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A New Supple Skink, Genus *Lygosoma* (Reptilia: Squamata: Scincidae), from the Western Philippines

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Abstract: The Palawan Pleistocene Aggregate Island Complex, a western Philippines island group, possesses a complex geologic history and numerous endemic vertebrates. On the basis of multiple unique morphological features, bolstered by genetic data supporting divergent lineages, we describe the first Philippine endemic species of *Lygosoma* from Palawan and Cuyo islands. This new semifossorial species is phenotypically similar to *Lygosoma quadrupes*, a widespread Southeast Asian scincid lizard. We recognize the Palawan lineage as a new species, the second member of the *L. quadrupes* species complex, and comment on its ecology and conservation status. This new species increases species-level diversity in the genus to 31, including 19 species distributed across Southeast Asia.

Key words: Cryptic diversity; Cuyo Island; Endemism; Huxley's Line; Palawan Island; Semifossorial; Sunda Shelf

The Western island arc in the Philippines composing the Palawan Pleistocene Aggregate Island Complex (Palawan PAIC) includes several moderately sized islands (Balabac, Bugsuk, Busuanga, Culion, Cuyo and Palawan islands) as well as numerous small islands. This area represents a unique group of islands containing a complex biogeographic and geologic history. Components of the modern-day Palawan PAIC were once part of mainland Asia, but they separated as the South China Sea formed ~30 million years ago (mya) during the Oligocene (Hall 1996, 1998; Zamoras and Matsuoka 2004; Yumul et al. 2009a,b). Following its separation from Asia, the Palawan microcontinental block moved south-eastward, until it collided with the Philippine mobile belt ~20 mya during the Miocene (Hall 2002; Zamoras et al. 2008; Yumul et al. 2009a). The unique flora and fauna of the Palawan PAIC have been the focus of numerous studies over the years, from older investigations of biogeographic patterns (e.g., Huxley 1868; Boulenger 1894; Steere 1890; Holloway 1982) to modern tests of biogeographical hypotheses (e.g., Evans et al. 2003; Esselstyn et al. 2010; Siler et al. 2012a). Historically, the mammal and bird communities on Palawan Island have been allied most closely to those of Borneo (e.g., Dickerson et al. 1928; Inger 1954; Heaney 1985; Esselstyn et al. 2004). More recent studies that included a wider variety of taxa, however, suggest that species diversity in the island chain is composed of endemic and widespread species of various regional affiliations (Brown and Guttman 2002; Evans et al. 2003; Esselstyn et al. 2010; Linkem et al. 2013; Brown et al. 2016; Fig. 1). Unfortunately, many vertebrate groups found throughout the Palawan PAIC remain poorly understood, including amphibians and reptiles.

With more than 1600 recognized species, Scincidae is one of the most diverse squamate families (Pyron et al. 2013; Uetz and Hošek 2016). More than 105 species are known in the Philippines (Brown and Diesmos 2009; Brown et al. 2013), and they exhibit a diverse array of ecomorphologies. However, only two genera include semifossorial taxa: *Brachymeles* and *Lygosoma* (Siler et al. 2012b; Davis et al. 2014). Whereas 39 of 41 species in *Brachymeles* are endemic to the Philippines (Davis et al. 2016), this genus has never been recorded in the Palawan PAIC. Two species of *Lygosoma* (*L. bowringii* and *L. quadrupes*) are known from the Palawan PAIC and the Sulu Archipelago of southern Philippines (Fig. 2).

The genus *Lygosoma* has a complicated taxonomic history, beginning with its original description of *L. quadrupes* (Linnaeus 1766), and including recent debate over whether they belong to *Lygosoma* vs. the genus *Riopa* (Geissler et al. 2011). The validity of the latter assignment, and what genera occur in Southeast Asia, remain open questions (Greer 1977; Moravec and Böhme 2008; Pauwels et al. 2008; Nguyễn et al. 2009; Das 2010; Geissler et al. 2011). Currently, 29 species of *Lygosoma* are recognized, with 17 present in Southeast Asia (Geissler et al. 2011; Uetz and Hošek 2016). Several species possess widespread distributions spanning recognized faunal demarcations (Geissler et al. 2011).

One widespread taxon, *L. quadrupes*, was first described from Java, Indonesia (Linnaeus 1766). Since the original description, populations of phenotypically similar, semifossorial lizards have been assigned to this species, expanding its perceived distribution across Cambodia, southern China, Indonesia, Laos, Peninsular Malaysia, Thailand, Vietnam, and Palawan and Cuyo islands in the western Philippines (Geissler et al. 2011; Fig. 1).

