miscalled bases and heterozygous sites. Primer-binding sites were trimmed off both ends of the sequences. For R35 and ND1, we aligned each gene by eye incorporating sequences of *Plestiodon marginatus* and *Brachymeles bicolor* from GenBank (see Table S1) as outgroups, which together form a clade of scincine species outside of *Lygosoma* (Pyron *et al.* 2013). The two alignments were placed in the correct reading frame in Geneious and examined for misplaced indels and erroneous internal stop codons. When we were satisfied with our alignments, we generated individual gene trees in RAxML to confirm there was no strong discordance (results not shown), and then concatenated the two genes for phylogenetic analysis.

We also conducted a separate phylogenetic analysis incorporating the four 16s rRNA sequences we generated with a dataset including 41 other sequences of *Lygosoma*, *Lepidothyris*, *Mochlus*, and outgroups, combining datasets of other *Lygosoma* phylogenies available on GenBank (Datta-Roy *et al.* 2014; Honda *et al.* 2003; Skinner *et al.* 2011). Outgroups were chosen based on the close relationship recovered by Pyron *et al.* (2013). As the dataset is similar to Datta-Roy *et al.* (2014), we did not conduct this analysis to provide strong support for phylogenetic relationships within the genus, but the inclusion was useful for confirming the distinctiveness of the new species compared to these other taxa.

The ND1 alignment consisted of 966 bp, the R35 alignment 662 bp, and the 16s alignment 516 bp. We partitioned the concatenated ND1 and R35 alignment for Bayesian and Maximum Likelihood analyses based on the results of PartitionFinder v1.1.1 (Lanfear *et al.* 2012) using the greedy algorithm and BIC. PartitionFinder supported three partitions for the Maximum Likelihood analysis (ND1 codon position 1 with R35 codon positions 1 and 3; ND1 codon position 2 with R35 codon position 2; and ND1 codon position 3) which we ran in the program

RAxML v8.1.15 (Stamatakis 2014) using the nucleotide GTR + Γ model for each partition and 1000 bootstrap replicates. We ran the Bayesian analysis in MrBayes v3.2.1 (Ronquist & Huelsenbeck 2003) for 10 million generations sampling every 1000 and discarding the first 25% of trees as burnin specifying five different partitions with separate models (R35 codon positions 1 and 3 under K80 + I; R35 position 2 with HKY + Γ ; ND1 position 1 with SYM + Γ ; ND1 position 2 with HKY + I; and ND1 position 3 with HKY + I + Γ). We assessed convergence of the Bayesian analysis in MrBayes by eye and by confirming ESS values were well over 200. The separate 16s analysis was run using RAxML with no partitions and otherwise identical settings.

We calculated uncorrected pairwise distances for each gene separately in Paup* v4.0b10 (Swofford 2003). Prior to the analysis, we removed the outgroup species so that distances were only calculated between ingroup (*Lygosoma*) species.

Systematics

Phylogenetic analysis places the new species as sister to *Lygosoma herberti* Smith, 1916 from the Malay Peninsula with strong support (Figs. 1, S1). The new species is genetically distinct from *L. herberti*, showing 16.1% uncorrected pairwise distance for ND1 and 1.2% uncorrected pairwise distance for R35 (Table 1), as well as 4.3–4.7% for 16s (data not shown). Additionally, both species are found to be closely related to *L. bowringii*, a widely distributed south-east Asian species.

TABLE 1. Uncorrected pairwise distances (%) between species in this study. Values for mitochondrial DNA (ND1) are above the diagonal and shaded in gray, values for nuclear DNA (R35) are below the diagonal and unshaded.

	<i>bowringii</i>	<i>corpulentum</i>	<i>herberti</i>	<i>lineolatum</i>	<i>quadrupes</i>	<i>samajaya</i> sp.nov.	<i>tabonorum</i>
<i>bowringii</i>	—	18.32	15.42	20.70	19.67	17.70	21.43
<i>corpulentum</i>	4.57	—	180.1	18.63	16.77	19.98	18.84
<i>herberti</i>	1.64	4.23	—	19.88	18.32	16.05	20.19
<i>lineolatum</i>	4.56	6.34	3.02	—	20.18	21.64	21.22
<i>quadrupes</i>	4.58	2.42	3.93	6.65	—	19.46	15.84
<i>samajaya</i> sp.nov.	1.48	4.23	1.21	4.38	3.93	—	21.33
<i>tabonorum</i>	5.07	3.02	4.38	7.10	0.60	4.38	—

Given that *Lygosoma herberti* is the closest relative of the new species, we confirmed that there were no available synonyms for the new specimens. There exists only one synonym for *L. herberti*: *Lygosoma hughi* (Cochran, 1927) from Koh Tao Island in the Gulf of Thailand (Cochran 1930). Based on our interpretation of the description, we are in agreement with Smith (1935:317) that *L. hughi* represents a synonym of *L. herberti* and does not refer to the specimens we collected from Borneo.

The results of our analyses suggest that the new species is both morphologically and genetically distinct from other species in *Lygosoma*. Therefore, in accordance with the general lineage concept of species (de Queiroz 1998, 1999), we recognize a new species from Sarawak, Borneo.

Lygosoma samajaya sp. nov.

Figs. 1–6

Holotype. An adult of unknown sex (CAS 259777; field number SS 0137) collected on 24 June 2014 by Indraneil Das, Benjamin Karin, and Samuel Shonleben from a pitfall trap placed in Sama Jaya Forest Reserve, Kuching, Sarawak, Malaysia (1.523683°N, 110.38793°E; WGS84; elevation 25 m; Figs. 2–4). The specimen was spotted at the edge of the pitfall trap, and directed into the bucket by hand.

