Journal of Herpetology, Vol. 52, No. 3, 332–347, 2018

New Supple Skink, Genus *Lygosoma* (Reptilia: Squamata: Scincidae), from Indochina and Redescription of *Lygosoma quadrupes* (Linnaeus, 1766)

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Abstract.—**Based on molecular and morphological data sets, we describe a new species of scincid lizard of the genus *Lygosoma* from Indochina, and redescribe true *Lygosoma quadrupes* (Linnaeus, 1766). The new species is small and slender, and represents the third member of the *L. quadrupes* complex, increasing the diversity of *Lygosoma* species recognized in Southeast Asia to 24. Based on the reevaluation of vouchered specimens from the type locality of *L. quadrupes* sensu Linnaeus (1766), the recognized geographic distribution of true *L. quadrupes* is restricted to the island of Java in Indonesia. With 10 species of *Lygosoma* recognized in Thailand, the country possesses considerable species-level diversity of these enigmatic, semifossorial skinks. In addition to being one of the smallest species in the genus, the new species can be distinguished from all congeners by features of its external morphology, including having small relative limb lengths, longer trunk length, and greater numbers of axilla–groin and paravertebral scale rows. Phylogenetic analyses support three divergent lineages corresponding to recognized and newly described members of the *L. quadrupes* complex. The descriptions underscore the need for continued and comprehensive biodiversity survey work throughout much of Southeast Asia, particularly in Indochina, where scincid diversity remains poorly understood.**

บทคัดย่อ.—การศึกษาข้อมูลทางชีวโมเลกุลและสัณฐานวิทยาทำให้มีการค้นพบจิ้งเหลนชนิดใหม่ในสกุล *Lygosoma* จากประเทศไทยและทบทวนการบรรยายลักษณะของจิ้งเหลนเรียวขาเล็ก *L. quadrupes* **(Linnaeus, 1766)** จากที่เคยบรรยายไว้ก่อนหน้านี้ดยจิ้งเหลนชนิดใหม่มีขนาดเล็กเรียวและเป็นสมาชิกชนิดลำดับที่สามของกลุ่มชนิดพันธุ์ซับซ้อน *L. quadrupes* จึงทำให้มีความหลากหลายของชนิดในสกุล *Lygosoma* ในเอเชียตะวันออกเฉียงใต้รวมเป็น **20** ชนิดซึ่งจากการศึกษาตัวอย่างอ้างอิงที่เก็บมาจากพื้นที่เดียวกับตัวอย่างต้นแบบของ *L. quadrupes sensu* **Linnaeus (1766)** พบว่าการแพร่กระจายทางภูมิศาสตร์ของ *L. quadrupes* พบเฉพาะบนเกาะชวาประเทศอินโดนีเซียและจากรายงานชนิดจิ้งเหลนสกุล *Lygosoma* จำนวน **10** ชนิดในประเทศไทยนั้นแสดงให้เห็นว่าประเทศไทยมีความหลากหลายของชนิดของจิ้งเหลนกลุ่มที่กึ่งอาศัยใต้ดินนอกจากนี้จิ้งเหลนชนิดใหม่จัดว่ามีขนาดเล็กและมีความแตกต่างจากชนิดอื่นๆในสกุลเดียวกันในลักษณะทางสัณฐานวิทยาภายนอกรวมทั้งลักษณะบางประการเช่นความยาวของรยางค์สั้นกว่าความยาวของลำตัวมากกว่าและมีจำนวนแถวของเกล็ดคือ **axilla–groin** และ **paravertebral scale** มากกว่าส่วนการวิเคราะห์สายสัมพันธ์ทางวิวัฒนาการพบว่าสายวิวัฒนาการแยกออกไปเป็นสามสายประกอบด้วยชนิดที่มีการตั้งชื่อไว้แล้วและชนิดใหม่ในกลุ่มชนิดพันธุ์ซับซ้อน *L. quadrupes* ดังนั้นผลจากการศึกษาครั้งนี้แสดงให้เห็นว่าควรมีการสำรวจและศึกษาความหลากหลายของชนิดจิ้งเหลนในพื้นที่เอเชียตะวันออกเฉียงใต้อย่างละเอียดรวมทั้งในประเทศไทยซึ่งยังขาดแคลนข้อมูลของสัตว์กลุ่มนี้.

The genus *Lygosoma* consists of 32 semifossorial species, representing a diversity of pentadactyl body forms from large, robust lineages to small, slender species (Geissler et al., 2011, 2012; Heitz et al., 2016; Grismer et al., 2018; Karin et al., 2018). The diversity in the genus spans much of the Old World tropics, from central and southern Africa, through India and Indochina, to Southeast Asia, including the Philippines (Smith, 1937; Greer, 1977; Chan-ard et al., 2015; Heitz et al., 2016). More than one-half of the species-level diversity occurs throughout Indochina (17 species: *Lygosoma albopunctatum*, *Lygosoma angeli*, *Lygosoma anguinum*, *Lygosoma boehmei*, *Lygosoma bowringii*, *Lygosoma corpulentum*, *Lygosoma frontoparietale*, *Lygosoma haroldyoungi*, *Lygosoma herberti*, *Lygosoma isodactylum*, *Lygosoma koratense*, *Lygosoma lineolatum*, *Lygosoma peninsulare*, *Lygosoma popae*, *Lygosoma punctata*, *Lygosoma quadrupes*, and *Lygosoma veunsaiensis*), with only a handful of species reaching maritime Southeast Asia (*Lygosoma bampfyldei*, *Lygosoma bowringii*, *Lygosoma kinabatanganensis*, *Lygosoma opisthorhodum*, *Lygosoma quadrupes*, *Lygosoma samajaya*, and *Lygosoma schneideri*; Werner, 1910; Heitz et al., 2016; Uetz and Hošek, 2016). With 10 species documented from Thailand (Geissler et al., 2011, 2012; Chan-ard et al., 2015; Uetz and Hošek, 2016; Grismer et al., 2018; Karin et al., 2018), the country possesses the largest diversity of *Lygosoma* in the region; however, only two are Thailand endemics (*L. frontoparietale* and *L. koratense*; Smith, 1917; Taylor, 1962, 1963). The country's diversity can be split largely into two body size classes: species with large, robust bodies (*L. angeli*, *L. corpulentum*, *L. haroldyoungi*, *L. isodactylum*, and *L. koratense*), and species with small, slender bodies (*L. anguinum*, *L. bowringii*, *L. frontoparietale*, *L. herberti*, and *L. quadrupes*; Geissler et al., 2011, 2012; Chan-ard et al., 2015).

Several species of *Lygosoma* are known to occur across broad geographic distributions, but only two species possess distributions that span both continental and oceanic landmasses (*L. bowringii* and *L. quadrupes*; Heitz et al., 2016; Uetz and Hošek, 2016). Over the last decade, numerous studies have revealed that few scincid taxa have truly widespread distributions across Southeast Asia, and often, such historically recognized "widespread" species represent complexes of unique evolutionary lineages (Siler and Brown, 2010; Siler et al., 2011, 2012; Davis et al., 2014; Grismer et al., 2018). Although there have been efforts to revise both polytypic and widespread species complexes in the region, diversity remains poorly understood in Thailand and Indochina for many scincid clades (e.g., *Eutropis*, *Lipinia*,

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DOI: 10.1670/16-064

FIG. 1. Map of Southeast Asia showing the distribution of focal lineages of the *Lygosoma quadrupes* complex. The distribution of the Sunda Shelf is represented by 120-m submarine bathymetric contour lines and light grey shading.

Isopachys, *Sphenomorphus*; Das and Austin, 2007; Das et al., 2008; Grismer and Chan, 2010; Datta-Roy et al., 2014; Grismer et al., 2016; Luu et al., 2016).

Recently, evaluation of vouchered collections of *Lygosoma* on Palawan Island in the western Philippines resulted in the revision of the *L. quadrupes* complex and recognition of a Philippine endemic species (Fig. 1; Heitz et al., 2016). This previous study underscored the importance of reevaluating regional populations of this complex, as similar body plans and external morphology likely have contributed to the longheld recognition of *L. quadrupes* as a widespread species across Southeast Asia (Fig. 2; Geissler et al., 2011, 2012; Heitz et al., 2016). Herein, we further revise the *L. quadrupes* complex and describe a new, semifossorial species from Indochina (Figs. 1, 3).

Taxonomic History.—*Lygosoma quadrupes* has had a long and complicated taxonomic history since the initial description by Linnaeus (1766) as *Anguis quadrupes*. In this description, Linnaeus (1766) incorrectly described this species as a snake that lacked external ear openings. Because of these errors, it was later redescribed by Bloch (1776) as *Lacerta serpens* based on additional available material (see Bauer and Günther, 2006). The taxonomy of this species continued to be changed by numerous authors, including Schneider (1801; *Scincus brachypus*), Daudin (1802; *Seps pentadactylus*), and Fitzinger (1826; *Mabuya serpens*). Hardwicke and Gray (1827) then designated this species as the type species for the newly formed genus *Lygosoma* (*L. serpens*). Taxonomic placement within the genus *Lygosoma* generally was accepted by most, except for Wiegmann (1834) who recognized the species as *Podophis quadrupes*, Gray (1845) who recognized the species as *Podophis chalcides*, and Günther (1864) and Leidy (1884) who recognized the species as *Eumeces chalcides*. Within *Lygosoma*, the taxonomy of this species continued to change, including descriptions as *Lygosoma brachypoda* (Duméril and Bibron, 1839; Gravenhorst, 1851), *Lygosoma abdominalis* (Gray, 1839), and *Lygosoma chalcides* (Boulenger, 1887; de Rooij, 1915; Taylor, 1922), until Cochran (1930) and Smith (1935) described this species as *L. quadrupes*. Although the type locality of *L. quadrupes* sensu Linnaeus (1766) is supported widely as Java (Indonesia), the recognized geographic distribution of the species has increased significantly since its original description. To the best of our knowledge after an extensive review of the literature, however, no taxonomic name has ever been applied in specific

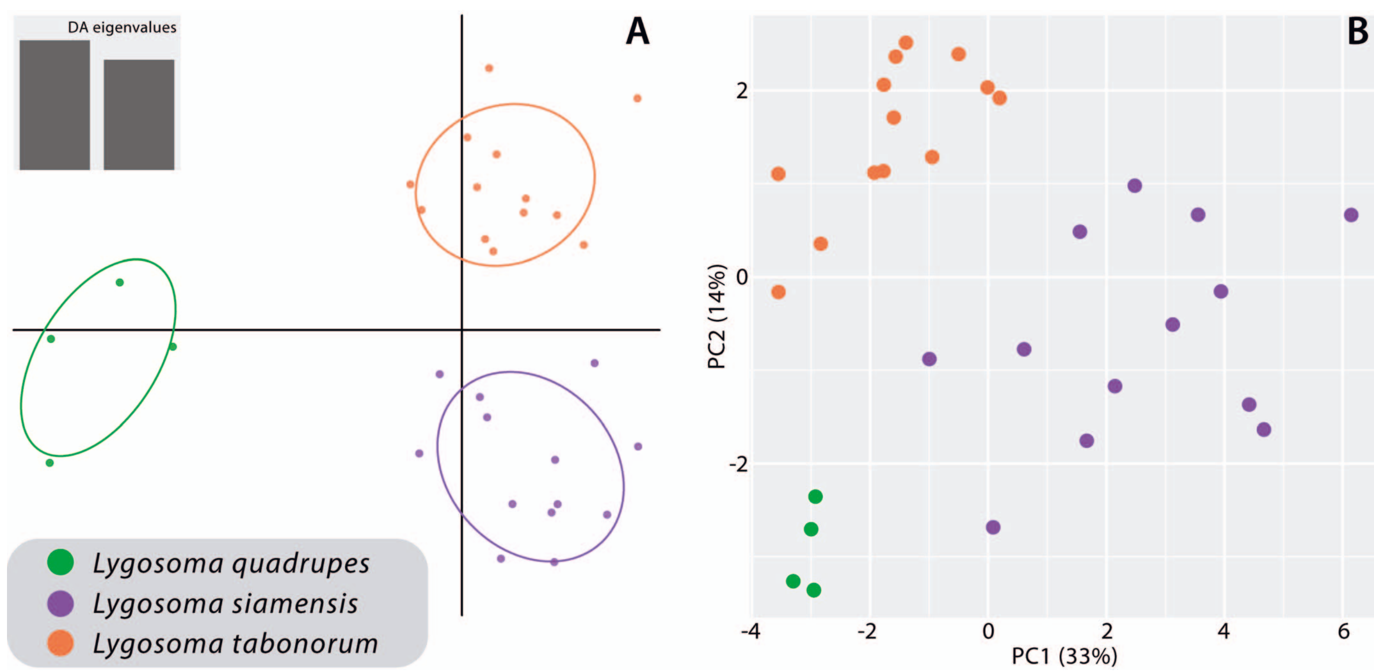

FIG. 2. (A) Results of DAPC analysis based on the first four component scores showing the greatest between-group and smallest within-group variance illustrated by the 95% confidence ellipses. (B) PCA plot showing complete separation of *Lygosoma quadrupes*, *Lygosoma siamensis*, and *Lygosoma tabonorum* in morphospace. Mensural and meristic characters used in the PCA include AGD, MBW, MBD, TW, TD, HL, HW, HD, ED, END, SNL, IND, FLL, HLL, MBSRC, AGSRC, PVSRC, F3lam, SL, IFL, SO, and SC (see text for definitions).