In the course of our examination of specimens of *L. quadrupes* collected from the islands of Palawan and Cuyo, it became clear that the Philippine populations of *L. quadrupes* sensu Linnaeus (1766), represent a distinct evolutionary lineage worthy of species recognition. Guided by observed genetic divergence between the new species and specimens of *L. quadrupes* from the type locality (Java,

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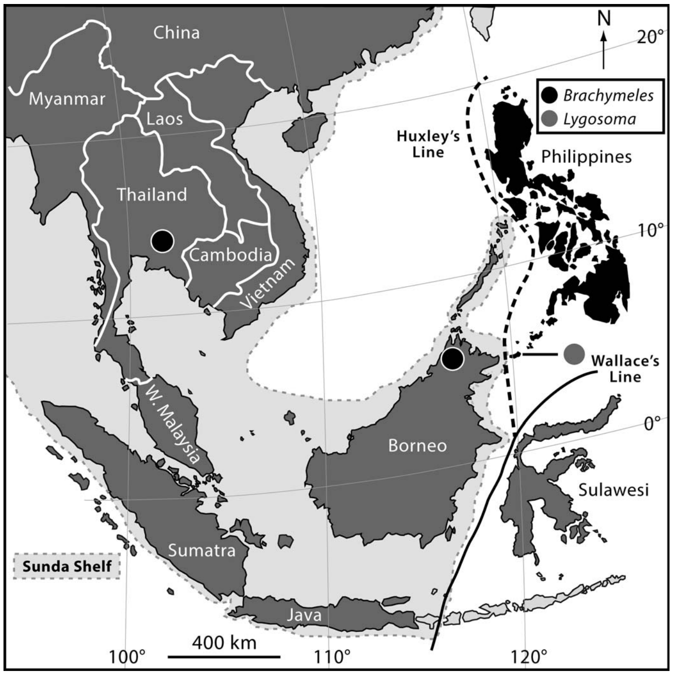

FIG. 1.—Map of Southeast Asia showing the distributions of the scincid genera *Lygosoma* (dark gray shading) and *Brachymeles* (black shading). Black and gray circles represent occurrences of *Lygosoma* and *Brachymeles*, respectively, that are exceptions to both genera's distributions across Huxley's Line. The positions of Wallace's and Huxley's lines are shown for reference. The location of the Sunda Shelf is represented by 120-m submarine bathymetric contour lines and light gray shading.

Indonesia), we describe the Palawan PAIC lineage, diagnose it with a suite of unique, morphological characters, and describe what is known of its ecology, distribution, and conservation status.

MATERIALS AND METHODS

Fieldwork and Specimen Collection

Specimens of the new species were collected from Palawan and Cuyo islands in the Philippines (Fig. 2). Field surveys by ACD and field companions from Palawan Island resulted in the collection of specimens from under rotting logs and in loose leaf litter in secondary forest. Specimens were euthanized with aqueous chloretone, dissected for tissue samples (liver preserved in 95% ethanol), fixed in 10% formalin, and later transferred to 70% ethanol. Museum abbreviations for specimens examined or sequenced in this study follow those of Sabaj Pérez (2014). Previously collected material deposited at the CAS and MVZ includes fluid-preserved specimens collected by A.C. Alcala and L.C. Alcala, J. Vindum, and E. Dujon.

Assessment of Genetic Divergence

To assess genetic divergence between the focal lineage in the Philippines and true *Lygosoma quadrupes* from Java, Indonesia, we extracted DNA from liver tissue preserved in 95% ethanol by using a high salt extraction method (Aljanabi and Martinez 1997) for four individuals of *Lygosoma* sp. nov. (Palawan Island) and one individual of *L. quadrupes* (Java). We amplified two loci: the mitochondrial NADH dehydrogenase subunit 1 (ND1) gene and the nuclear RNA fingerprint protein 35 (R35) gene by using published primers and protocols (Siler et al. 2011). 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 (v. 3.1, Applied Biosystems, Foster City, CA), purified by ethanol precipitation, and sent to Eurofins Scientific (Louisville, KY) for sequencing. Initial alignments were produced in Muscle (Edgar 2004) and manual adjustments were made in Geneious (v. 9.0.5, Biomatters Limited, Auckland, New Zealand). All sequences were deposited in GenBank (ND1 accessions KX774340–44; R35 accessions KX774335–38).