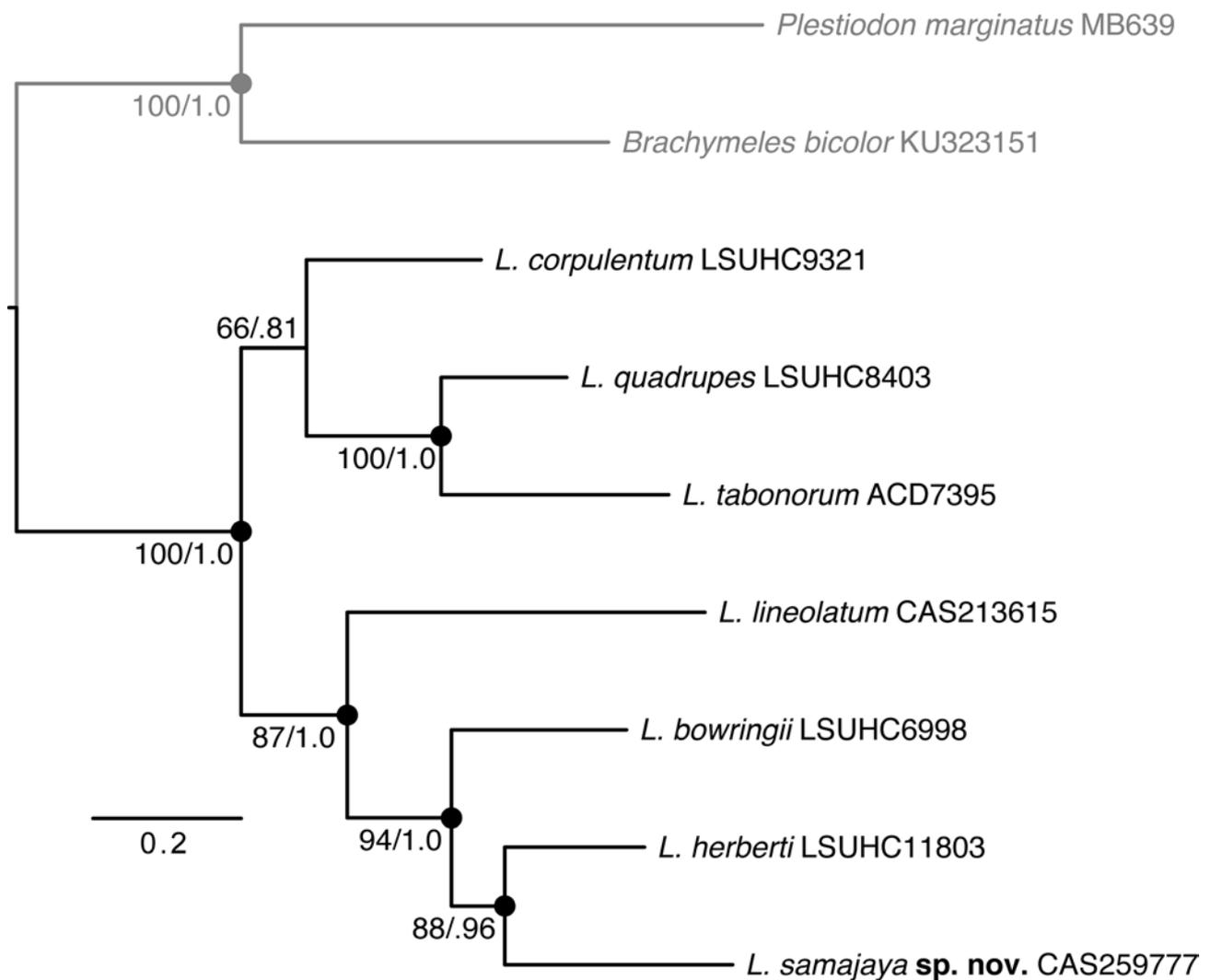


FIGURE 1. Phylogenetic position of *Lygosoma samajaya* sp. nov. within the genus *Lygosoma*. Topology of Bayesian analysis, with support shown by RAxML bootstrap replicates (left value) and Bayesian posterior probabilities (right value). Black circles denote nodes supported by greater than 70/.95. Species in the genus *Lygosoma* are in black; outgroup species are in gray.

Paratype. An adult of unknown sex (UNIMAS 9503; field number SS 0031) collected on 2 February 2013 by Samuel Shonleben and Indraneil Das from a pitfall trap at the foothills of Gunung Gumbang, Kuching Division, Sarawak, Malaysia (1.267°N, 110.050°E; WGS84; elevation 167 m; Figs. 2, 4). No tissue sample was collected.

Diagnosis. *Lygosoma samajaya* sp. nov. is distinguished from all other south-east Asian congeners by the following combination of characters: (1) quinquecarinate dorsal and lateral scales; (2) 13 or 14 subdigital lamellae on the fourth toe; (3) 10 or 11 subdigital lamellae on the fourth finger; (4) paravertebral scale rows 61; (5) midbody scale rows 28–30; (6) lacking enlarged nuchals; (7) supranasals in medial contact; (8) paired frontoparietals; (8) seven supralabials; (9) six infralabials; (10) adult SVL 70 mm; and (11) tail shorter than SVL.

Description of Holotype. Medium sized, SVL 70.1 mm; head weakly differentiated from neck; head width 9.0 mm, 6.8 mm at center of eyes; neck width 8.7 mm; head height 4.8 mm; head length 11.0 mm; nostril–snout length 1.6 mm; nostril–eye length 3.1 mm; internarial distance 2.8 mm; interocular distance 5.1 mm; ear opening small, 0.7 mm in length and 0.6 mm in height. Body slightly dorsoventrally depressed, 9.6 mm in width and 6.7 mm in height at widest point, about midway between the limbs; axilla–groin length 39.8 mm; snout–forelimb length 22.7 mm (axilla–groin length 1.75x snout–forelimb length); forelimb 13.2 mm; hindlimb 18.2 mm; fourth fingers (left/right) 3.4/3.3 mm in length; fourth toes (left/right) 6.9/6.2 mm in length; tail narrower than body, incomplete, 18.2 mm in length from vent; tail width 6.7 mm at its base.