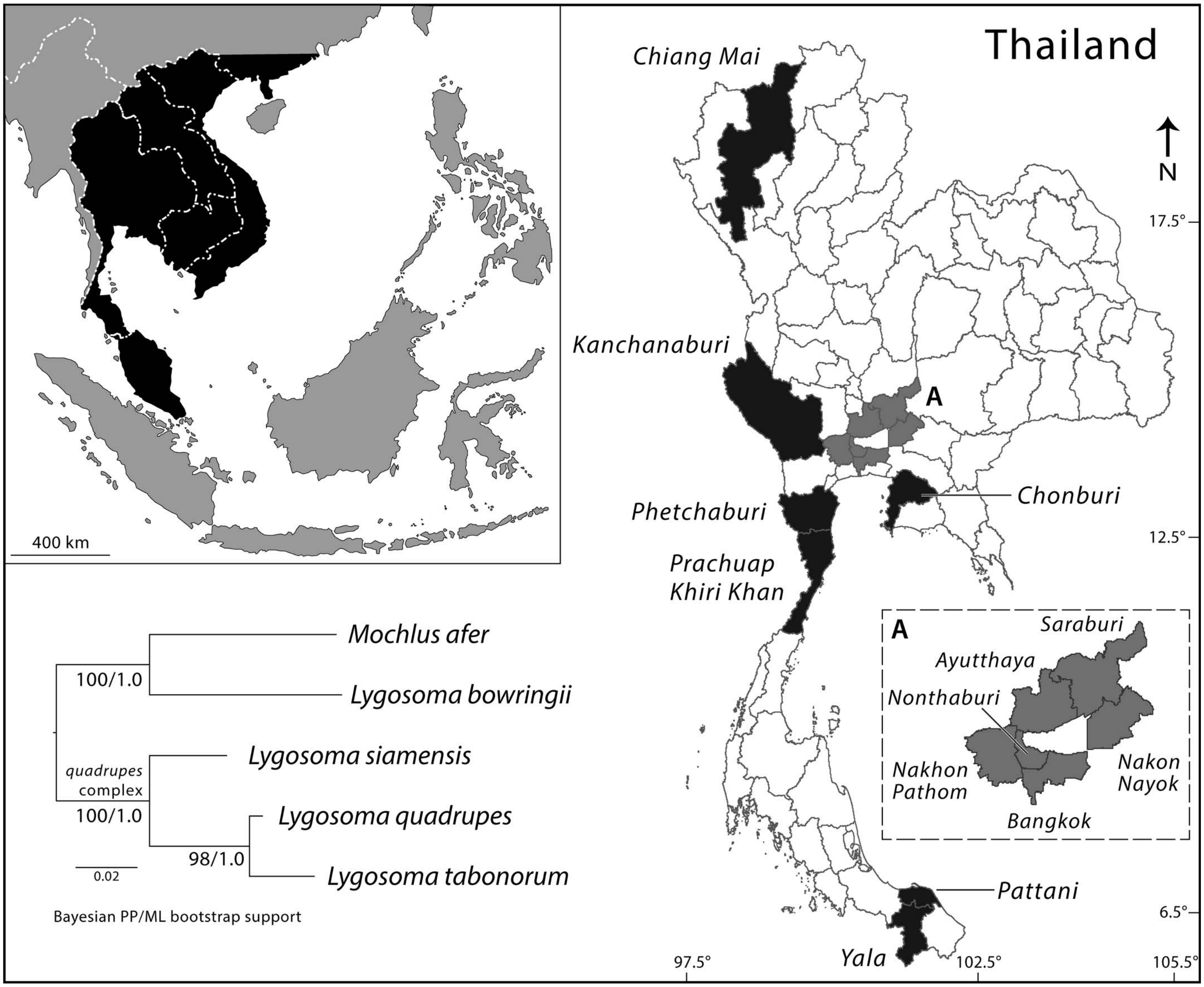

FIG. 3. (Inset) Map of Southeast Asia showing the distribution of *Lygosoma siamensis* across Indochina shaded in black. (Right) Map of Thailand showing known provincial distribution of *Lygosoma siamensis* based on vouchered museum specimens (black and grey provinces), with focal provincial names shown for reference. Close-up view of provinces in grey shown within box A. (Bottom left) Hypothesized relationships among species of the *Lygosoma quadrupes* complex illustrated by the maximum clade credibility tree resulting from Bayesian analyses of 16S. Nodes supported by ≥95% Bayesian posterior probability and P ≥ 70% Maximum–likelihood bootstrap support were considered significantly supported.

reference to populations from Indochina, specifically Cambodia, Laos, West Malaysia, Thailand, and Vietnam.

MATERIALS AND METHODS

We recorded morphometric data from fluid-preserved specimens that were fixed in 10% formalin (Appendix 1). We determined sex by gonadal inspection and recorded measurements with digital calipers to the nearest 0.1 mm. Measurements of the new species were scored by CDS, with comparative measurements collected and scored by ESF, E. Ellsworth, and CDS for a recent systematic study of the *L. quadrupes* complex (Heitz et al., 2016). We based morphometric comparisons on adult specimens only; color descriptions were based on preserved specimens. Museum abbreviations for additional specimens examined or sequenced in this study follow those of Sabaj (2016).

We chose meristic and mensural characters based on Heitz et al. (2016) and Geissler et al. (2011): snout–vent length (SVL: distance from tip of snout to vent), axilla–groin distance (AGD: distance between posterior edge of forelimb insertion and anterior edge of hind-limb insertion), total length (TotL: distance from tip of snout to tip of tail), midbody width (MBW: measured from lateral surface to opposing lateral edge at midpoint of axilla–groin region), midbody depth (MBD: measured from ventral surface to dorsal surface at midpoint of axilla–groin region), tail length (TL: measured from posterior margin of vent to tip of tail), tail width (TW: measured at widest section of tail posterior to hemipene bulge), tail depth (TD: measured from ventral to dorsal surface of tail at the same point as TW), head length (HL: measured from tip of snout to posterior margin of retroarticular process), head width (HW: widest measure of head width at jaw articulations), head depth (HD: measured from ventral to dorsal surface of head at jaw articulations), eye diameter (ED: at widest point), eye–narial distance (END: from anterior margin of eye to posterior margin of nares), snout length (SNL: from anterior margin of eye to tip of snout), internarial distance (IND: from dorsal aspect between most laterally distal edges of nares), forelimb length (FLL: measured from forelimb insertion to tip of Finger III or longest digit), hind-limb length (HLL: measured from hind-limb insertion to tip of Toe IV or longest digit), midbody scale-row count (MBSR: number of longitudinal scale rows measured around widest point of midbody), paravertebral scale-row count (PVSR: number of scale rows counted between parietals and the base of the tail opposite the vent), axilla–groin scale-row count (AGSR: number of scale rows counted between posterior edge of forelimb insertion and anterior edge of hind-limb insertion), Finger III lamellae count (F3lam: number of enlarged, undivided lamellae beneath Finger III), Toe IV lamellae count (T4lam: number of enlarged, undivided lamellae beneath Toe IV), supralabial count (SL), infralabial count (IFL), superciliary count (SC), and supraocular count (SO). Additionally, the following head scalation patterns were scored: supranasal contact (SN), prefrontal contact (PF), frontoparietal contact (FP), parietal contact (P), enlarged, differentiated nuchal presence/absence (NU), and enlarged, first chin shield pair contact (1stChin). In the description, ranges are followed by mean ± SD in parentheses. For focal relative size comparisons, some measurements were converted to ratiometric values.

To date, sequence data for one individual only of *Lygosoma* cf. *quadrupes* from Thailand has been published for the mitochondrial ribosomal RNA (rRNA) genes 12S and 16S (Honda et al., 2000). To the best of our knowledge, no other tissue samples for the putative new species from Indochina exist in vouchered and publicly available natural history collections. To evaluate phylogenetic support for the focal lineage from Thailand and other members of the *L. quadrupes* complex, we used DNA extractions available from the recent study by Heitz et al. (2016) to amplify the mitochondrial 16S rRNA gene for comparison with sequence data available on GenBank. The small phylogenetic data set consisted of three ingroup samples representing the *L. quadrupes* complex (Fig. 3): *L.* cf. *quadrupes* from Thailand, *Lygosoma tabonorum* from Palawan Island in the Philippines, and true *L. quadrupes* from Java, as well as the two outgroup species, *L. bowringii* and *Mochlus sundevallii*. Protocols and primers for PCR amplification of 16S followed Datta-Roy et al. (2014). We visualized the PCR products with gel electrophoresis and then purified them by using ExoSAP-IT (Affymetrix, Santa Clara, CA). Cycle sequencing reactions were run using ABI Prism BigDye Terminator chemistry (v3.1; Applied Biosystems, Foster City, CA), purified by ethanol precipitation, and sent to Eurofins Scientific (Louisville, KY) for sequencing. Novel sequences were deposited in GenBank (accession: AB028818 [*L.* cf. *quadrupes*, Thailand]; MG367367 [*L. tabonorum*, Philippines]; MG367368 [*L. quadrupes*, Java]; AY308263 [*L. bowringii*], KU705386 [*M. sundevallii*]).

Initial alignments were produced in Muscle (Edgar, 2004), and manual adjustments were made in Geneious (v9.0.5; Biomatters Limited, Auckland, New Zealand). The 528 bp region of 16S was treated as a single partition. The best-fit model of nucleotide substitution was GTR + Γ, inferred by the Akaike Information Criterion (AIC) as implemented in jModelTest v2.1.10 (Posada, 2008). We performed Bayesian analyses in MrBayes v3.2.6 (Ronquist et al., 2012) using the inferred model of sequence evolution. A rate multiplier model was used to allow substitution rates to vary among subsets, and default priors were used for all model parameters. We ran two independent MCMC analyses, each with four Metropolis-coupled chains, an incremental heating temperature of 0.02, and an exponential distribution with a rate parameter of 25 as the prior on branch lengths (Marshall, 2010). Both analyses were run for 5 million generations, with parameters and topologies sampled every 1,000 generations. We assessed stationarity with Tracer v1.4 (Rambaut and Drummond, 2007) and confirmed convergence with AWTY (Wilgenbusch et al., 2004). Stationarity was achieved after 2 million generations, and we conservatively discarded the first 50% of samples as burn-in.

Additionally, we performed 100 replicate maximum-likelihood (ML) analyses in RAxML-VI-HPC v7.0 (Stamatakis, 2006). Each inference was initiated with a random starting tree, and nodal support was assessed with 100 bootstrap pseudoreplicates (Stamatakis et al., 2008). We calculated percentage uncorrected pairwise distances using PAUP* v4.0 (Swofford, 2002).