Morphological Data

We examined 134 fluid-preserved specimens of the genus *Lygosoma* for variation in qualitative, meristic, and mensural characters (Appendix). Sex was determined by gonadal inspection when necessary (e.g., when a hemipene bulge or everted hemipenes were not visible), and measurements were taken with digital calipers (±0.01 mm) by EDE and ESF. Meristic and mensural characters were chosen based on Siler et al. (2009; 2010a,b) and Geissler et al. (2011, 2012) and defined as follows: 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), 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; from tip of snout to posterior margin of jaw articulation), 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 counts (MBSRC; number of longitudinal scale rows measured around widest point of midbody), axilla–groin scale-row counts (AGSRC; number of scale rows measured between posterior edge of forelimb insertion and anterior edge of hind limb insertion), and paravertebral scale-row counts (PVSRC; number of scale rows measured between parietals and the base of the tail opposite the vent), Finger III lamellae (F3lam; all enlarged, undivided lamellae beneath Finger III), Toe IV lamellae (T4lam; all enlarged, undivided lamellae beneath Toe IV), supralabial (SL), infralabial (IFL), supraocular (SO), and supraciliary (SC) counts, 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). Additional morpho-

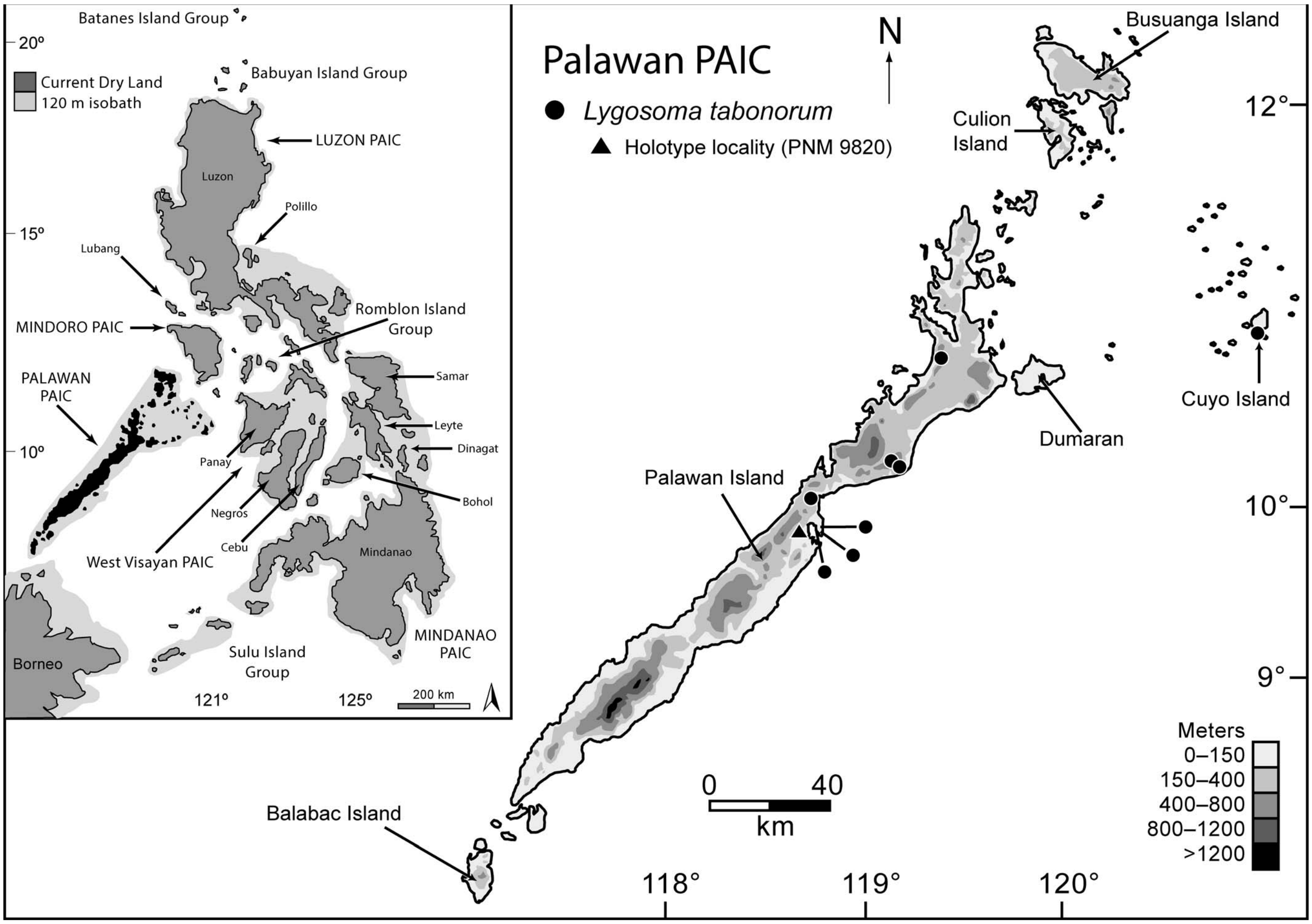

Fig. 2.—Map of the Philippines (top left) with putative distribution of *Lygosoma tabonorum* sp. nov. shaded in black. The Philippine Islands are shaded in gray, with a 120-m bathymetric contour in light gray (the hypothesized maximum range of land during the mid-to-late Pleistocene). The symbols on the islands of the Palawan Pleistocene Aggregate Island Complex (right) indicate locations where *Lygosoma tabonorum* sp. nov. has been documented (triangle = holotype; circles = paratypes).