FIGURE 2. Map of Borneo indicating sampling localities for holotype (red) and paratype (orange).

Scales glossy; ventral scales smooth; dorsal scales with five keels (Fig. 5); keels indistinct and nearly smooth near the neck and becoming more prominent posteriorly; scales on limbs much smaller than body scales, moderately keeled; 30 midbody scale rows; 60 paravertebral scale rows; 58 ventral scale rows; four slightly enlarged precloacal scales; 36 rows of scales between the forelimb and hindlimb insertions; limbs well-developed, pentadactyl; keeled scales on dorsal surface of limbs; adpressed hindlimb does not reach halfway to base of adpressed forelimb; lamellae under fingers (left/right) I:3/3, II:9/9, III:10/10, IV:11/11, V:5/5; lamellae under toes (left/right) I:4/4, II:9/8, III:12/12, IV:13/13, V:10/10 (Fig. 5).

Rostral separated from frontonasal by supranasals, nearly trapezoidal with slight projection along midline towards frontonasal; supranasals in contact along the midline; nasal contacts supranasal, rostral, first supralabial, and the anterior loreal; supranasal enters the nostril opening; two loreals, posterior loreal almost twice the length of the slightly taller anterior loreal; frontonasal in broad contact with the frontal; prefrontals widely separated; four

supraoculars, first two in contact with frontal, second to fourth in contact with frontoparietal; frontoparietals in broad contact; interparietal with pineal eyespot near the posterior margin; parietals in broad contact behind the interparietal; no enlarged nuchals; seven supraciliaries; three preoculars, uppermost largest; lower eyelid scaly, without window; seven supralabials, fifth below the eye; six infralabials; mental much wider than long; postmental slightly larger than mental; two pairs of enlarged chin shields; first pair of chin shields in medial contact; second pair of chin shields separated by two small gular scales, slightly larger than first pair. A small tick is preserved between the fourth and fifth gular scale rows (see Fig. 6 for dorsal and lateral diagram of head scales).



FIGURE 3. Photo in life of the holotype of *Lygosoma samajaya* sp. nov.

Colour in Alcohol. Dorsal surface of head, body, limbs, and tail uniform brown; ventral surface of head, body and limbs uniform cream-coloured; a dark brown lateral stripe extends from nostril through the eye and fades to the brown dorsum colour halfway between the limbs, bordered above by a thin whitish line that begins above the eye and terminates above the forelimb insertion; ventral surface of tail begins to darken posteriorly (though incomplete).

Variation. The paratype matches the holotype in size and form, but differs in having 28 (vs. 30) scale rows around the midbody; 61 (vs. 60) paravertebral scale rows; 60 (vs. 58) ventral scale rows; 58 subcaudals (tail of holotype incomplete); (left/right) 10/11 (vs. 11/11) lamellae under the fourth finger (see Table 1 for comparison and other measurements of paratype). Though we do not have molecular data for the paratype, we regard it as a member of this species due to the high degree of morphological similarity observed.

Distribution. Only known from two localities in western Sarawak that are approximately 50 km apart (Fig. 2). It is presumed to occur more widely in lowland rainforest with dense leaf-litter at other sites in western Borneo. No genetic data is available for the paratype, so we cannot assess molecular divergence or connectivity between the two localities and we are assuming that based on morphology, they are conspecific and not cryptic species.

Natural History. Both specimens were collected in pitfall traps placed among leaf litter in dense, closed-canopy forest. In Sama Jaya, the area is primarily heath forest (Kerangas), while in Gumbang it is disturbed, partially logged, mixed dipterocarp forest. We presume the new species is semi-fossorial as its elongate body morphology suggests (Grismer 2011).



FIGURE 4. Preserved holotype (upper) and paratype (lower) of *Lygosoma samajaya* sp. nov.

Etymology. The species epithet *samajaya* is a proper noun in apposition that refers to the locality of collection of the holotype at the Sama Jaya Forest Reserve in Kuching, Sarawak, Malaysia. This name draws attention to the importance of small urban rainforest parks in sustaining species diversity (see Discussion).

Comparisons. Here, we focus comparisons on the 17 congeners that occur in south-east Asia. As our phylogenetic analysis places the new species outside of the Indian radiation of *Lygosoma* (Fig. S1), we exclude Indian congeners from the analysis. *Lygosoma samajaya* sp. nov. differs from nearly all other *Lygosoma* in having five distinct keels on the dorsal scales, an uncommon feature in *Lygosoma*. Of the south-east Asian congeners, most have smooth dorsal scales—*L. angeli* (Smith, 1937), *L. anguinum* (Theobald, 1868), *L. bampfyldei*, *L. corpulentum* Smith, 1921, *L. frontoparietale* (Taylor, 1962), *L. haroldyoungi* (Taylor, 1962), *L. isodactylum* (Günther, 1864), *L. koratense* Smith, 1916, *L. lineolatum*, *L. popae* (Shreve, 1940), *L. quadrupes* (Linnaeus, 1766), *L. tabonorum* Heitz, Diesmos, Freitas, Ellsworth & Grismer, 2016; juveniles and subadults of one species possess pseudokeels (i.e., the optical illusion of keels underlying a smooth scale; sensu Ziegler *et al.* (2007))—*L. boehmei* Ziegler, Schmitz, Heidrich, Vu & Nguyen, 2007; two species usually possess smooth scales but occasionally show weak keels—*L. bowringii* and *L. veunsaiensis* Geissler, Hartmann, & Neang, 2012; and one species possesses tricarinate scales—*L. opisthorhodum* Werner, 1910. Only one other species of south-east Asian *Lygosoma* also possesses quinquecarinate scales, *Lygosoma herberti* from southern Thailand and Peninsular Malaysia, to which *Lygosoma samajaya* sp. nov. is most closely related. The new species is distinguished from *L. herberti* in possessing fewer lamellae under the fourth toe (13–14 vs. 15) and fourth finger (10–11 vs. 12), more paravertebral scale rows (61 vs. 54–58), and being slightly larger in adult body size (SVL 69–71 mm vs. 56–66 mm).