Analyses of variance (ANOVA) were performed to ascertain whether statistically significant mean differences ($P < 0.05$) existed among the populations for the mensural and meristic characters. ANOVAs having a *P*-value less than 0.05 indicating that statistical differences existed were subjected to a Tukey HSD test to ascertain which population pairs differed significantly.

Principal Component Analysis (PCA) and Discriminant Analysis of Principal Components (DAPC) were used to determine the degree to which the morphological variation coincided with species boundaries delimited by the molecular phylogenetic and univariate analyses. PCA, implemented by the "prcomp" command in R v3.2.1 (R Core Team, 2015), searches for the best overall low-dimensional representation of significant morphological variation in the data. Characters used in the PCAs and DAPCs were discrete meristic data from the scale counts MBSRC, AGSRC, PVSRC, F3lam, SL, IFL, SO, and SC and the continuous mensural data from AGD, MBW, MBD, TW, TD, HL, HW, HD, ED, END, SNL, IND, FLL, and HLL. To remove the effects of body size from the latter, we used the following equation: $Xadj = X - \beta(SVL - SVLmean)$, where Xadj = adjusted value; X = measured value; β = unstandardized regression coefficient for each OTU; SVL = measured snout–vent length; SVLmean = overall average SVL of all OTU's (Thorpe, 1975, 1983; Turan, 1999; Lleonart et al., 2000). All PCA data were natural log-transformed prior to analysis and scaled to their one standard deviation to normalize their distribution so as to ensure characters with very large and very low values did not overleverage the results owing to intervariable nonlinearity and to transform meristic and mensural data into comparable units for analysis.

To characterize clustering and separation in morphospace, a DAPC was performed to search for linear combinations of morphological variables having the greatest between-group variance and the smallest within-group variance (Jombart et al., 2010). DAPC relies on log transformed data from the PCA as a prior step to ensure that variables analyzed are not correlated and number fewer than the sample size. Principal components with eigenvalues greater than one were retained for the DAPC according to the criterion of Kaiser (1960). Separate PCA and DAPC analyses were performed on the scale count (discrete) and mensural (continuous) data to ascertain which, if any category of characters, performed better at delimiting species with respect to the phylogenetic analyses. Total evidence PCA and DAPC analyses also were performed using a concatenated data set to illustrate an unbiased morphospatial relationship of the OTUs. All statistical analyses were performed in R.

TABLE 1. Matrix of species pairs having significantly different ($P < 0.05$) mean values of varying combinations of characters based on a TukeyHSD test. Abbreviations are listed in the Materials and Methods.

	siamensis	*quadrupes*	*tabonorum*
siamensis	**	**	**
quadrupes	PVSRC, MBW, SL	**	**
tabonorum	IFL, SL, T4lam	IFL, PVSRC, SL, T4lam	**

We follow the General Lineage Concept of species (de Queiroz, 1998, 1999) and consider populations as unique evolutionary lineages when sufficient, diagnostic morphological features exist and, when available, genetic divergence, support their distinction from congeners, especially if allopatric. For this study, we used estimated phylogenetic relationships to guide and bolster our recognition of species boundaries; however, our diagnoses of a new species is restricted to lineages that are identified clearly based on fixed diagnostic character differences in nonoverlapping morphological character states.

RESULTS

Genetic and morphological data support the presence of three evolutionary lineages within the *L. quadrupes* complex (Figs. 2, 3). The PCA and DAPC analyses corroborate the molecular analyses in that there is complete separation in morphospace between *L. quadrupes*, *L.* sp. nov., and *L. tabonorum* (Fig. 2A,B). *Lygosoma quadrupes* and *L.* sp. nov. are further separated along principal component 1 (PC1), and *L. quadrupes* and *L. tabonorum* are further separated along PC2 (Fig. 2B). PC1 accounted for 33% of the total variation and loaded most heavily for MBD, TW, HW, and IND. The second principal component (PC2) accounted for an additional 14% of the total variation and loaded heavily for HD. The third principal component (PC3) accounted for an additional 8% of the total variation and loaded most heavily for HL. The first seven principal components had eigenvalues ranging from 1.102–7.682 and accounted for 82% of the total variance (Appendix 2), and these were retained for the DAPC analysis (Fig. 2A). Additionally, all three species differ in having varying combinations of statistically different character means (Table 1). Therefore, in addition to *L. tabonorum* from Palawan Island in the Philippines, and true *L. quadrupes* from Java, Indonesia, we recognize a new species from Thailand.

TAXONOMIC ACCOUNTS

Lygosoma ***quadrupes*** (Linnaeus, 1766)

Figure 4, Tables 2, 3

Anguis quadrupes Linnaeus, 1766:390.
Lacerta serpens Bloch, 1776
Scincus brachypus Schneider, 1799:192.
Seps pentadactylus Daudin, 1802:325.
Mabuya serpens Fitzinger 1826:53.
Lygosoma serpens Hardwicke and Gray, 1827:228.
Podophis quadrupes Wiegmann, 1834:11.
Lygosoma abdominalis Gray, 1839:332.
Lygosoma brachypoda Duméril and Bibron, 1839:721; Gravenhorst, 1851:367.
Podophis chalcides Gray, 1845:88.
Eumeces chalcides Günther, 1864:90; Leidy, 1884:66.
Lygosoma chalcides Boulenger, 1887:340; de Rooij, 1915:225; Taylor, 1922:233.
Lygosoma quadrupes Cochran, 1930:16; Smith, 1935:290, 1937:219; Mittleman, 1952:29; Taylor, 1963:1049; Greer, 1977:515; Brown and Alcala, 1980:108; Frank and Ramus, 1995:191; Bobrov, 1995:16; Manthey and Grossmann, 1997:267; Cox et al., 1998:115; Gaulke, 1999:273; Honda et al., 2000:453; Bauer and Günther, 2006:17; Ziegler et al., 2007:399; Wagner et al., 2009:2; Chan-ard et al., 2010:132; Das, 2010:240; Geissler et al., 2011:1169, 2012:56; Pyron et al., 2013:14; Datta-Roy et al., 2014:165; Heitz et al., 2016:352.

Syntype.—ZMB 1276. Bloch (1776) redescribed this species based on two specimens and provided illustrations of both. Investigation by Bauer and Günther (2006) revealed that only a single syntype of this species remains (ZMB 1276) which was the larger of the two specimens illustrated in Bloch's (1776) redescription and that the missing syntype may have been lost or destroyed prior to the receipt of these specimens to ZMB.

Referred Specimens.—FMNH 122264 (male), MCZ 7667 (female), USNM 43677 (female), 43257 (female), 43578 (juvenile), 43780 (juvenile), 29414 (male).

Diagnosis.—*Lygosoma quadrupes* can be distinguished from congeners by the following combination of morphological characters: 1) body size small (SVL 66.8–78.3 mm); 2) limb length short; 3) supralabials 6 or 7; 4) infralabials 5 or 6; 5) superciliaries 7; 6) supraoculars 4; 7) Finger III lamellae 5 or 6; 8) Toe IV lamellae 6 or 7; 9) midbody scale rows 25 or 26; 10) axilla–groin scale rows 99–101; 11) paravertebral scale rows 117–121; and 12) single, enlarged, fused frontoparietal (Tables 2, 3).

Comparisons.—*Lygosoma quadrupes* is phenotypically most similar to *Lygosoma siamensis* and *L. tabonorum* but can be distinguished from both by having longer relative forelimbs (FLL 4.7–5.9% SVL vs. 2.3–4.9% [*L. siamensis*], 3.3–4.6% [*L. tabonorum*]), a tendency toward longer relative hind limbs (HLL 6.6–9.7% SVL vs. 4.0–8.0% [*L. siamensis*], 5.1–6.8% [*L. tabonorum*]), and a greater number of axilla–groin scale rows (99–101 vs. 88–98 [*L. siamensis*], 83–90 [*L. tabonorum*]). Additionally, *L. quadrupes* differs from *L. tabonorum* by having a greater number of paravertebral scale rows (117–121 vs. 106–111) and superciliaries (7 vs. 5 or 6) (Tables 2, 3).

Compared with all other small, slender species recognized to occur in Southeast Asia (*L. albopunctatum*, *L. anguinum*, *L. bowringii*, *L. frontoparietale*, *L. herberti*, *L. lineolatum*, *L. popae*, and *L. veunsaiensis*), *L. quadrupes* can be distinguished from *L. albopunctatum*, *L. anguinum*, *L. bowringii*, *L. frontoparietale*, *L. herberti*, *L. lineolatum*, *L. popae*, and *L. veunsaiensis* by having a larger body size (SVL 66.8–78.3 mm vs. ≤64.0 mm), longer axilla–groin distance (AGD 47.9–61.0 mm vs. ≤42.0 mm), and a greater number of axilla–groin (99–101 vs. ≤76) and paravertebral (117–121 vs. ≤99) scale rows; from *L. albopunctatum*, *L. frontoparietale*, *L. lineolatum*, and *L. popae* by having a longer tail length (TL; 54.0–71.8 mm vs. ≤54.0 mm); from *L. anguinum*, *L. frontoparietale*, *L. lineolatum*, and *L. popae* by having longer forelimbs (3.9–4.4 mm vs. ≤4.3 mm); from *L. albopunctatum* by having a greater number of midbody scale rows (25 or 26 vs. 14); from *L. frontoparietale* by having fewer midbody scale rows (25 or 26 vs. 28 or 29); from *L. albopunctatum*, *L. bowringii*, *L. frontoparietale*, *L. herberti*, and *L. samajaya* by having fewer Finger III lamellae (5 or 6 vs. >7); and from *L. albopunctatum*, *L.*