logical data used for comparisons with larger congener species were obtained from the literature (Günther 1864; Werner 1910; Geissler et al. 2011, 2012).

Species Concept

We follow the general lineage concept of species (de Queiroz 1998, 1999) and consider allopatric populations that are morphologically and genetically diagnosable, as unique evolutionary lineages, and thus distinct species. Although we use estimated sequence divergences in support, our recognition of the new species is based on a diagnosable population identified on the basis of fixed diagnostic character differences and nonoverlapping ranges of morphological characters.

Species Description

Lygosoma ***tabonorum*** sp. nov.
(Tables 1 and 2; Figs. 3–5)

Lygosoma quadrupes Gaulke 1999; Linkem et al. 2010:76.

Holotype.—An adult male (PNM 9820; Field no. ACD 7395; Figs. 3–5) collected on 10 November 2011 at 1100 h in secondary growth forest, Santa Lucia Penal Colony, Barangay Santa Lucia, Municipality of Puerto Princesa, Palawan Province, Palawan Island, Philippines (9.743269°N, 118.665306°E, elevation 6 m above sea level; in all cases, datum = WGS84; Fig. 2), by ACD, E. Jose, and J.V. Bienen.

Paratypes (paratopotypes).—One adult male (PNM 9821) and two juveniles (PNM 9822, 9823) collected on 10 November 2011 by ACD, E. Jose, and J.V. Bienen.

Other paratypes.—One adult male (PNM 9824), one adult female (PNM 9825), and one juvenile (PNM 9826) collected on 8 November 2011 in secondary growth forest, El Nido Airport Area, Municipality of El Nido, Palawan Province, Palawan Island, Philippines, by ACD and K. Soriano. Two adults (CAS 152030, 152032) and one juvenile (CAS 152031) collected on 16 April 1975 in Maringit Ringit, Municipality of Cuyo, Palawan Province, Cuyo Island, Philippines (10.8433°N, 121.044°E), by L.C. Alcala. Three adult males (MCZ 26523, 26525, 183651), one adult female (MCZ 26521), and three juveniles (MCZ 26514, 26515, 26524) collected in 1923 in Puerto Princesa, Palawan Province, Palawan Island, Philippines (9.935372°N, 118.736267°E). One juvenile (CAS-SUR 28465) collected on 12 April 1961 in Palawan Province, Palawan Island, Philippines (9.740638889°N, 118.636°E), by E. Dujon. One juvenile (CAS 157345) collected on 18 June 1984 in Tinitian

TABLE 1.—Summary of mensural characters in *Lygosoma tabonorum* sp. nov. and other small species of slender skinks that occur in Southeast Asia. Sample sizes of adult specimens are indicated in parentheses below specific epithets. Measurements (mm) are listed as range (mean ± 1 SD); relative limb lengths (FLL/SVL and HLL/SVL) are listed as percentages.