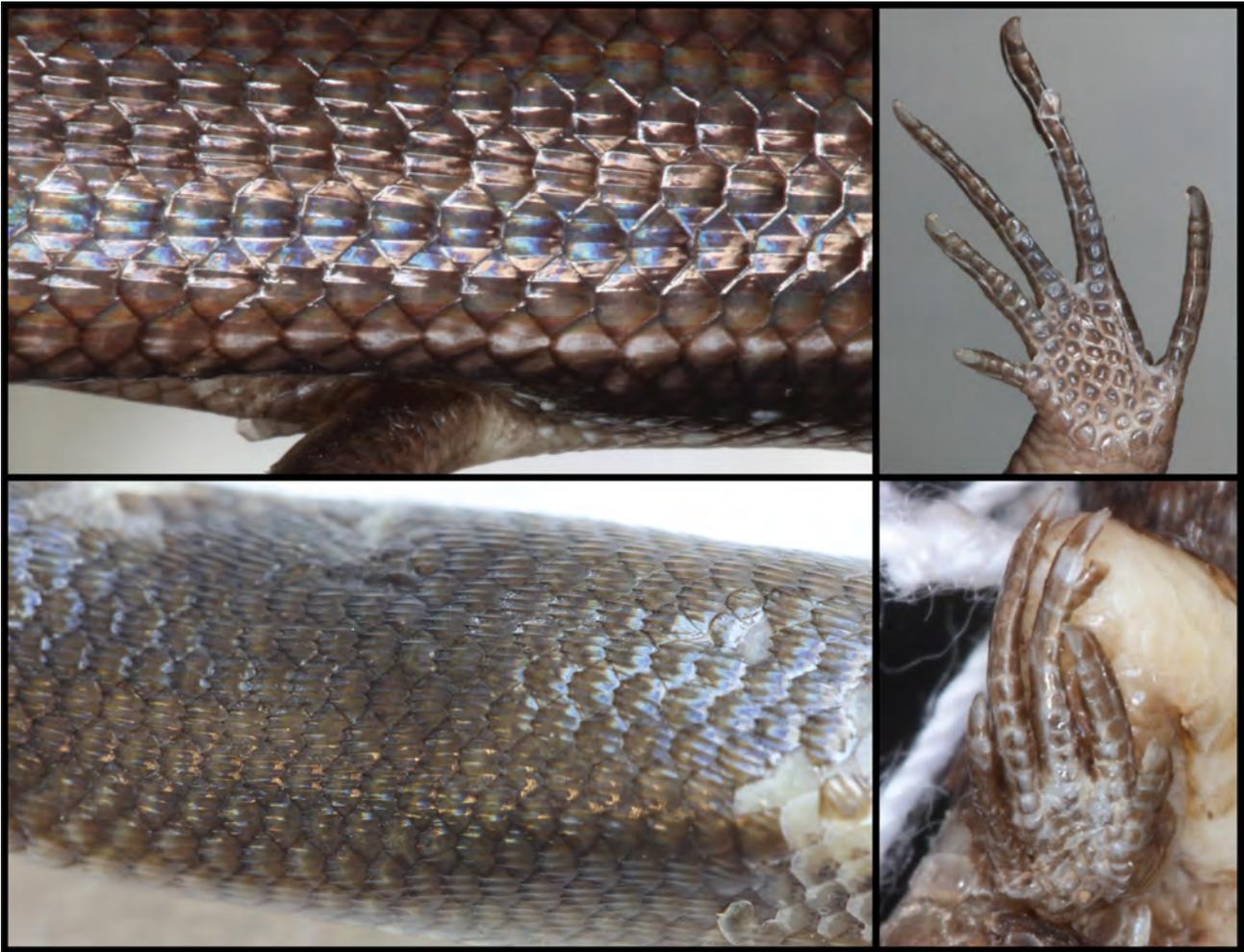


FIGURE 5. Close-up photographs of holotype (upper panels) and paratype (lower panels) showing quincocarinated dorsal scales (left) and hind foot (right). Left foot displayed for holotype and right foot displayed for paratype.

We further differentiate the new species from the south-east Asian congeners that possess some degree of dorsal scale keeling. *Lygosoma samajaya* **sp. nov.** is distinguished from *L. boehmei* by smaller body size (SVL 69–71 mm vs. 91 mm), in possessing a tail shorter than SVL (vs. longer), six infralabials (vs. seven) possessing true keels (vs. pseudokeels); from *L. bowringii* in lacking enlarged nuchal scales (though some *L. bowringii* may also lack nuchals) and in coloration (sides same color as dorsal surface, fading to white vs. sides with red and yellow, fading to white) and in pigmentation patterns (sides solid vs. a lateral stripe and spotting); and from *L. veunsaicensis* by possessing supranasals in contact (vs. separated), seven supralabials (vs. five), six infralabials (vs. five), external ear openings present (vs. absent), 28–30 midbody scale rows (vs. 22), more lamellae under the fourth toe (13–14 vs. 9) and fourth finger (10–11 vs. 5).