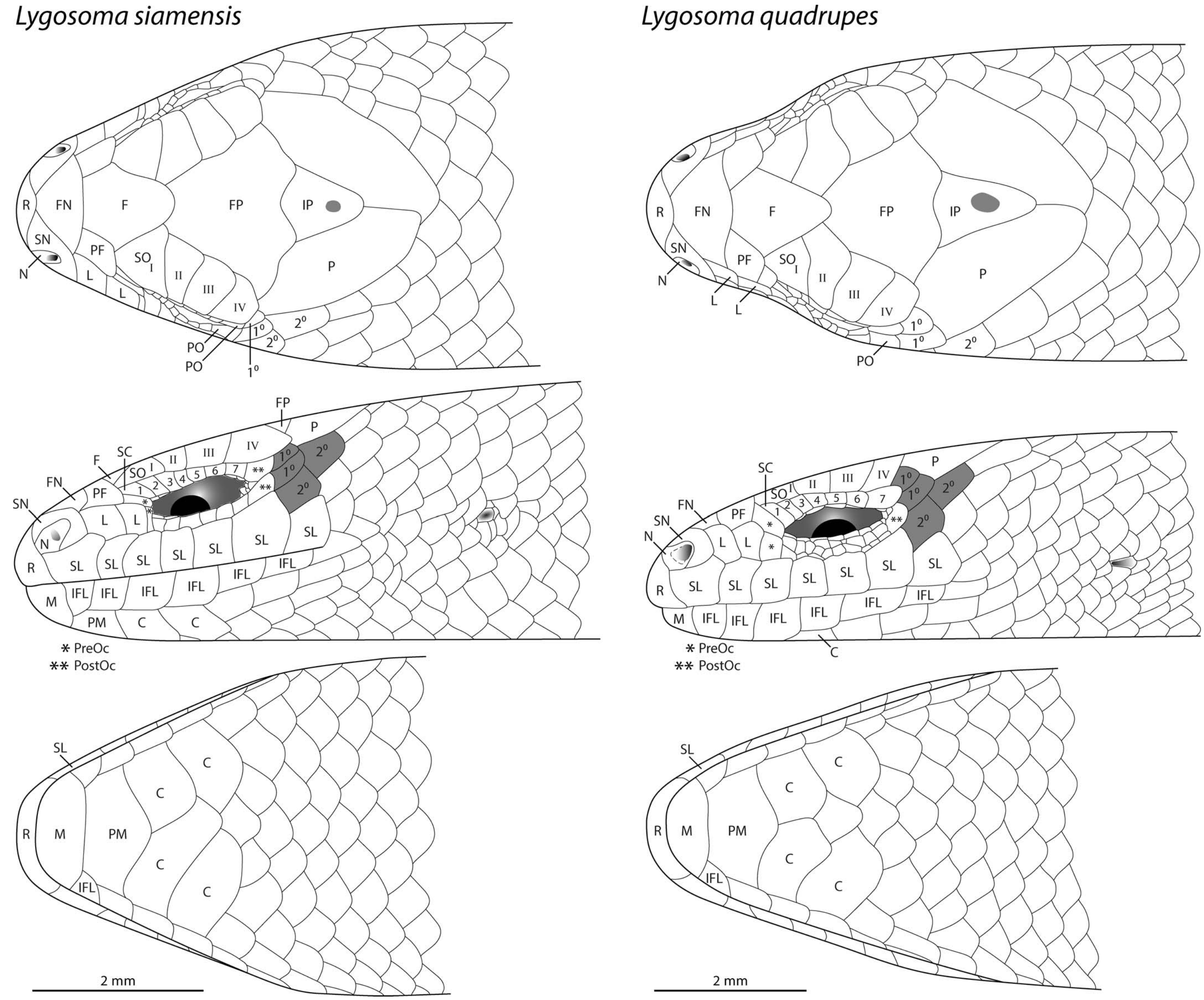

FIG. 4. Illustrations of the heads of male holotype of *Lygosoma siamensis* (FMNH 177496) and subadult specimen of *Lygosoma quadrupes* (USNM 43578) in dorsal, lateral, and ventral views. Taxonomically useful head scales within *Lygosoma* are labeled as follows: C, chin shield; F, frontal; FN, frontonasal; FP, frontoparietal; IL, infralabial; IP, interparietal; L, loreal; M, mental; N, nasal; P, parietal; PF, prefrontal; PM, postmental; PN, postnasal; PreOc, preocular; PostOc, postocular; R, rostral; SC, superciliary; SL, supralabial; SN, supranasal; SO, supraocular; 1°, primary temporal; 2°, secondary temporal. Roman numerals indicate scales in the supraocular series, with arabic numerals indicating scales in the superciliary series. Temporal scales highlighted in gray. Illustrations by CDS and BBH.

anguinum, *L. bowringii*, *L. frontoparietale*, *L. herberti*, *L. popae*, and *L. samajaya* by having fewer Toe IV lamellae (6 or 7 vs. >8); and from *L. samajaya* by having a longer axilla-groin distance (AGD 47.9–61.0 mm vs. ≤43.4 mm), shorter forelimbs (3.9–4.4 mm vs. ≥13.2 mm), and a greater number of paravertebral scale rows (117–121 vs. ≤61) (Tables 2 and 3).

From larger species recognized to occur in Southeast Asia (*L. angeli*, *L. bampfyldei*, *L. boehmei*, *L. corpulentum*, *L. haroldyoungi*, *L. isodactylum*, *L. kinabatanganensis*, *L. koratense*, *L. opisthorhodum*, *L. peninsulare*, *L. punctatum*, and *L. schneideri*), *L. quadrupes* differs from *L. boehmei*, *L. corpulentum*, and *L. koratense* by having a smaller body size (SVL 66.8–78.3 mm vs. 86.0 mm [*L. boehmei*], 97.8–168.0 mm [*L. corpulentum*], 101.0–106.0 mm [*L. koratense*]) and shorter tail length (TL 54.0–71.8 mm vs 91.0 mm [*L. boehmei*], 97.6–159.8 mm [*L. corpulentum*], 93.0–95.0 mm [*L. koratense*]); from *L. bampfyldei*, *L. haroldyoungii*, *L. isodactylum*, *L. kinabatanganensis*, *L. opisthorhodum*, *L. peninsulare*, *L. punctata*, and *L. schneideri* by having a smaller body size (SVL 66.8–78.3 mm vs. 110.0–119.0 mm [*L. bampfyldei*], 114.8–148.0 mm [*L. haroldyoungi*], 82.5–117.0 mm [*L. isodactylum*], 141.0 mm [*L. kinabatanganensis*], 93.0 mm [*L. opisthorhodum*], 119.0 mm [*l. peninsulare*], 85.0 mm [*L. punctata*], 129.0 mm [*L. schneideri*]); from *L. boehmei*, *L. corpulentum*, *L. haroldyoungi*, *L. herberti*, *L. isodactylum*, and *L. koratense*, *L. quadrupes* differs by having a shorter head length (HL 4.4–5.6 mm vs. 12.3 mm [*L. boehmei*], 16.9–30.3 mm [*L. corpulentum*], 15.2–18.1 mm [*L. haroldyoungi*], 6.8–8.8 mm [*L. herberti*] 11.7–14.0 mm [*L. isodactylum*], 18.0–19.0 mm [*L. koratense*]) and shorter head width (HW 4.6–5.2 mm vs. 10.5 mm [*L. boehmei*], 12.0–21.8 mm [*L. corpulentum*], 9.5–12.0 mm [*L. haroldyoungi*], 7.5–8.4 [*L. herberti*], 7.7–9.0 mm [*L. isodactylum*], 13.0 mm [*L. koratense*]); from *L. boehmei*, *L. corpulentum*, *L. isodactylum*, and *L. koratense* by having fewer

TABLE 2. Summary of mensural characters in *Lygosoma siamensis* and specimens of all other small, slender species recognized to occur in Southeast Asia. Adult sample size shown in parentheses following species names. Measurements given as ranges followed by mean ± SD; relative limb lengths given as percentage over mean ± SD).

	siamensis (16)	*tabonorum* (13)	*quadrupes*[a] (5)	*albopunctatum* (4)	*anguinum* (6)
SVL	51.0–79.0 (63.0 ± 6.7)	60.0–79.0 (68.5 ± 5.4)	66.8–78.3 (71.6 ± 5.7)	35.0–47.0 (39.5 ± 5.7)	35.0–58.0 (51.5 ± 8.4)
TL	50.0–74.0 (60.5 ± 9.2)	55.0–72.0 (65.5 ± 5.4)	54.0–71.8 (63.9 ± 9.0)	33.0–37.0 (35 ± 2.8)	40.0–55.0 (47.3 ± 6.1)
AGD	33.0–57.0 (46.2 ± 5.7)	45.0–63.0 (51.7 ± 4.7)	47.9–61.0 (54.5 ± 5.7)	20.0–27.0 (24.3 ± 3.0)	26.0–41.0 (35.7 ± 5.1)
MBW	3.5–4.8 (4.1 ± 0.3)	3.8–6.1 (4.8 ± 0.6)	4.7–5.7 (5.2 ± 0.5)	3.4–5.8 (4.4 ± 1.0)	4.0–5.0 (4.5 ± 0.4)
HL	3.4–5.1 (4.3 ± 0.5)	4.1–5.6 (5.0 ± 0.4)	4.4–5.6 (4.9 ± 0.5)	4.2–5.4 (4.7 ± 0.6)	3.7–5.6 (4.6 ± 0.7)
HW	3.4–5.3 (3.9 ± 0.5)	3.9–7.8 (4.7 ± 1.0)	4.6–5.2 (4.8 ± 0.2)	3.9–4.9 (4.5 ± 0.5)	3.5–4.7 (4.0 ± 0.4)
SNL	1.7–2.4 (2.0 ± 0.2)	2.1–3.0 (2.4 ± 0.3)	2.6–2.9 (2.7 ± 0.1)	2.0–2.9 (2.5 ± 0.4)	2.0–2.8 (2.3 ± 0.2)
FLL	1.8–2.8 (2.3 ± 0.3)	2.2–3.2 (2.8 ± 0.3)	3.9–4.4 (4.2 ± 0.3)	3.1–9.7 (6.2 ± 3.2)	1.7–3.2 (2.3 ± 0.6)
HLL	3.1–4.9 (3.8 ± 0.5)	3.5–4.9 (4.1 ± 0.4)	4.7–7.2 (6.0 ± 1.2)	3.5–6.4 (5.3 ± 1.3)	3.2–4.1 (3.7 ± 0.4)
FLL/SVL	2.3–4.9 (3.7 ± 0.7)	3.3–4.6 (4.2 ± 0.5)	4.7–5.9 (5.8 ± 0.1)	8.1–23.7 (15.9 ± 8.7)	3.1–5.7 (4.4 ± 1.0)
HLL/SVL	4.0–8.0 (6.2 ± 0.9)	5.1–6.8 (6.1 ± 0.6)	6.9–9.7 (8.3 ± 1.2)	9.9–16.7 (13.5 ± 2.8)	6.1–10.4 (7.3 ± 1.6)

[a] Specimens from type locality island of Java, Indonesia only.

midbody (25 or 26 vs. 32 [*L. boehmei*], 36–40 [*L. corpulentum*], 30–34 [*L. isodactylum*], 32–34 [*L. koratense*]) and a greater number of paravertebral scale rows (117–121 vs. 66 [*L. boehmei*], 78–86 [*L. corpulentum*], 88–98 [*L. isodactylum*], 63 [*L. koratense*]); from *L. angeli* by having fewer midbody scale rows (25 or 26 vs. 30); and from *L. punctata* by having a greater number of paravertebral scale rows (117–121 vs. 62–76); and from *L. boehmei* and *L. koratense* by having fewer infralabials (5 or 6 vs. 7 [*L. boehmei*], 7 [*L. koratense*]).

Description.—Based on the type description and examination of five adult (FMNH 122264, MCZ 7667, USNM 29414, 43257, 43677) and two juvenile (USNM 43578, 43780) specimens (mensural measurements summarized for adults specimens only). Body small, slender, SVL 66.8–78.3 mm; head weakly differentiated from neck and roughly equal in width to body, HW 6.4–7.5% SVL, 91.4–117.9% HL; snout rounded in dorsal and lateral profile, SNL 47.0–64.9% HL; ear opening small; eyes small, ED 21.6–32.4% HL, 72.5–92.3% END; body moderately depressed, nearly uniform in thickness, MBW 107.8–147.2% MBD; scales smooth, glossy, imbricate; longitudinal scale rows at midbody 25 or 26; paravertebral scale rows 117–121; axilla–groin scale rows 99–101; limbs short, diminutive, pentadactyl; Finger III lamellae five or six, Toe IV lamellae six or seven; FLL 7.3–8.2% AGD, 5.7–5.9% SVL; HLL 8.9–12.7% AGD, 6.9–9.7% SVL; tail nearly as wide as body, gradually tapered toward end, TW 71.5–84.1% MBW, tail length shorter than SVL, TL 72.5–97.0% SVL.

Rostral projecting onto dorsal snout to level in line with anterior edge of nasal opening, wider than long, in contact with frontonasal; frontonasal wider than long; nostril ovoid, in posterior portion of single nasal, longer axis directed posterodorsally and anteroventrally; supranasals present; postnasals absent; prefrontals moderate in size, widely separated; frontal large, its anterior margin in broad contact with frontonasal, in contact with first two anterior supraoculars, 2.5 times larger than anterior supraocular; supraoculars four; frontoparietals fused into single large scale, in contact with supraoculars two, three, and four; interparietal moderate in size, shorter in length than frontoparietal, longer than wide, triangular-shaped, wider anteriorly, pineal eyespot circular, visible in posterior one-third of interparietal; parietals in broad contact medially behind interparietal; in contact distally with posteriormost supraocular, primary temporals, and dorsalmost secondary temporal; enlarged nuchals present; loreals two, anterior loreal slightly longer and higher than posterior loreal; preoculars two; superciliaries seven, anteriormost contacting prefrontal and first supraocular; subocular scale row complete, in contact with supralabials; lower eyelid scaly, with one complete row of scales on dorsal edge; postoculars two, dorsal postocular larger in size; primary temporals two; secondary temporals two, larger than primary temporals; supralabials six or seven, fourth and fifth subocular; infralabials five or six (Fig. 4).