	Skink species								
Trait[a]	*tabonorum* (13)	*quadrupes*[b] (2)	*albopunctata* (4)	*anguinum* (6)	*bowringii* (84)	*frontoparietale* (2)	*herberti* (3)	*lineolatum* (11)	*popae* (11)
SVL	60.0–79.0 (68.5 ± 5.4)	51.0–67.0 (59.0 ± 11.3)	35.0–47.0 (39.5 ± 5.7)	35.0–58.0 (51.5 ± 8.4)	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)
TL	55.0–72.0 (65.5 ± 5.4)	54.0–65.0 (59.5 ± 7.8)	33.0–37.0 (35 ± 2.8)	40.0–55.0 (47.3 ± 6.1)	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)	35.0–42.0 (38.5 ± 4.9)
AGD	45.0–63.0 (51.7 ± 4.7)	42.0–52.0 (47.0 ± 7.1)	20.0–27.0 (24.3 ± 3.0)	26.0–41.0 (35.7 ± 5.1)	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)
MBW	3.8–6.1 (4.8 ± 0.6)	3.4–5.6 (4.5 ± 1.5)	3.4–5.8 (4.4 ± 1.0)	4.0–5.0 (4.5 ± 0.4)	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)
HL	4.1–5.6 (5.0 ± 0.4)	4.0–4.6 (4.3 ± 0.4)	4.2–5.4 (4.7 ± 0.6)	3.7–5.6 (4.6 ± 0.7)	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)
HW	3.9–7.8 (4.7 ± 1.0)	4.0–4.6 (4.3 ± 0.4)	3.9–4.9 (4.5 ± 0.5)	3.5–4.7 (4.0 ± 0.4)	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)
SNL	2.1–3.0 (2.4 ± 0.3)	2.0–2.7 (2.4 ± 0.5)	2.0–2.9 (2.5 ± 0.4)	2.0–2.8 (2.3 ± 0.2)	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)
FLL	2.2–3.2 (2.8 ± 0.3)	3.0–3.2 (3.1 ± 0.1)	3.1–9.7 (6.2 ± 3.2)	1.7–3.2 (2.3 ± 0.6)	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)
HLL	3.5–4.9 (4.1 ± 0.4)	3.5–3.7 (3.6 ± 0.1)	3.5–6.44 (5.3 ± 1.3)	3.2–4.1 (3.7 ± 0.4)	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)
FLL/SVL	3.3–4.6 (4.2 ± 0.5)	4.4–6.2 (5.3 ± 1.2)	8.1–23.7 (15.9 ± 8.7)	3.1–5.7 (4.4 ± 1.0)	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)
HLL/SVL	5.1–6.8 (6.1 ± 0.6)	5.4–6.9 (6.2 ± 1.0)	9.9–16.7 (13.5 ± 2.8)	6.1–10.4 (7.3 ± 1.6)	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)

[a] SVL = distance from tip of snout to vent; TL = tail length (measured from posterior margin of vent to tip of tail); AGD = axilla–groin distance (distance between posterior edge of forelimb insertion and anterior edge of hind limb insertion); MBW = midbody width (measured from lateral surface to opposing lateral edge at midpoint of axilla–groin region); HL = head length (from tip of snout to posterior margin of jaw articulation); HW = head width (widest measure of head width at jaw articulations); SNL = snout length (from anterior margin of eye to tip of snout); FLL = forelimb length (measured from forelimb insertion to tip of Finger III or longest digit); HLL = hind limb length (measured from hind limb insertion to tip of Toe IV or longest digit).

[b] Specimens from type locality only.

TABLE 2.—Summary of qualitative diagnostic characters (present, absent) in *Lygosoma tabonorum* sp. nov. and other small species of slender skinks that occur in Southeast Asia. Sample sizes of adult specimens are indicated in parentheses below specific epithets. The pairs of enlarged scales posterior to the postmental scale are abbreviated as chin shield pairs with reference to contact between the first pair.

	Skink species								
Trait[a]	*tabonorum* (13)	*quadrupes*[b] (2)	*albopunctata* (4)	*anguinum* (6)	*bowringii* (84)	*frontoparietale* (2)	*herberti* (3)	*lineolatum* (11)	*popae* (11)
MBSRC	25 or 26	26	14	20–25	14–32	28 or 29	24 or 25	22–24	24–26
AGSRC	83–90	99–101	37–49	69–76	21–46	40 or 41	37	57–72	68–72
PVSRC	106–111	117–119	59–71	90–99	51–71	60	54–58	78–93	90–96
F3lam	5 or 6	5 or 6	8–10	5–7	7–12	9 or 10	11 or 12	6–9	5–7
T4lam	6 or 7	6 or 7	13–16	8	10–17	13–15	15	6–12	8–9
SL	6 or 7	6 or 7	6 or 7	7	6–8	7	6 or 7	6 or 7	7
IFL	5 or 6	5 or 6	5 or 6	6	6 or 7	6	6	6	6
SO	4	4	4	4	4	4	4	4	4
SC	5 or 6	7	—	6 or 7	6–8	5	—	7 or 8	6 or 7
FP fusion	Fused	Fused	Separate	Fused or separate	Fused or separate	Fused	Fused or separate	Fused or separate	Fused or separate
Enlarged nuchals	Present or absent	Present	Present or absent	Present or absent	Present or absent	Present	Absent	Present or absent	Present
First chin shield pair	Contact medially	Contact medially	Contact medially or no contact	Contact medially	Contact medially or no contact	No contact	Contact medially or no contact	Contact medially	Contact medially

[a] MBSRC = midbody scale-row counts (number of longitudinal scale rows measured around widest point of midbody); AGSRC = axilla–groin scale-row counts (number of scale rows measured between posterior edge of forelimb insertion and anterior edge of hind limb insertion); PVSRC = paravertebral scale-row counts (number of scale rows measured between parietals and the base of the tail opposite the vent); F3lam = Finger III lamellae (all enlarged, undivided lamellae beneath Finger III); T4lam = Toe IV lamellae (all enlarged, undivided lamellae beneath Toe IV); SL = supralabial, IFL = infralabial; SO = supraocular; SC = supraciliary counts; FP = frontoparietal contact.