The new species is easily distinguished from the two congeners known to occur on Borneo, *L. bowringii* and *L. bampfyldei*: from *L. bowringii* as above; and from *L. bampfyldei* in being much smaller in body size (SVL 69–71 vs. 110–142 mm), in possessing keeled (vs. unkeeled) dorsal scales, and in having fewer midbody scale rows (28–30 vs. 38).

Four other species of *Lygosoma* (*L. albopunctata*, *L. opisthorhodum*, *L. quadrupes*, and *L. tabonorum*) occur in close enough proximity to Borneo (Sunda Shelf or the Philippines) to warrant further comparison beyond differences in carination. *Lygosoma samajaya* **sp. nov.** is further differentiated by the following characters: from *L. albopunctata* by showing a greater midbody scale row count (28–30 vs. 14) and larger body size (SVL 69–71 mm vs. 35–47 mm); from *L. opisthorhodum* by possessing quincocarinated (vs. tricarinate) dorsal scales, in being larger in size (SVL 69–71 mm vs. SVL 45 mm), with tail shorter (vs. longer) than SVL, and in color pattern (uniform brown with dark anterolateral stripe vs. black-brown, brighter toward posterior, with a bright lateral stripe, starting

at subocular region and extending below tympanic region to the midbody); and from *L. quadrupes* and *L. tabonorum* by possessing separated frontoparietals (vs. fused), absence (vs. presence) of enlarged nuchals, and a greater fourth toe lamellae count (13–14 vs. 6–7 in each).

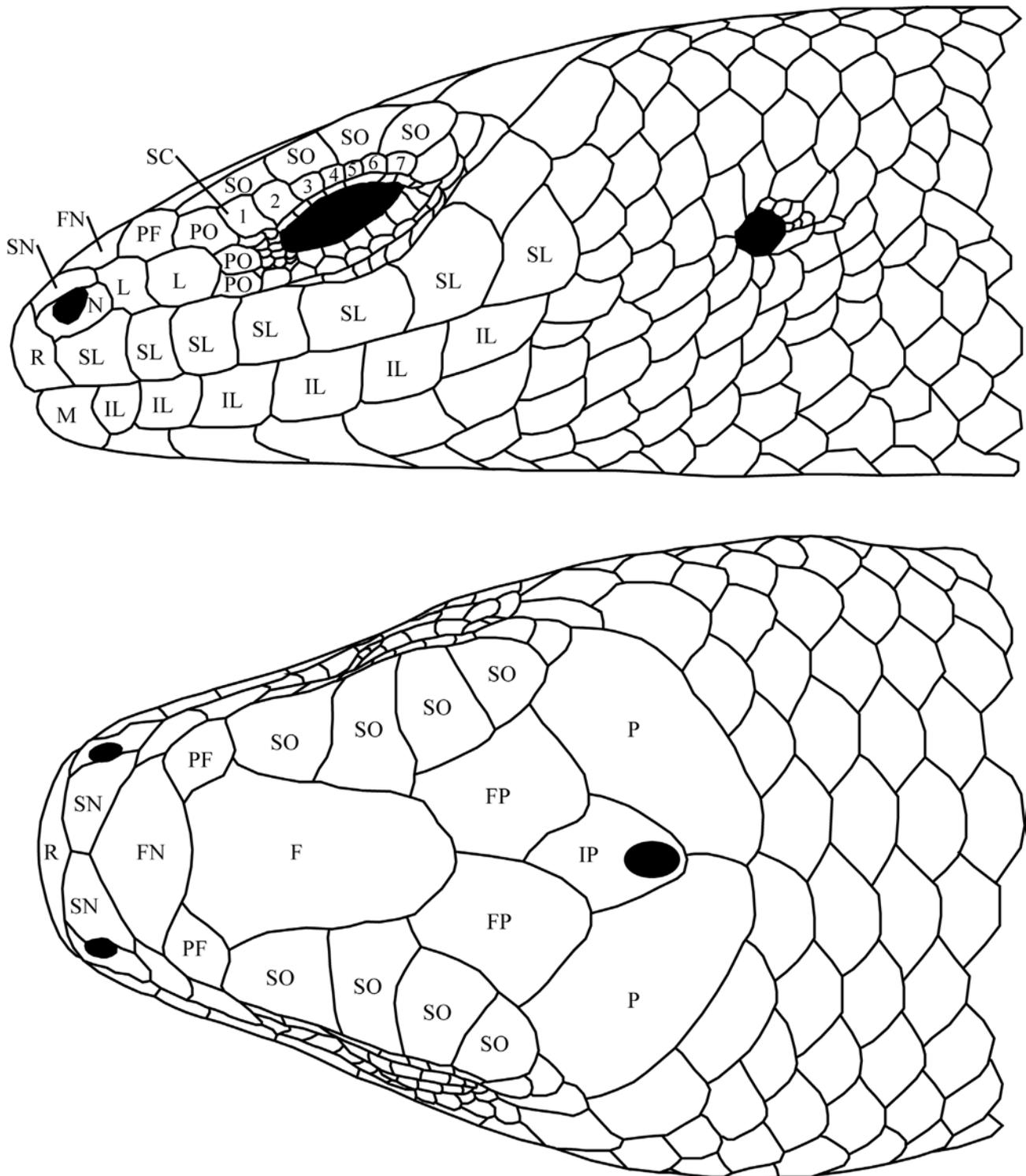


FIGURE 6. Diagram of head scales of holotype of *Lygosoma samajaya* sp. nov. M=Mental; R=Rostral; IL=Infralabial; SL=Supralabial; N=Nasal; SN=Supranasal; L=Loreal; PO=Preocular; FN=Frontonasal; PF=Prefrontal; SC=Supraciliary (numbered 1–7); SO=Supraocular; F=Frontal; FP=Frontoparietal; IP=Interparietal; P=Parietal.