Mental wider than long, in contact with first infralabial; postmental single, enlarged, slightly wider than mental; followed by two pairs of enlarged chin shields, first pair in contact, second pair separated by single medial scale, second

TABLE 3. Summary of qualitative diagnostic characters (present, absent) in *Lygosoma siamensis* and specimens of all other small, slender species recognized to occur in Southeast Asia. Adult sample size shown in parentheses following species names. The pairs of enlarged scales posterior to the postmental scale are abbreviated as chin shield pairs with reference to contact between the first pair. For character abbreviation definitions, see Materials and Methods.

	siamensis (16)	*tabonorum* (13)	*quadrupes*[a] (5)	*albopunctatum* (4)	*anguinum* (6)
MBSR	26–28	25 or 26	25 or 26	14	20–25
AGSR	88–98	83–90	99–101	37–49	69–76
PVSR	113–124	106–111	117–121	59–71	90–99
F3lam	4–6	5 or 6	5 or 6	8–10	5–7
T4lam	5–7	6 or 7	6 or 7	13–16	8
SL	6 or 7	6 or 7	6 or 7	6 or 7	7
IFL	5 or 6	5 or 6	5 or 6	5 or 6	6
SO	4	4	4	4	4
SC	6–8	5 or 6	7	—	6 or 7
FP fusion	+	+	+	–, paired	+ or –, paired
Enlarged nuchals	+ or –	+ or –	+	+ or –	+ or –
1st chin shield pair	Contact medially	Contact medially	Contact medially	Contact medially or no contact	Contact medially

[a] Specimens from type locality island of Java, Indonesia only.

TABLE 2. Extended.

bowringii (84)	*frontoparietale* (2)	*herberti* (3)	*lineolatum* (11)	*popae* (11)
30.0–64.0 (46.2 ± 6.5)	36.0–43.0 (39.5 ± 4.9)	59.0–64.0 (61.0 ± 2.6)	44.0–55.0 (49.1 ± 4.4)	46.0–57.0 (52.0 ± 4.6)
24.0–89.0 (45.5 ± 12.0)	47.0–54.0 (50.5 ± 4.9)	54.0–67.0 (58.3 ± 7.5)	34.0–45.0 (39.3 ± 3.7)	33.0–42.0 (35.6 ± 3.6)
17.0–42.0 (27.3 ± 5.0)	20.0–26.0 (23.0 ± 4.2)	33.0–37.0 (35.3 ± 2.1)	25.0–41.0 (32.6 ± 5.2)	30.0–39.0 (35.4 ± 3.4)
4.5–10.0 (6.7 ± 1.2)	5.6–7.0 (6.3 ± 1.0)	8.6–9.4 (9.1 ± 0.5)	4.0–5.3 (4.6 ± 0.5)	4.3–6.1 (4.9 ± 0.6)
4.2–7.4 (6.1 ± 0.7)	5.5–6.1 (5.8 ± 0.4)	6.8–8.8 (7.6 ± 1.1)	4.0–5.2 (4.4 ± 0.4)	4.1–4.9 (4.5 ± 0.3)
4.0–9.7 (5.6 ± 0.8)	4.5–6.0 (5.2 ± 1.0)	7.5–8.4 (7.9 ± 0.4)	3.7–4.4 (4.1 ± 0.3)	3.8–4.6 (4.2 ± 0.3)
1.5–3.9 (2.8 ± 0.5)	1.3–1.5 (1.4 ± 0.1)	3.5–4.0 (3.8 ± 0.3)	2.0–2.4 (2.2 ± 0.1)	1.8–2.3 (2.1 ± 0.1)
2.2–6.1 (4.7 ± 0.7)	3.0–4.3 (3.6 ± 0.9)	6.6–6.8 (6.7 ± 0.1)	2.4–3.6 (2.9 ± 0.5)	2.4–3.5 (3.0 ± 0.5)
4.0–9.7 (6.3 ± 1.0)	5.5–6.7 (6.1 ± 0.8)	8.0–9.8 (9.1 ± 0.9)	3.7–5.5 (4.5 ± 0.8)	4.0–5.0 (4.4 ± 0.5)
3.8–13.5 (10.3 ± 1.7)	8.4–9.9 (9.1 ± 1.1)	10.6–11.5 (11.0 ± 0.4)	4.5–9.2 (6.4 ± 1.9)	4.6–6.9 (5.8 ± 1.0)
7.2–21.6 (13.8 ± 2.2)	15.3–15.5 (15.4 ± 0.2)	12.5–16.6 (15.0 ± 2.1)	7.9–10.9 (10.0 ± 1.4)	7.6–8.8 (8.4 ± 0.5)

pair equal in size to first pair (Fig. 4). Scales on limbs smaller than body scales.

Coloration in Life.—Although the original description by Linnaeus (1766) was highly abbreviated and lacked a description of color in life, Bloch's (1776) redescription of *Lacerta serpens* (syn. *Lygosoma quadrupes* [Linnaeus, 1766]) based on two syntypes did provide some notes on coloration.

Bloch (1776) described the body surfaces of the species as "ash gray" to "reddish brown" dorsally, with venter either "of a grey color" or covered with "white scales shining like silver." "The mouth...has a brown margin which extends to the eyes, which are framed by this brown color" and the tail was described to terminate in a "brown-colored point" (Bloch, 1776:30, 31; Bauer and Günther, 2006).

Coloration in Preservative.—The dorsal and lateral portions of the trunk appear medium to dark brown, with the ventral body coloration transitioning to a lighter shade of yellowish brown. With the exception of noticeable dorsolateral stripes that are lighter brown in coloration, general background coloration on the body is relatively homogeneous in historically collected material. A few head scales present minor shade differences to the body coloration, with the mental scale appearing slightly darker brown than ventral body coloration, and the rostral and anteriormost supralabial scales appearing slightly lighter brown than dorsal and lateral body coloration.

Variation.—Some variation in head scale patterns were observed among the examined specimens. All specimens had seven supralabials and six infralabials, except for a single specimen (FMNH 122264) which had six and five, respectively. Additionally, Finger III lamellae were observed to vary between five (MCZ 7667, USNM 29414, 43257) and six (FMNH 122264, USNM 43578, 43677, 43780), and Toe IV lamellae between six (MCZ 7667, USNM 29414, 43578, 43677, 43780) and seven (FMNH 122264, USNM 43257).

Distribution, Ecology, and Natural History.—*Lygosoma quadrupes* sensu Linnaeus (1766) is known only from the island of Java in Indonesia (Fig. 1) and is presumed to occur in forested habitats at lower elevations, similar to other members of the *L. quadrupes* complex (Chan-ard et al., 2015; Heitz et al., 2016).

Lygosoma ***siamensis*** sp. nov.
Figures 4, 5, Tables 2–4

Lygosoma quadrupes Honda et al., 2000:453; Ziegler et al., 2007:401; Wagner et al., 2009:4; Das, 2010:240; Geissler et al., 2011:1169.

Holotype.—FMNH 177496 (field no. EHT 1390; Figs. 4, 5), adult male, collected on 7 June 1956 in Thailand, Pattani Province by E. H. Taylor.

Paratypes.—One adult male (FMNH 176980), collected in December 1953 in Thailand, Chonburi Province by E. H. Taylor; two adult males (FMNH 177506, 177509) and one adult female (FMNH 177505), collected between 26 October 1953 and 26 October 1955 in Thailand, Kanchanaburi Province by E. H. Taylor; two adult females (FMNH 177495, 177497) collected on 7 June 1956 in Thailand, Pattani Province by E. H. Taylor; one adult

TABLE 3. Extended.

bowringii (84)	*frontoparietale* (2)	*herberti* (3)	*lineolatum* (11)	*popae* (11)
14–32	28 or 29	24 or 25	22–24	24–26
21–46	40 or 41	37	57–72	68–72
51–71	60	54–58	78–93	90–96
7–12	9 or 10	11 or 12	6–9	5–7
10–17	13–15	15	6–12	8–9
6–8	7	6 or 7	6 or 7	7
6 or 7	6	6	6	6
4	4	4	4	4
6–8	5	N/A	7 or 8	6 or 7
+ or –, paired	+	+ or –, paired	+ or –, paired	+ or –, paired
+ or –	+	–	+ or –	+
Contact medially or no contact	No contact	Contact medially or no contact	Contact medially	Contact medially

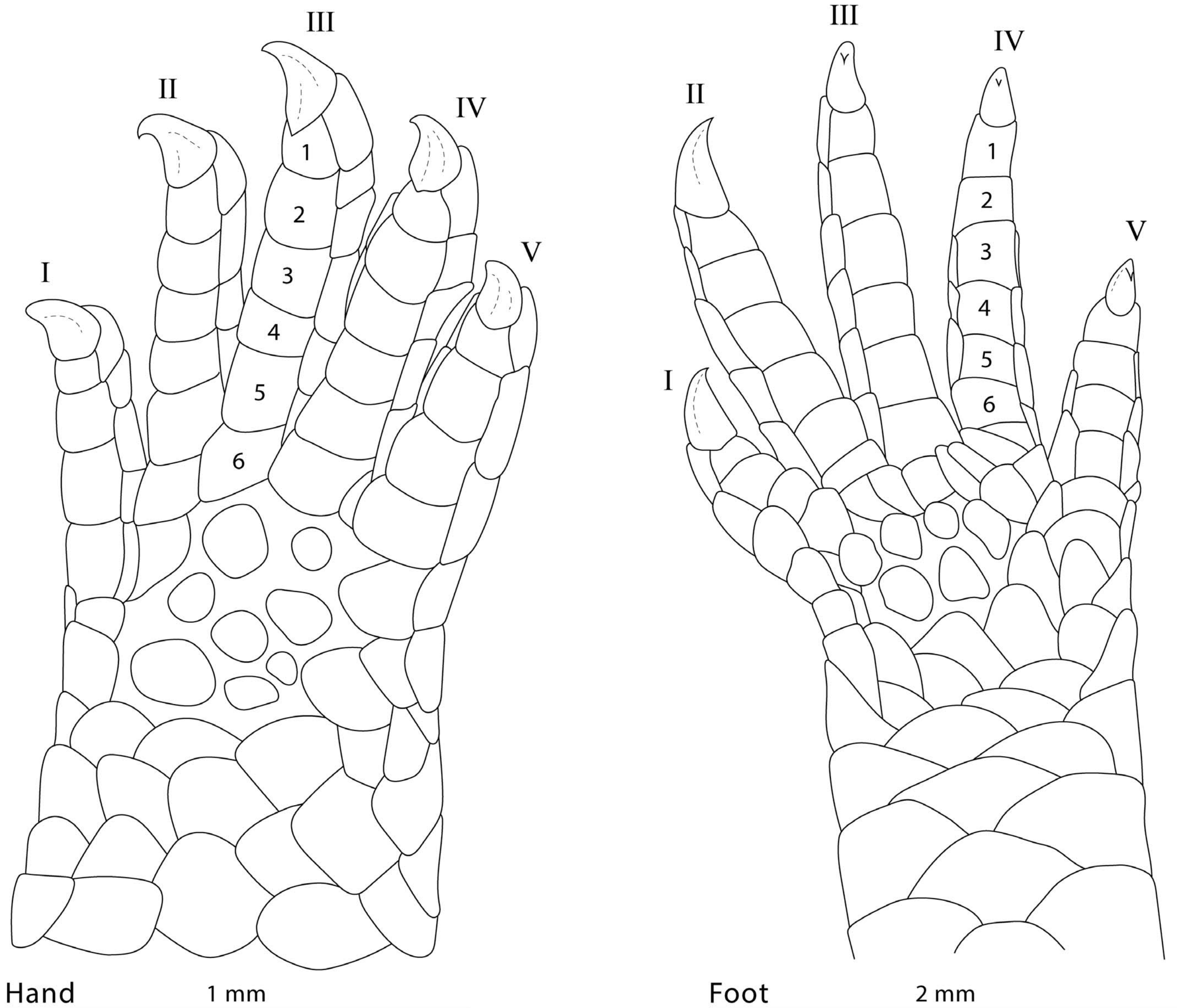

FIG. 5. Illustration of left hand and foot of male holotype of *Lygosoma siamensis* (FMNH 177496) in ventral view. Digit identities labeled with Roman numerals, subdigital lamellae labeled with arabic numerals. Illustrations by CDS and BBH.

male (FMNH 176979) collected on 15 September 1956 in Thailand, Phra Nakhon District by E. H. Taylor; one adult male (FMNH 177491) and one adult female (FMNH 177492) collected on 11 December 1955 in Thailand, Prachuap Khiri Khan Province by E. H. Taylor; one adult male (FMNH 177502) and one adult female (FMNH 177503), unknown date of collection, collected in Thailand, Yala Province by E. H. Taylor; one adult male (FMNH 152332), unknown date of collection, collected in Thailand by S. S. Flower; one adult male (MCZ 39280) and one adult female (MCZ 39281), unknown date of collection, collected in Thailand, Bangkok; one adult female (MCZ 39279), unknown date of collection, collected in Thailand, Bagnara, Pattani Province.