[b] Specimens from type locality only.

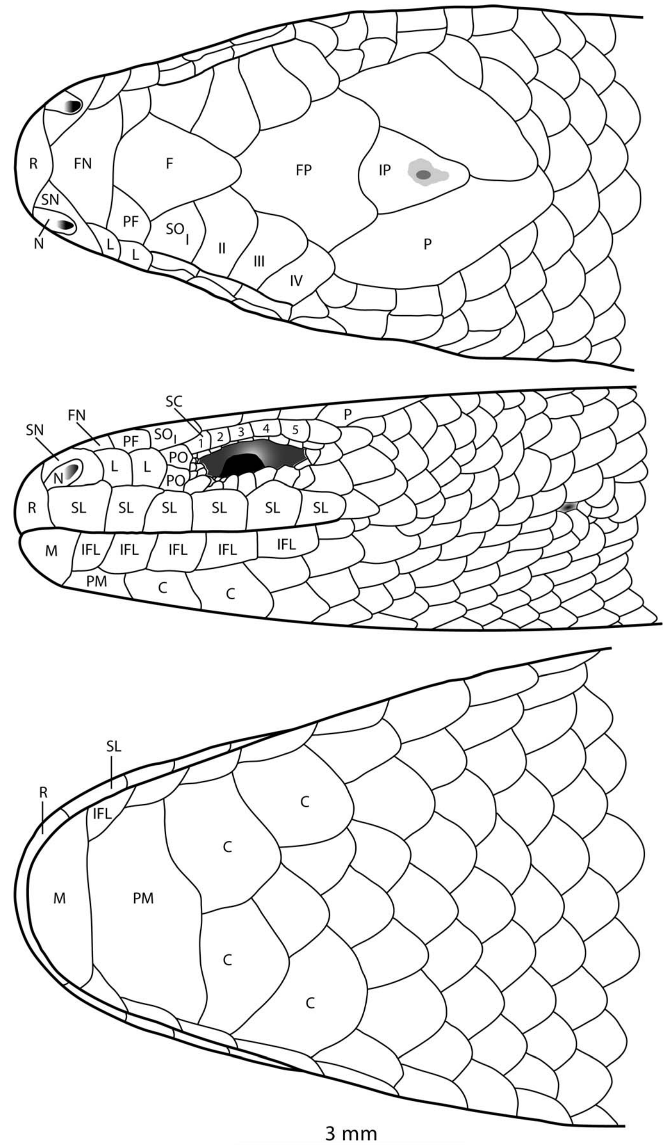

Fig. 3.—Illustrations of the head of *Lygosoma tabonorum* sp. nov. (holotype, PNM 9820) in dorsal, lateral, and ventral views. Taxonomically diagnostic head scales are labeled as follows: C = chin shield; F = frontal; FN = frontonasal; FP = frontoparietal; IFL = infralabial; IP = interparietal; L = loreal; M = mental; N = nasal; P = parietal; PF = prefrontal; PM = postmental; PN = postnasal; PO = preocular; R = rostral; SC = supraciliary; SL = supralabial; SN = supranasal; and SO = supraocular. Roman numerals indicate scales in the supraocular series, whereas Arabic numbers indicate scales in the supraciliary series. Illustrations by BBH and M.L. Penrod.

Barrio, Palawan Province, Palawan Island, Philippines, by A.C. Alcala and J.V. Vindum.

Diagnosis.—*Lygosoma tabonorum* can be distinguished from congeners by the following combination of morphological characters: (1) body size small (SVL = 60.0–79.0 mm); (2) limbs short (<5 mm); (3) SL 6 or 7; (4) IFL 5 or 6; (5) SC 5 or 6; (6) SO 4; (7) MBSRC 25 or 26; (8) AGSRC 83–90; (9) PVSRC 106–111; (10) prefrontal contact absent; and (11) single, enlarged, fused frontoparietal (Tables 1 and 2).