TABLE 2. Scale counts and measurements of the holotype (CAS 259777) and paratype (UNIMAS 9503) of *Lygosoma samajaya* **sp. nov.**

Character	Holotype	Paratype
Supralabials	7	7
Infralabials	6	6
Fourth toe lamellae	13/13	14/14
Midbody scale rows	30	28
Paravertebral scale rows	60	61
Ventral scale rows	58	60
SVL	70.1	69.5
Tail Length	—	67.0
Axilla–groin distance	39.8	43.4
Head Length	11.0	10.8
Head Width	9.0	7.9
Head Height	4.8	4.5
Nostril–snout Length	1.6	1.3
Nostril–eye length	3.1	2.9
Internarial distance	2.8	2.4
Interocular distance	5.1	4.7
Length of fourth finger	3.3	3.4
Length of fourth toe	6.2	5.9
Tail width at base	6.7	7.2
Forelimb length	13.2	13.2
Hindlimb length	18.2	18.2

Discussion

The description of *Lygosoma samajaya* **sp. nov.** from Sarawak, Malaysia increases the known diversity of *Lygosoma* on Borneo to three species and the total number of species in the genus to 31 (but see Introduction regarding African species). Though many areas across the distribution of *Lygosoma*, especially within south-east Asia, are relatively unexplored and it is likely that there is additional undiscovered diversity in the genus.

The discovery of *Lygosoma samajaya* **sp. nov.** from an urban forest in the vicinity of Sarawak's state capital city, Kuching, highlights the importance of urban rainforest parks for maintaining species diversity. Sama Jaya Forest Reserve is a small rainforest park in Kuching established in March 2000 that measures approximately 450 x 750 m (38 ha). Prior to its establishment, the area comprising the reserve was at the edge of Kuching and connected to the Stutong forest, a larger expanse of undeveloped peat swamp to the south-east spanning across a tributary of the Sarawak River (see Fig. 7). The expansion and development of this region into residential areas and an industrial zone led the Sama Jaya Forest Reserve to become fully encircled by residential and industrial development. Sama Jaya probably remained undeveloped for longer than surrounding areas as it was drier mixed heath and peat swamp forest that was not ideal for agriculture ('Kerangas', the Iban word for heath forest, means 'land that will not grow rice'). Today it is a popular urban greenspace that is frequented by locals and tourists for recreational activities and exercise. Despite its small size and high levels of human use, the forest in Sama Jaya Forest Reserve is well-managed and human impact is kept to a minimum on paved trails. For lizards, we have collected or observed 14 species from Sama Jaya Forest Reserve, some of which are associated with human-modified habitats (*Eutropis multifasciata*, *Bronchocela cristatella*, *Dasia vittata*, *Hemidactylus brookii*, *Draco sumatranus*, *Varanus salvator*) and others of which are generally only found in partially disturbed or primary forests (*Dasia grisea*, *Eutropis rudis*, *Eutropis rugifera*, *Gonocephalus borneensis*, *Gonocephalus liogaster*,

Lipinia vittigera, *Cyrtodactylus pubisculcus*, and *Cnemaspis kendallii*). We have also collected or observed several species of frogs in Sama Jaya that are forest specialists (e.g., *Chaperina fusca*, *Kalophrynus* sp.). Beyond this, tarsiers and colugos also occupy the Park (pers. obsv.). The presence of these rainforest species, along with the discovery of *Lygosoma samajaya* sp. nov. indicate that despite its small size, Sama Jaya Forest Reserve has remained a relatively healthy forest that is capable of harboring a wide variety of small vertebrate species.