Diagnosis.—*Lygosoma siamensis* can be distinguished from congeners by the following combination of morphological characters: 1) body size small (SVL 51.0–79.0 mm); 2) limb length short; 3) supralabials 6 or 7; 4) infralabials 5 or 6; 5) superciliaries 6–8; 6) supraoculars 4; 7) Finger III lamellae 4–6; 8) Toe IV lamellae 5–7; 9) midbody scale rows 26–28; 10) axilla–groin scale rows 88–98; 11) paravertebral scale rows 113–124; and 12) single, enlarged, fused frontoparietal (Tables 2 and 3).

Comparisons.—*Lygosoma siamensis* is phenotypically most similar to *L. quadrupes* sensu Linnaeus (1766) and *L. tabonorum* but can be distinguished from both based on a combination of characteristics. The new species differs from *L. tabonorum* by having more midbody (26–28 vs. 25 or 26) and paravertebral (113–124 vs. 106–111) scale rows and a tendency toward having more axilla–groin scale rows (88–98 vs. 83–90); and from *L. quadrupes* by having shorter relative forelimbs (FLL 2.3–4.9% SVL vs. 4.7–5.9%) and fewer midbody (26–28 vs. 25 or 26) and axilla–groin (88–98 vs. 99–101) scale rows (Tables 2 and 3).

Among the other species of *Lygosoma* recognized to occur in Southeast Asia (*L. albopunctatum*, *L. angeli*, *L. anguinum*, *L. bampfyldei*, *L. boehmei*, *L. bowringii*, *L. corpulentum*, *L. frontoparietale*, *L. haroldyoungi*, *L. herberti*, *L. isodactylum*, *L. kinabatanganensis*, *L. koratense*, *L. lineolatum*, *L. opisthorhodum*, *L. peninsularae*, *L. popae*, *L. punctata*, *L. samajaya*, *L. schneideri*, and *L.*

TABLE 4. Summary of morphological variation among meristic and mensural characters in the type series of *Lygosoma siamensis*. Values are given for adult specimens examined and summarized by sex. For mensural characters, ranges are given followed by means ± SD, for meristic characters, number of individuals with a given scale count shown in parentheses. For character abbreviation definitions, see Materials and Methods.

	Males $N = 9$	Females $N = 7$
SVL	51.0–79.0 (63.0 ± 7.9)	57.0–73.0 (63.0 ± 5.4)
TotL	101.0–138.0 (124.0 ± 14.9)	117.0–118.0 (117.5 ± 0.7)
MBW	3.5–4.4 (4.0 ± 0.2)	4.0–4.8 (4.4 ± 0.3)
MBD	2.6–3.6 (3.1 ± 0.4)	3.2–4.7 (3.7 ± 0.5)
TL	50.0–74.0 (62.8 ± 9.4)	50.0–57.0 (53.5 ± 4.9)
TW	2.3–3.4 (3.0 ± 0.4)	2.8–4.3 (3.3 ± 0.5)
TD	2.2–3.9 (2.9 ± 0.5)	2.5–4.0 (3.2 ± 0.6)
FLL	1.8–2.7 (2.3 ± 0.4)	2.1–2.8 (2.4 ± 0.3)
HLL	3.1–4.9 (3.7 ± 0.5)	3.3–4.4 (4.0 ± 0.4)
HL	3.4–4.9 (4.2 ± 0.5)	3.4–5.1 (4.3 ± 0.5)
HW	3.4–4.2 (3.9 ± 0.3)	3.4–5.3 (4.1 ± 0.7)
HD	2.4–3.2 (2.9 ± 0.3)	2.6–3.6 (3.2 ± 0.3)
ED	1.0–1.5 (1.3 ± 0.1)	1.1–1.6 (1.3 ± 0.2)
END	1.2–1.6 (1.4 ± 0.1)	1.3–1.6 (1.4 ± 0.1)
SNL	1.8–2.3 (2.1 ± 0.1)	1.7–2.4 (2.0 ± 0.3)
IND	0.9–1.2 (1.1 ± 0.1)	1.0–1.3 (1.2 ± 0.1)
MBSR	26 (6)	26 (5)
	27 (2)	27 (1)
	28 (1)	28 (1)
AGSR	88–98	91–98
PVSR	113–124	116–121
F3lam	4 (1)	4 (3)
	5 (4)	5 (3)
	6 (4)	6 (1)
T4lam	5 (2)	5 (2)
	6 (5)	6 (3)
	7 (2)	7 (2)
SL	6 (5)	6 (3)
	7 (4)	7 (4)
IFL	5 (5)	5 (4)
	6 (4)	6 (3)
SO	4 (9)	4 (7)
SC	6 (2)	6 (1)
	7 (7)	7 (5)
		8 (1)

veunsaiensis), *L. siamensis* differs on the basis of overall body size and relative limb lengths and a number of scale pattern characteristics (Tables 2 and 3). On the basis of body morphology, the new species can be distinguished from *L. albopunctatum* and *L. veunsaiensis* by having a larger body size (SVL 51.0–79.0 mm vs. 35.0–47.0 mm [*L. albopunctatum*], 33.6 mm [*L. veunsaiensis*]) and longer tail length (TL 50.0–74.0 mm vs. 33.0–37.0 mm [*L. albopunctatum*], 40.1 mm [*L. veunsaiensis*]); from *L. frontoparietale* by having a larger body size (SVL 51.0–79.0 mm vs. 36.0–43.0 mm); from *L. lineolatum* and *L. popae* by having a longer tail length (TL 50.0–74.0 mm vs. 34.0–45.0 [*L. lineolatum*], 33.0–42.0 [*L. popae*]); from *L. bampfyldei*, *L. boehmei*, *L. corpulentum*, *L. kinabatanganensis*, *L. koratense*, *L. peninsulare*, and *L. schneideri* by having a smaller body size (SVL 51.0–79.0 mm vs. 110.0–119.0 mm [*L. bampfyldei*], 86.0 mm [*L. boehmei*], 97.8–168.0 mm [*L. corpulentum*], 141.0 mm [*L. kinabatanganensis*], 101.0–106.0 mm [*L. koratense*], 119.0 mm [*L. peninsulare*], 129.0 mm [*L. schneideri*]) and shorter tail length (TL 50.0–74.0 mm vs. 75.0–130.0 mm [*L. bampfyldei*], 91.0 mm [*L. boehmei*], 97.6–159.8 mm [*L. corpulentum*], 93.0–95.0 mm [*L. koratense*], 150.0 mm [*L. peninsulare*], 96 mm [*L. schneideri*], original TL unknown but expected to be >74.0 mm [*L. kinabatanganensis*]); and from *L. bampfyldei*, *L. haroldyoungii*, *L. isodactylum*, *L. kinabatanganensis*, *L. opisthorhodum*, *L. peninsularae*, *L. punctata*, and *L. schneideri* by having a smaller body size (SVL 51.0–79.0 mm vs. 110.0–119.0 mm [*L. bampfyldei*], 114.8–148.0 mm [*L. haroldyoungi*], 82.5–117.0 mm [*L. isodactylum*], 141.0 mm [*L. kinabatanganensis*], 93.0 mm [*L. opisthorhodum*], 119.0 mm [*L. peninsularae*], 85.0 mm [*L. punctata*], 129.0 mm [*L. schneideri*]).

In comparing limb morphology, *L. siamensis* is distinguished from *L. albopunctatum*, *L. bampfyldei*, *L. boehmei*, *L. corpulentum*, *L. frontoparietale*, *L. haroldyoungi*, *L. herberti*, *L. isodactylum*, *L. kinabatanganensis*, *L. koratense*, *L. peninsulare*, *L. samajaya*, *L. schneideri*, and *L. veunsaiensis* by having shorter relative forelimb lengths (FLL/SVL 2.3–4.9% vs. 8.1–23.7% [*L. albopunctatum*], 15.0–21.0% [*L. bampfyldei*], 17.1% [*L. boehmei*], 12.7–22.7% [*L. corpulentum*], 8.4–9.9% [*L. frontoparietale*], 10.6–18.8% [*L. haroldyoungi*], 10.6–11.5% [*L. herberti*], 10.6–18.8% [*L. isodactylum*], 25.0% [*L. kinabatanganensis*], 22.6–24.8% [*L. koratense*], 21.0% [*L. peninsulare*], 18.8–19.0% [*L. samajaya*], 17.5% [*L. schneideri*], 18.5% [*L. veunsaiensis*]) and shorter relative hind-limb lengths (HLL/SVL 4.0–8.0% vs. 9.9–16.7% [*L. albopunctatum*], 17.0–32.0% [*L. bampfyldei*], 22.1% [*L. boehmei*], 9.8–19.6% [*L. corpulentum*], 15.3–15.5% [*L. frontoparietale*], 9.8–13.9% [*L. haroldyoungi*], 12.5–16.6% [*L. herberti*], 9.8–13.9% [*L. isodactylum*], 25.0% [*L. kinabatanganensis*], 14.2–15.8% [*L. koratense*], 32.0% [*L. peninsulare*], 26.0–26.2% [*L. samajaya*], 24.8% [*L. schneideri*], 12.8% [*L. veunsaiensis*]).

From *L. bampfyldei*, *L. boehmei*, *L. corpulentum*, *L. haroldyoungi*, *L. herberti*, *L. isodactylum*, *L. kinabatanganensis*, *L. koratense*, *L. peninsulare*, *L. samajaya*, and *L. schneideri*, *L. siamensis* differs by having a shorter head length (HL 3.4–5.1 mm vs. 16.6–18.8 mm [*L. bampfyldei*], 12.3 mm [*L. boehmei*], 16.9–30.3 mm [*L. corpulentum*], 15.2–18.1 mm [*L. haroldyoungi*], 6.8–8.8 mm [*L. herberti*] 11.7–14.0 mm [*L. isodactylum*], 23.8 mm [*L. kinabatanganensis*], 18.0–19.0 mm [*L. koratense*], 19.1 mm [*L. peninsulare*], 10.8–11.0 mm [*L. samajaya*], 21.1 mm [*L. schneideri*]) and shorter head width (HW 3.4–5.3 mm vs. 12.5–18.9 mm [*L. bampfyldei*], 10.5 mm [*L. boehmei*], 12.0–21.8 mm [*L. corpulentum*], 9.5–12.0 mm [*L. haroldyoungi*], 7.5–8.4 [*L. herberti*], 7.7–9.0 mm [*L. isodactylum*], 23.8–20.8 mm [*L. kinabatanganensis*], 13.0 mm [*L. koratense*], 14.5 mm [*L. peninsulare*], 7.9–9.0 mm [*L. samajaya*], 18.5 mm [*L. schneideri*]); and from *L. angeli* and *L. frontoparietale* by having a shorter head length (HL 3.4–5.1 mm vs. 9.4–12.1 mm [*L. angeli*], 5.5–6.1 mm [*L. frontoparietale*]).