Comparisons.—*Lygosoma tabonorum* is phenotypically most similar to *L. quadrupes* sensu Linnaeus (1766), but it can be distinguished by having fewer AGSR (83–90 vs. 99–101) and PVSR (106–111 vs. 117–119), and fewer SC (5 or 6 vs. 7). Among other species of *Lygosoma* recognized to occur in Southeast Asia (*L. albopuncata*, *L. angeli*, *L. anguinum*, *L. bampfyldei*, *L. boehmei*, *L. bowringii*, *L. corpulentum*, *L. frontoparietale*, *L. haroldyoungi*, *L. herberti*, *L. isodactylum*, *L. koratense*, *L. lineolatum*, *L. opisthorhodum*, *L. popae*, *L. punctata*, and *L. veunsaiensis*), *L. tabonorum* differs on the basis of overall body size, relative limb lengths and a number of scale pattern characteristics (Tables 1 and 2).

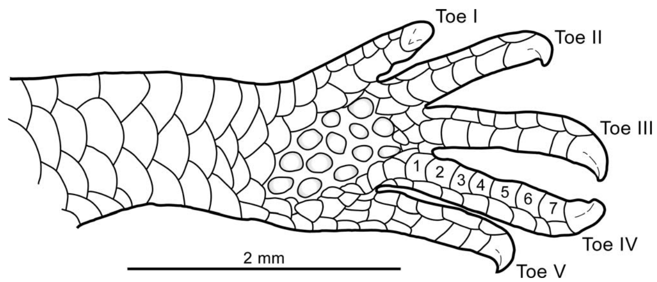

Fig. 4.—Illustration of the ventral surface of the foot of *Lygosoma tabonorum* sp. nov. (holotype, PNM 9820). Digit identities and Toe IV lamellae labeled for reference. Illustration by BBH and M.L. Penrod.

On the basis of body morphology, *L. tabonorum* can be distinguished from *L. albopunctata*, *L. anguinum*, *L. frontoparietale*, *L. lineolatum*, *L. popae*, and *L. veunaiensis* by having a larger SVL (60.0–79.0 mm vs. 35.0–47.0 mm [*L. albopunctata*], 35.0–58.0 mm [*L. anguinum*], 36.0–43.0 mm [*L. frontoparietale*], 44.0–55.0 mm [*L. lineolatum*], 46.0–57.0 mm [*L. popae*], 33.6 mm [*L. veunaiensis*]) and longer TL (55.0–72.0 mm vs. 33.0–37.0 mm [*L. albopunctata*], 40.0–55.0 mm [*L. anguinum*], 47.0–54.0 mm [*L. frontoparietale*], 34.0–45.0 mm [*L. lineolatum*], 35.0–42.0 mm [*L. popae*], 40.1 mm [*L. veunaiensis*]); from *L. boehmei*, *L. corpulentum*, and *L. koratense* by having a smaller SVL (60.0–79.0 mm vs. 86.0 mm [*L. boehmei*], 97.8–168.0 mm [*L. corpulentum*], 101.0–106.0 mm [*L. koratense*]) and shorter TL (55.0–72.0 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. opisthorhodum*, and *L. punctata* by having a smaller SVL (60.0–79.0 mm vs. 142.1 mm [*L. bampfyldei*], 114.8–148.0 mm [*L. haroldyoungi*], 82.5–117.0 mm [*L. isodactylum*], 93.0 mm [*L. opisthorhodum*], 85.0 mm [*L. punctata*]); and from *L. herberti* by having a slimmer body profile (AGD = 45.0–63.0 mm vs. 33.0–37.0 mm; MBW = 3.8–6.1 mm vs. 8.6–9.4 mm).

On the basis of limb morphology, the new species can be distinguished from *L. albopunctata*, *L. boehmei*, *L. corpulentum*, *L. frontoparietale*, *L. haroldyoungi*, *L. herberti*, *L. isodactylum*, *L. koratense*, and *L. veunaiensis* by having shorter relative FLL (FLL/SVL = 3.3–4.6% vs. 8.1–23.7% [*L. albopunctata*], 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*], 22.6–24.8% [*L. koratense*], 18.5% [*L. veunaiensis*]) and shorter relative HLL (HLL/SVL = 5.1–6.8% vs. 9.9–16.7% [*L. albopunctata*], 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*], 14.2–15.8% [*L. koratense*], 12.8% [*L. veunaiensis*]); and from *L. lineolatum* and *L. popae* by having shorter relative HLL (HLL/SVL = 5.1–6.8% vs. 7.9–10.9% [*L. lineolatum*], 7.6–8.8% [*L. popae*]).

FIG. 5.—The holotype of *Lygosoma tabonorum* sp. nov. (PNM 9820) in dorsal and ventral views. A color version of this figure is available online.