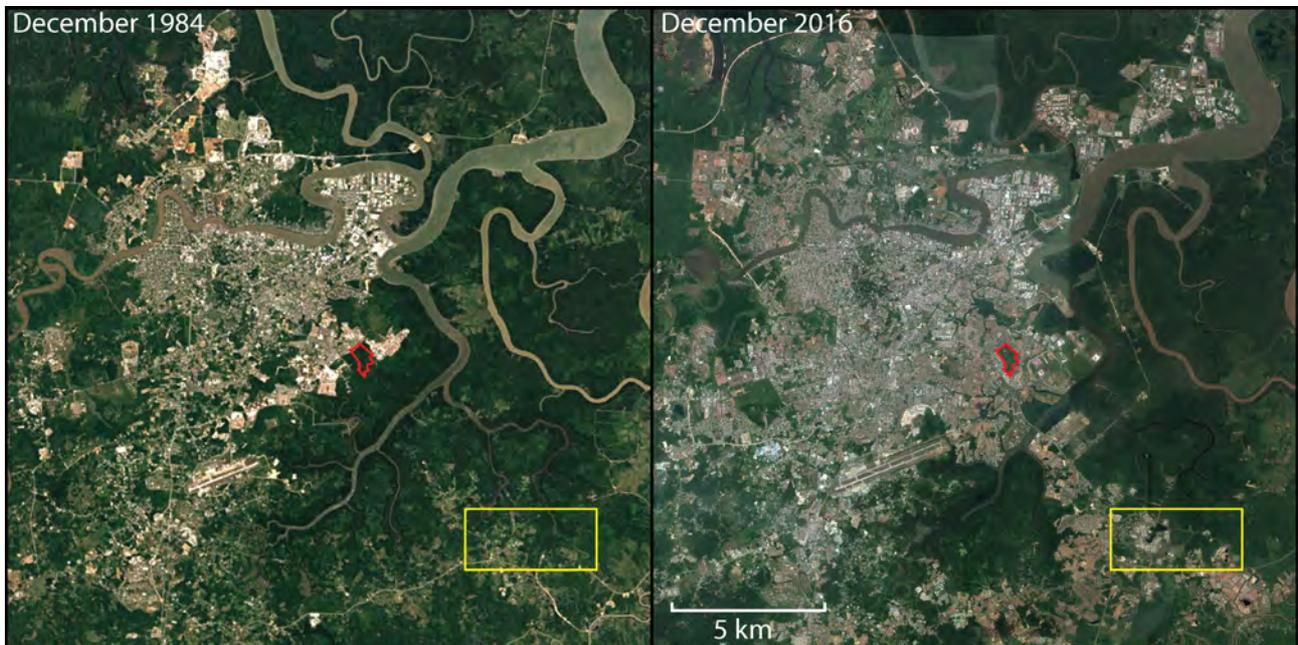


FIGURE 7. Satellite imagery of Kuching, Malaysia and surrounding areas showing land use change from December, 1984 to December, 2016. The red shape denotes the boundary of the Sama Jaya Forest Reserve (type locality), which was the edge of a large peat and heath forest in 1984, but is now totally enclosed within urban housing development. Within the yellow box is the location of the Universiti Malaysia Sarawak campus, provided to highlight the rapid development in its vicinity in the past decades. Continuous forests have not existed between the holotype and paratype collection localities since at least 1973 (Gaveau *et al.* 2014).

However, given that the park was recently (since about 16–17 years ago) disconnected from a larger forested region due to urbanization (see Fig. 7), the question remains if the relatively high species diversity in this park can survive the gradual erosion of genetic diversity and increase in frequency of deleterious mutations that occurs in confined populations (Woodruff 2001), and that may eventually lead to extinction (e.g., Rogers & Slatkin 2017). Though we only sequenced the DNA of the holotype and cannot assess genetic divergence from the paratype, gene flow is unlikely to be occurring between the small and restricted urban forest at Sama Jaya Forest Reserve and other populations of this species, especially those as far as Gunung Gumbang near the Indonesian border. Habitat fragmentation has been shown to have varied effects on genetic diversity in different groups (for review see Radespiel & Bruford 2014), but viable populations can live for long periods of time even in very small, confined populations. For example, fire salamanders (*Salamandra salamandra*) have been isolated for over 1000 years within the inner city walls of Oviedo, Spain, an area a third the size of Sama Jaya Forest Reserve, yet they have only suffered a small loss in genetic diversity (Lourenço *et al.* 2017). However, other confined populations, such as dusky salamanders (*Desmognathus fuscus*) in New York City, have undergone more substantial declines in genetic diversity (Munshi-South *et al.* 2013). The prickly forest skink (*Gnypetoscincus queenslandiae*), a leaf-litter specialist in the Australian wet tropics, has only experienced a slight decrease in genetic diversity in rainforest fragments of comparable size over 50–80 years (Sumner *et al.* 2004), likely due to its small home range size (Sumner *et al.* 2001) and naturally limited movement. We expect the population dynamics (e.g., populations sizes, generation times) for leaf-litter skinks such as *Lygosoma samajaya* sp. nov. to be similar to those of the prickly forest skink, and expect that a slow decline in genetic diversity may occur, but that the populations in Sama Jaya Forest Reserve could remain viable for a very long period of time, (possibly for more than 1000 years). However, we will not fully understand the viability of fragmented populations in Sama Jaya Forest Reserve and the role that

urban rainforest parks can play in maintaining species diversity until future studies assess the effective population sizes, generation times, and home range sizes of the inhabitants.

Development and urbanization of tropical cities is occurring at a rapid rate that is unlikely to be abated, and primary tropical rainforests harbor levels of biodiversity unparalleled to other regions (Gibson *et al.* 2011). Habitat degradation and loss in Borneo is the greatest threat to the region's biodiversity (Sodhi *et al.* 2004), and Borneo has suffered from some of the highest deforestation rates in the world. Sarawak in particular has experienced the worst of it, with only 14.6% of its forest remaining intact (compared to 56.9% remaining in Brunei, 32.6% in Kalimantan, and 19.1% in Sabah) (Gaveau *et al.* 2014). As a result, preserved forest areas, particularly primary forests, are becoming increasingly more important for protecting biodiversity (Gibson *et al.* 2011). The question remains: can rainforest species coexist in urban environments (Mitchell & Jung Brown 2008)? Developing cities, especially those near relatively undeveloped tropical rainforest areas, will face the decision of whether to develop urban greenspaces into manicured parks with lawns and planted (often invasive) trees, or to maintain them as urban forests in the most natural state possible. Our findings suggest that even small parks that have been preserved as forests through periods of development can maintain biodiversity, and even host species that have yet to be discovered. We believe that preserving even small tracts of natural rainforest in parts of the world with high species richness is incredibly beneficial for maintaining biodiversity. Given the relatively high species diversity observed in Sama Jaya Forest Reserve compared to most urban parks, future efforts to document and understand biodiversity in Borneo should focus not only on pristine forest but also on secondary forests and disturbed habitats to understand how population growth, tourism, and anthropogenic factors affect biodiversity through habitat fragmentation, pollution, and climate change.

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APPENDIX I. List of comparative material examined.