On the basis of scale patterns and counts, the new species differs from *L. albopunctatum*, *L. anguinum*, *L. herberti*, and *L. lineolatum* by having a greater number of midbody (26–28 vs. 14 [*L. albopunctatum*], 20–25 [*L. anguinum*], 24 or 25 [*L. herberti*], 22–24 [*L. lineolatum*]), axilla-groin (88–98 vs. 37–49 [*L. albopunctatum*], 69–76 [*L. anguinum*], 37 [*L. herberti*], 57–72 [*L. lineolatum*]), and paravertebral (113–124 vs. 59–71 [*L. albopunctatum*], 90–99 [*L. anguinum*], 54–58 [*L. herberti*], 78–93 [*L. lineolatum*]) scale rows; from *L. bampfyldei*, *L. boehmei*, *L. corpulentum*, *L. isodactylum*, *L. kinabatanganensis*, *L. koratense*, *L. peninsulare*, and *L. schneideri* by having fewer midbody (26–28 vs. 36–40 [*L. bampfyldei*], 32 [*L. boehmei*], 36–40 [*L. corpulentum*], 30–34 [*L. isodactylum*], 42 [*L. kinabatanganensis*], 32–34 [*L. koratense*], 41 [*L. peninsulare*], 45 [*L. schneideri*]) and more paravertebral (113–124 vs. 81–85 [*L. bampfyldei*], 66 [*L. boehmei*], 78–86 [*L. corpulentum*], 88–98 [*L. isodactylum*], 98 [*L. kinabatanganensis*], 63 [*L. koratense*], 87 [*L. peninsulare*], 95 [*L. schneideri*]) scale rows; from *L. bowringii*, *L. frontoparietale*, and *L. popae* by having a greater number of axilla–groin (88–98 vs. 21–46 [*L. bowringii*], 40 or 41 [*L. frontoparietale*], 68–72 [*L. popae*]) and paravertebral (113–124 vs. 51–71 [*L. bowringii*], 60 [*L. frontoparietale*], 90–96 [*L. popae*]) scale rows; from *L. angeli* by having fewer midbody scale rows

(26–28 vs. 30); from *L. veunsaiensis* by having a greater number of midbody (26–28 vs. 22) and paravertebral (113–124 vs. 51) scale rows; and from *L. punctata* by having a greater number of paravertebral scale rows (113–124 vs. $\leq$ 76).

The new species further differs from *L. albopunctatum*, *L. bampfyldei*, *L. boehmei*, *L. bowringii*, *L. corpulentum*, *L. frontoparietale*, *L. herberti*, *L. kinabatanganensis*, *L. koratense*, *L. peninsulare*, *L. schneideri*, and *L. samajaya* by having fewer Finger III lamellae (4–6 vs. 8–10 [*L. albopunctatum*], 10 [*L. bampfyldei*], 8–10 [*L. boehmei*], 7–12 [*L. bowringii*], 9 or 10 [*L. frontoparietale*], 11 or 12 [*L. herberti*], 10 [*L. kinabatanganensis*], 9 [*L. koratense*], 11 [*L. peninsulare*], 10 [*L. schneideri*], 10 [*L. samajaya*]) and Toe IV (5–7 vs. 13–16 [*L. albopunctatum*], 17 [*L. bampfyldei*], 14 [*L. boehmei*], 10–17 [*L. bowringii*], 13–15 [*L. frontoparietale*], 15 [*L. herberti*, *L. kinabatanganensis*], 13 or 14 [*L. koratense*, *L. samajaya*], 16 [*L. peninsulare*, *L. schneideri*]) lamellae; and from *L. anguinum*, *L. corpulentum*, *L. popae*, *L. punctata*, and *L. veunsaiensis* by having fewer Toe IV lamellae (5–7 vs. 8 [*L. anguinum*], 11–15 [*L. corpulentum*], 8 or 9 [*L. popae*], 11–14 [*L. punctata*], 9 [*L. veunsaiensis*]) (Fig. 5).

Finally, *L. siamensis* can be distuingished from *L. boehmei* and *L. koratense* by having fewer infralabials (5 or 6 vs. 7 [*L. boehmei*], 7 [*L. koratense*]); from *L. veunsaiensis* by having a greater number of supralabials (6 or 7 vs. 5); from *L. albopunctatum* by the presence of a single, enlarged, fused frontoparietal (vs. distinct pair or lack of frontoparietals); and from *L. frontoparietale* by the presence of medial contact between enlarged, first chin shields (vs. separation) (Fig. 4).

Description.—Adult male, body small, slender, SVL 61.0 mm; head weakly differentiated from neck and roughly equal in width to body, HW 6.9% SVL, 101.2% HL; snout rounded in dorsal and lateral profile, SNL 46.7% HL; ear opening small; eyes small, ED 60.6% HL, 87.1% END; body moderately depressed, nearly uniform in thickness, MBW 123.9% MBD; scales smooth, glossy, imbricate; longitudinal scale rows at midbody 26; paravertebral scale rows 113; axilla–groin scale rows 88; limbs short, diminutive, pentadactyl; Finger III lamellae five, Toe IV lamellae six (Fig. 4); FLL 5.7% AGD, 4.4% SVL; HLL 10.4% AGD, 8.0% SVL; tail nearly as wide as body, gradually tapered towards end, TW 70.6% MBW, tail length equal to SVL (Figs. 4, 5).

Rostral projecting onto dorsal snout to level in line with anterior edge of nasal opening, wider than long, in contact with frontonasal; frontonasal wider than long; nostril ovoid, in posterodorsal portion of single nasal, longer axis directed posterodorsally and anteroventrally; supranasals present; postnasals absent; prefrontals small, widely separated; frontal large, its anterior margin in broad contact with frontonasal, in contact with first two anterior supraoculars on right side of head, first anterior supraocular on left side of head, 2 times larger than anterior supraocular; supraoculars four; frontoparietals fused into single large scale, in contact with supraoculars two, three, and four on right side of head, and all four supraoculars on left side of head; interparietal small, shorter in length than frontoparietal, longer than wide, triangular-shaped, wider anteriorly, pineal eyespot circular, visible in posterior one-third of interparietal; parietals in broad contact medially behind interparietal; in contact distally with posteriormost supraocular and dorsalmost primary and secondary temporals; enlarged nuchals absent; loreals two, anterior loreal slightly longer and higher than posterior loreal; preoculars two, dorsal preocular extending in width anteriorly past midline of posterior loreal; superciliaries seven, anteriormost contacting prefrontal and first supraocular; subocular scale row complete, in contact with supralabials; lower eyelid scaly, with one complete row of scales on dorsal edge; postoculars two, roughly equal in size; primary temporals two; secondary temporals two, larger than primary temporals; supralabials seven, first and sixth largest, fourth and fifth subocular; infralabials six (Fig. 4).

Mental wider than long, in contact with first infralabial; postmental single, enlarged, its width equal to width of mental; followed by two pairs of enlarged chin shields, first pair in contact, second pair narrowly separated by single medial scale, second pair equal in size to first pair (Fig. 4). Scales on limbs smaller than body scales.

Coloration in Life.—Chan-ard et al. (2015) described coloration in life as greyish-brown to brown, noting darker brown longitudinal lines present on the edges of scales and continuing onto the tail. Darker pigmentation can be observed on portions of the head, particularly across the supralabial scales, with the ventral surface of the body and tail described as pale pink (Chan-ard et al., 2015).

Coloration in Preservative.—The dorsal, lateral, and ventral portions of the trunk appear a light milky brown with slight speckling on the lateral and dorsal regions of the body. The ventral surfaces of the body are lighter in shade than the dorsal and lateral surfaces. Speckled pigmentation patterns on dorsal and lateral body scales appear to be composed of irregularly spaced, small, dark spots that become less distinct toward the lateral surfaces of the body. These spots are absent from the ventral surfaces of the body. The supralablials and supraoculars are a darker shade of brown as compared with the trunk, and the supralabials possess a higher density of dark, scale pigmentation spots than dorsal and lateral body scales.

Measurements (mm) and Scale Counts of Holotype.—SVL 61.0; TotL 122.0; MBW 4.4; MBD 3.5; TL 61.0; TW 3.1; TD 3.1; HL 4.2; HW 4.2; HD 3.2; ED 1.3; END 1.5; SNL 2.0; IND 1.1; FLL 2.7; HLL 4.9; MBSR 26; AGSR 88; PVSR 113; F3lam 6; T4lam 6; SL 7; IFL 6; SC 7; SO 4.

Variation.—Summaries of variation in meristic and mensural characters in the type series are presented in Table 4. Additionally, the presence of enlarged, differentiated nuchal scales varies in the type series from present (FMNH 152332, 176979, 176980, 177492, 177495, 177505, 177506, MCZ 39280, 39281) to absent (FMNH 177491, 177496 [holotype], 177497, 177502, 177503, 177509, MCZ 39279).

Distribution, Ecology, and Natural History.—*Lygosoma siamensis* is known from Cambodia, Laos, West Malaysia, Thailand, and Vietnam (Figs. 1, 3) and is presumed to occur in forested habitats at lower elevations, similar to other members of the *L. quadrupes* complex (Chan-ard et al., 2015; Heitz et al., 2016). The new species is semifossorial and has been reported from leaf litter substrates (Chan-ard et al., 2015), as well as oviparous, with two or three eggs per clutch observed (Chan-ard et al., 2015).

Etymology.—The new species name was derived from the exonym "Siam," a term formerly used as the name of Thailand. The name was chosen in recognition of Thailand as the center of the species' known distribution. Suggested common name: Siamese Supple Skink.

Discussion

Members of the *L. quadrupes* complex are distributed across a landscape of continential landmasses and isolated oceanic islands, each possessing complex topographic structure involving mountain ranges, intervening river valleys, and isolated volcanic peaks (Woodruff and Turner, 2009; Grismer, 2011;

Brown et al., 2013; Heitz et al., 2016). Within this region, the Thai-Malay Peninsula has served as an important system for research investigating patterns and processes of diversification, with a large number of prior studies focused on biogeographic patterns related to the Isthmus of Kra (Jansa et al., 2006; Esselstyn et al., 2009, 2010; Woodruff and Turner, 2009; Grismer, 2011; Brown et al., 2013; Parnell, 2013). Phylogenetic studies have now shown that the dramatic ecotone has indeed acted as a barrier to gene flow for a number of organisms, including some starfish (Benzie, 1999), marine gastropod species (Crandall et al., 2008), and even brackish water snakes (*Cerberus rynchops*; Karns et al., 2000; Alfaro et al., 2004), among others (Parnell, 2013). However, the expectation of this north–south barrier to gene flow resulting in higher population genetic structure and contributing to lineage diversification has not been supported universally by recent work. In fact, some studies have found quite the opposite, with low genetic diversity across the peninsula for several widespread species (i.e., mangrove plant species in the genera *Ceriops* and *Excoecaria* [Zhang et al., 2008; Parnell, 2013], or the Asiatic honeybee, *Apis cerana* [Rueppel et al., 2011]). Although the growing number of studies employing denser population-level sampling and genetic data sets has shed light on the region's varied impact on species-level diversification, clearly much work remains. In fact, for many animal and plant species alike, our understanding of species-specific geographic distributions and population genetic structure remains poor (Parnell, 2000, 2013; Middleton, 2003; Parnell et al., 2003).

With the description of the new species, there are now 24 species of *Lygosoma* recognized to occur in Southeast Asia (Heitz et al., 2016; Uetz and Hošek, 2016), 11 of which occur in Thailand. *Lygosoma frontoparietale* and *L. koratense* continue to be the only Thailand endemic species in the genus; however, the number may increase as future studies continue to investigate species boundaries in this group of more secretive, burrowing lizards. Interestingly, many recent discoveries and descriptions of scincid diversity throughout the region have been of smaller and more secretive species, most often semifossorial or leaf-litter specialists (Grismer et al., 2009, 2014, 2017; Grismer, 2011). In fact, across Indochina, numerous taxonomic problems pertaining to burrowing genera continue to present (e.g., *Isopachys*, *Larutia*, *Leptoseps*, *Lygosoma*; Geissler et al., 2011, 2012; Grismer, 2011; Linkem et al., 2011; Datta-Roy et al., 2014). Semifossorial lizards in general represent an ecomorph class of reptiles that remains poorly understood on our planet, largely attributable to the logistical difficulty in locating and studying populations in the wild (Siler et al., 2011, 2012; Davis et al., 2014; Grismer et al., 2016, 2017).

Currently, three species comprise the *L. quadrupes* complex (*L. siamensis*, *L. tabonorum*, and *L. quadrupes*; Fig. 1; Heitz et al., 2016). Phylogenetic analyses of available sequence data support each of these lineages as genetically distinct from its congeners (Fig. 3). The results of ML analyses support *L. siamensis* as the sister lineage to a clade composed of *L. tabonorum* from Palawan Island in the Philippines and true *L. quadrupes* from Java (Fig. 3). Based on the available 16S data set, we observe significant uncorrected pairwise sequence divergences between the new species and *L. tabonorum* (5.8%) and *L. quadrupes* (4.4%). The combination of genetic data, nonoverlapping mensural and meristic character state data, and biogeographic information provides unequivocal support for the recognition of this lineage of *Lygosoma* as a unique species.

With the recognized distribution of true *L. quadrupes* now restricted to Java, Indonesia, future studies are needed to further evaluate the widespread distribution of *L. siamensis* across much of Indochina, particularly populations documented in Cambodia, southern China, Laos, West Malaysia, and Vietnam (Figs. 1, 3; Geissler et al., 2011, 2012; Heitz et al., 2016). Continued efforts to survey focal microhabitats (i.e., rotting logs, forest leaf litter, tree root networks) throughout Indochina, islands of the Sunda Shelf, and the oceanic Philippines are needed, including the collection of high-quality voucher specimens and genetic tissue samples. Without such vouchered material available in museum natural history collections, more comprehensive systematic and phylogenetic studies of species boundaries, regional genetic diversity, and levels of cryptic diversity will not be possible (Datta-Roy et al., 2014). Furthermore, such work also must be undertaken across Thailand. At present, little is known about the ecology of the new species. Therefore, we consider the status of the new species "data deficient," pending the collection of additional information on distribution, abundance, and habitat requirements.

Acknowledgments.—For specimen loans, we thank J. Vindum and A. Leviton (CAS), A. Resetar and H. Voris (FMNH), K. de Queiroz and A. Wynn (USNM), J. McGuire and C. Spencer (MVZ), R. Brown and L. Welton (KUBI), and J. Hanken, J. Losos, and J. Rosado (MCZ). For access to a tissue sample of true *L. quadrupes* from Java, we thank E. Smith and P. Thammachoti (UTA). For access to the Sam Noble Museum Invertebrate Paleontology Stacking Photography Lab, we thank S. Westrop and R. Burkhalter. Critical reviews of the manuscript were provided by J. L. Watters. Financial support was provided by NSF grants (IOS 1353683 and DEB 1657648) to CDS and Kasetsart University Research and Development Institute to AA.

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Accepted: 16 April 2018.
Published online: 24 August 2018.

ZooBank ID: urn:lsid:zoobank.org:pub:37EFCAEE-2A28-4EBE-800F-3A0EA849812C

Appendix 1

Specimens Examined.—Numbers in parentheses indicate the number of specimens examined. Several sample sizes are greater than those observed in the description attributable to the examination of subadult specimens, which were excluded from morphometric analyses. Within the locality string for each specimen, countries are written in all capital letters, islands are written in small capital letters, higher-order administrative boundaries (i.e., provinces, regions, states) are italicized, and lower-order administrative boundaries (i.e., districts) are not italicized. When possible, the locality for each specimen was identified to district.

Lygosoma albopunctatum (4). PAKISTAN (FMNH 82911); INDIA: *Madhya Pradesh State*: Balaghat District (FMNH 60662); INDIA: *Madhya Pradesh State*: Mandla District (FMNH 152402); INDIA: *Kerala State*: Thiruvananthapuram District (FMNH 74942).

Lygosoma anguinum (6). MYANMAR: *Bago Region*: Taungoo District (CAS 222127); MYANMAR: *Chin State*: Mindat District (CAS 234962); MYANMAR: *Rakhine State*: Sittwe District (CAS 221110); MYANMAR: *Sagaing Region* (CAS 206645, 206646); MYANMAR: *Sagaing Region*: Monywa District (CAS 215732).

Lygosoma bowringii (84). CAMBODIA: *Kratie Province*: Sambour District (MVZ 258372, 258373); INDONESIA: Java Island (FMNH 119684); MALAYSIA: Borneo Island: *Sarawak State* (FMNH 134715, 134716); MALAYSIA: Borneo Island: *Sarawak State*: Bintulu Division (FMNH 158736, 158737); INDONESIA: Sulawesi Island: *South Sulawesi Province* (MVZ 268478, 268480); INDONESIA: Sulawesi Island: *West Sulawesi Province* (MVZ 268482, 268484); MALAYSIA: *Selangor State* (FMNH 125889, 125893, 125896, 125899); MYANMAR: *Kachin State*: Myitkyina District (CAS 232587, 233085); MYANMAR: *Mandalay Region*: Myingyan District (CAS 214002, 214163, 231439); PHILIPPINES: Mindanao Island (FMNH 83488); PHILIPPINES: Palawan Island: *Palawan Province* (FMNH 125640–125642, CAS 157408, 157411, 157412, 157415, PNM 9827–9830); PHILIPPINES: Jolo Island: *Sulu Province* (CAS 60741, 60742, 60744); PHILIPPINES: *Sulu Province* (CAS 60861, 60862); PHILIPPINES: *Tawi-tawi Province* (CAS 62495); THAILAND (CAS 123960, CAS-SUR 23577, 23579, 23580, MCZ 16666); THAILAND: *Chiang Mai Province* (FMNH 188764, 188856, 188859, 188885); THAILAND: *Chiang Mai Province*: Mueang Chiang Mai District (CAS 172730, 172731); THAILAND: *Chonburi Province* (FMNH 17146, 178327, 179456, 188828, 188829, 188833); THAILAND: *Nakhon Ratchasima Province* (FMNH 181847, 181880, 182044, 182054, 182059, 182234); THAILAND: *Nakhon Ratchasima Province*: Wang Nam Khiao District (KU 328482–328486); THAILAND: *Nakhon Si Thammarat Province* (FMNH 179449); THAILAND: *Pattani Province* (FMNH 177494, 188868, 188869); THAILAND: *Phetchabun Province* (MCZ 16667); THAILAND: *Prachuap Khiri Khan Province* (FMNH 188836, 188837, 188843); THAILAND: *Nakhon Ratchasima Province*: Wang Nam Khiao District, Udom Sap Subdistrict (ZMKU R 00612, 00713); THAILAND: *Prachuap Khiri Khan Province*: Thap Sakae District District, Huai Yang Subdistrict (ZMKU R 00712, 00714, 00715);VIETNAM: *Lam Dong Province* (MVZ 222214, 222215).

Lygosoma frontoparietale (2). THAILAND: *Saraburi Province*: Muak Lek District, Mittraphap Subdistrict (ZMKU R 00705, 00706).

Lygosoma herberti (3). THAILAND: *Nakhon Si Thammarat Province* (FMNH 176974–176976).

Lygosoma lineolatum (7). MYANMAR: *Kachin State*: Myitkyina District (CAS 232549); MYANMAR: *Magway Region* (CAS 213615); MYANMAR: *Mandalay Region*: Nyaung-u District (CAS 231273); MYANMAR: *Sagaing Region*: Mon Ywa District (CAS 215536, 215537). MYANMAR: *Yangon Region* (CAS 206533).

Lygosoma popae (7). MYANMAR: *Kachin State*: Myitkyina District (CAS 232550, 233106); MYANMAR: *Mandalay Region*: Nyaung-u District (CAS 231327); MYANMAR: *Sagaing Region* (CAS 210503): MYANMAR: *Sagaing Region*: Hkamti District (CAS 232289); *Shan State*: Kyaukme District (CAS 216328, 216329).

Lygosoma quadrupes (2). INDONESIA: Java Island (FMNH 122264) INDONESIA: Java Island: *West Java Province* (MCZ 7667).

Lygosoma siamensis (16). See taxonomic account.

Lygosoma tabonorum (19). PHILIPPINES: Cuyo Island: *Palawan Province* (CAS 152030–152032); PHILIPPINES: Palawan Island: *Palawan Province* (CAS 157345, CAS-SUR 28465, MCZ 26514, 26515, 26521, 26523–26525, 183651, PNM 9820–9826).

APPENDIX 2. Morphometric analyses. Summary statistics and principal component (PC) scores for meristic and mensural characters shown for principal components with eigenvalues > 1 (PC1–7) that were retained for DAPC analyses (Kaiser, 1960). Abbreviations are listed in the Materials and Methods.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Standard deviation	2.77178	1.79045	1.39079	1.37397	1.24067	1.21549	1.05002
Proportion of variance	0.33403	0.13938	0.0841	0.08208	0.06692	0.06424	0.04794
Cumulative proportion	0.33403	0.47341	0.55751	0.63959	0.70651	0.77075	0.81868
Eigenvalue	7.68274	3.2057	1.93429	1.88778	1.53927	1.47741	1.10254
AGD	−0.0805	0.03272	−0.3816	0.35765	−0.26079	0.26004	−0.12499
MBW	−0.25049	−0.10148	0.2375	0.22745	−0.11166	0.02775	−0.25281
MBD	−0.27478	−0.16611	0.17784	0.11461	0.02604	0.08083	−0.06496
TW	−0.27106	−0.13233	−0.0133	0.23094	−0.11744	−0.17727	−0.10726
TD	−0.23218	−0.20382	0.0812	0.10167	0.0099	−0.19461	0.04948
HL	−0.2384	−0.03429	0.38741	−0.01562	0.04852	−0.14668	−0.11461
HW	−0.2865	−0.21051	−0.06761	0.01402	0.15441	−0.0612	0.16886
HD	−0.18882	0.27075	−0.05914	−0.18023	0.19515	−0.27453	0.30745
ED	−0.15689	0.10347	−0.09215	−0.4554	−0.1678	−0.31691	−0.1363
END	−0.28547	−0.13418	−0.16863	−0.17818	0.15573	0.15095	−0.07486
SNL	−0.22569	0.045	−0.22668	0.20707	0.39388	0.13603	0.15385
IND	−0.27714	−0.02819	−0.0834	−0.09824	0.32115	−0.04085	0.01412
FLL	−0.2567	0.16162	0.03202	0.08922	−0.10271	−0.10088	−0.0683
HLL	−0.22376	−0.24516	−0.24683	−0.01134	0.05278	0.15139	−0.1359
MBSRC	0.11664	−0.09109	−0.01425	0.34783	0.02308	−0.36038	0.54238
AGSRC	0.03873	−0.4899	−0.08915	−0.21938	0.03991	−0.06031	0.05519
PVSRC	0.17412	−0.44	−0.01131	−0.17238	0.04353	−0.0935	0.12756
F3lam	−0.13353	0.13362	0.23776	−0.395	0.06582	0.41225	0.11562
T4lam	−0.09479	0.23483	−0.23052	−0.04502	−0.07274	−0.46714	−0.32055
SL	−0.23471	−0.02035	−0.05825	−0.16624	−0.46315	−0.0049	0.29932
IFL	−0.19785	−0.02495	−0.11211	−0.07306	−0.51173	0.1663	0.33254
SO	−0.08726	−0.00943	0.55703	0.11438	−0.08178	−0.01078	0.07215
SC	0.17153	−0.38654	0.00326	−0.08905	−0.14124	−0.14297	−0.24482