- Lygosoma albopunctata* (Gray, 1846). India: “Madras” (BMNH 1946.8.18.87–90; four syntypes).
- Lygosoma anguinum* (Theobald, 1868). Myanmar: ‘Pegu (Tonghu, Rangoon, & c.)’ (ZSI 5197; holotype).
- Lygosoma bampfyldei* Bartlett, 1895. Malaysia: Sungei Rejang, Sri Aman Division, Sarawak (BMNH 1946.8.10.84 and BMNH 1946.8.6.84, syntypes of *Lygosoma Bampfyldei* Bartlett, 1895); Deramakot, Kinabatangan District, Sabah (FMNH 76226); Fernarium, Crocker Range National Park, Keningau District, Sabah (SP 06841).
- Lygosoma bowringii* (Günther, 1864). China: “Hong Kong”, eastern China; in error) (BMNH 1946.8.18.82; ex-BMNH 56.11.17.41; holotype); Thailand: Kosichang (ZRC 2.1565–1566); Malaysia: Near Sri Hartamas 1.2 km from National Tennis Centre, Kuala Lumpur (ZRC 2.3476); Pulau Tioman, Tekek–Juara Trail, Pahang (ZRC 2.5128); Telok Kemang, Negeri Sembilan (ZRC 2.1567–1573); Pulau Aur, Johor (ZRC 2.5115–5116); Kuching, Kuching Division, Sarawak (SM c.c.b.2.7.r [30 specimens]; FMNH 134712–16); Bintulu, Bintulu Division, Sarawak (FMNH 158735–37); UNIMAS Campus, Kota Samarahan, Samarahan Division, Sarawak (ZRC 2.4960–61 and ZRC 2.4964); also, “Sarawak” (BMNH 97.6.1.3–4); Labuan (BMNH 94.6.30.23); Sabah Museum Campus, Kota Kinabalu, Kota Kinabalu District, Sabah (SSM 681); Universiti Kebangsaan Malaysia Sabah campus, Kota Kinabalu, Kota Kinabalu District, Sabah (UKMS [at present UMS] Re. 167 and 239); Kota Kinabalu, Kota Kinabalu District, Sabah (BMNH 97.12.28.19); Tambunan, Tambunan District, Sabah (UMS 5882); also, “Sabah” (MNHN 1889.316; holotype of *Lygosoma Whiteheadi* Mocquard, 1890); Brunei: Gadong, Bandar Seri Begawan, Brunei Muara District (UBD 02–04, 239, 531, 607); Jalan Manggis Dua, Bandar Seri Begawan, Brunei Muara District (UBD 554); Brunei Museum compound, Bandar Seri Begawan, Brunei Muara District (BM 1993.10); Tasek Lama, Bandar Seri Begawan, Brunei Muara District (UBD 661); Singapore: ZRC 2.1574; ZRC 2.1577; Eng Neo Avenue (ZRC 2.3198–3199); Bukit Mandai (ZRC 2.1575); Mandai (ZRC 2.1576); Changi (ZRC 2.2539); Kent Ridge Campus (ZRC 2.3475, ZRC 2.4863, ZRC 2.5630, ZRC 2.5646); Sungei Buloh Wetland Reserve (ZRC 2.4819); Lim Chu Kang (ZRC 2.4819); Kranji (ZRC 2.1578, cited by Sworder, 1925c); Holland Close (ZRC 2.5262); Indonesia: Sumatra, Riau Islands, Pulau Bulang (ZRC 2.1579).
- Lygosoma quadrupes* (Linnaeus, 1758). Thailand: Ban Sac along tributary of Sungai Kolok, Narathiwat Province (ZRC 2.4569).
- Lygosoma goaensis* (Sharma, 1976). India: “ca. 5 km N.E. of Foret (sic) Rest House, Mollem” (Goa, south-western India) (ZSI 22032; holotype).
- Lygosoma herberti* Smith, 1916. Malaysia: Sungai Menora near Kangsar, Perak (ZRC 2.1580).
- Lygosoma lineata* (Gray, 1839). “India” (BMNH 1946.8.18.83; holotype).
- Lygosoma lineolatum* (Stoliczka, 1870). “Martaban” (BMNH 1946.8.6.85, ZSI 3218, NMW 16645.1–2; syntypes); ‘Pegu, British Barma’ (ZSI 5547–48; syntypes of *Riopa cyanella* Stoliczka, 1872).
- Lygosoma pruthi* (Sharma, 1977). India: “Chitteri range, lat. 11° 50’N, long. 78° 25’E, Salem District, Tamil Nadu, India” (ZSI 22393; holotype).
- Lygosoma singha* (Taylor, 1950). “Sri Lanka”. USNM 29411 (holotype).
- Lygosoma vosmaerii* (Gray, 1839). “Java”, emended to “Bengal” (MNHN 777; ex-MNHN 3007; holotype).

TABLE S1. Samples and GenBank accession numbers for specimens included in molecular analyses in this study. Newly sequenced samples for this study are arranged at the top of the table (MG and MF accession numbers).

Species	Country	Museum No.	16S	ND1	R35
<i>Lygosoma samajaya</i> sp. nov.	Malaysia	CAS 259777	MG020475	MF981879	MF981876
<i>Lygosoma bowringii</i>	Malaysia	LSUHC 11885	MG020474	—	—
<i>Lygosoma herberti</i>	Malaysia	LSUHC 10995	MG020472	—	—
<i>Lygosoma herberti</i>	Malaysia	LSUHC 12098	MG020473	—	—
<i>Lygosoma herberti</i>	Malaysia	LSUHC 11803	—	MF981877	MF981874
<i>Lygosoma lineolatum</i>	Myanmar	CAS 213615	—	MF981878	MF981875
<i>Lygosoma bowringii</i>	Malaysia	LSUHC 6998	—	HQ907328	HQ907637
<i>Lygosoma corpulentum</i>	Cambodia	LSUHC 9321	—	HQ907329	HQ907638
<i>Lygosoma quadrupes</i>	Cambodia	LSUHC 8403	—	HQ907330	HQ907639
<i>Lygosoma tabonorum</i>	Philippines	PNM 9820	—	KX774343	KX774338
<i>Brachymeles bicolor</i>	Philippines	KU 323151	—	HQ907379	HQ907689
<i>Plestiodon marginatus</i>	Japan	MCB 639	—	HM160833	HM161116

16s rRNA Maximum Likelihood Tree

RAxML – 1000 Bootstrap Replicates
 Newly generated sequences in bold
 Genbank accession numbers listed