Lygosoma tabonorum differs from *L. boehmei*, *L. corpulentum*, *L. haroldyoungi*, *L. isodactylum*, and *L. koratense* by having shorter HL (4.1–5.6 mm vs. 12.3 mm [*L. boehmei*], 16.9–30.3 mm [*L. corpulentum*], 15.2–18.1 mm [*L. haroldyoungi*], 11.7–14.0 mm [*L. isodactylum*], 18.0–19.0 mm [*L. koratense*]) and shorter HW (3.9–7.8 mm vs. 10.5 mm [*L. boehmei*], 12.0–21.8 mm [*L. corpulentum*], 9.5–12.0 mm [*L. haroldyoungi*], 7.7–9.0 mm [*L. isodactylum*], 13.0 mm [*L. koratense*]); and from *L. angeli* and *L. herberti* by having a shorter HL (4.1–5.6 mm vs. 9.4–12.1 mm [*L. angeli*], 6.8–8.8 mm [*L. herberti*]).

On the basis of scale patterns and counts, *L. tabonorum* differs from *L. albopunctata* and *L. lineolatum* by having more MBSR (25 or 26 vs. 14 [*L. albopunctata*], 22–24 [*L. lineolatum*]), AGSR (83–90 vs. 37–49 [*L. albopunctata*], 57–72 [*L. lineolatum*]), and PVSR (106–111 vs. 59–71 [*L. albopunctata*], 78–93 [*L. lineolatum*]); from *L. frontoparietale* by having fewer MBSR (25 or 26 vs. 28 or 29), more AGSR (83–90 vs. 40 or 41), and more PVSR (106–111 vs. 60); from *L. bohemei*, *L. corpulentum*, *L. isodactylum*, and *L. koratense* by having fewer MBSR (25 or 26 vs. 32 [*L. bohemei*], 36–40 [*L. corpulentum*], 30–34 [*L. isodactylum*], 32–34 [*L. koratense*]) and more PVSR (106–111 vs. 66 [*L. bohemei*], 78–86 [*L. corpulentum*], 88–98 [*L. isodactylum*], 63 [*L. koratense*]); from *L. anguinum*, *L. bowringii*, *L. herberti*, and *L. popae* by having more AGSR (83–90 vs. 69–76 [*L. anguinum*], 21–46 [*L. bowringii*], 37 [*L. herberti*], 68–72 [*L. popae*]) and PVSR (106–111 vs. 90–99 [*L. anguinum*], 51–71 [*L. bowringii*], 54–58 [*L. herberti*], 90–96 [*L. popae*]); from *L. angeli* by having fewer MBSR (25 or 26 vs. 30); from *L. popae* by having more AGSR (83–90 vs. 68–72) and PVSR (106–111 vs. 90–96); from *L. veunaiensis* by having more MBSR (25 or 26 vs. 22) and PVSR (106–111 vs. 51); and from *L. punctata* by having more PVSR (106–111 vs. 62–76).

The new species further differs from *L. albopunctata*, *L. boehmei*, *L. bowringii*, *L. corpulentum*, *L. frontoparietale*, *L. herberti*, and *L. koratense* by having fewer F3lam (5 or 6 vs. 8–10 [*L. albopunctata*], 8–10 [*L. boehmei*], 7–12 [*L. bowringii*], 9 or 10 [*L. frontoparietale*], 11 or 12 [*L. herberti*], 9 [*L. koratense*]) and T4lam (6 or 7 vs. 13–16 [*L. albopunctata*], 14 [*L. boehmei*], 10–17 [*L. bowringii*], 13–15 [*L. frontoparietale*], 15 [*L. herberti*], 13 or 14 [*L. koratense*]); and from *L. anguinum*, *L. corpulentum*, *L. popae*, *L. punctata*, and *L. veunaiensis* by having fewer T4lam (6 or 7 vs. 8 [*L. anguinum*], 11–15 [*L. corpulentum*], 8 or 9 [*L. popae*], 11–14 [*L. punctata*], 9 [*L. veunaiensis*]).

Lygosoma tabonorum can be distinguished from *L. boehmei* and *L. koratense* by having fewer IFL (5 or 6 vs. 7 [*L. boehmei* and *L. koratense*]); from *L. haroldyoungi* and *L. isodactylum* by having fewer SC (5 or 6 vs. 7 [*L. haroldyoungi* and *L. isodactylum*]); from *L. koratense* by having fewer SL (6 or 7 vs. 8); from *L. veunaiensis* by having a greater number of SL (6 or 7 vs. 5); from *L. lineolatum* by having fewer SC (5 or 6 vs. 7 or 8); from *L. albopunctata* by the presence of a single, enlarged, fused FP (vs. distinct pair or lack of frontoparietals); and from *L. frontoparietale* by the presence of contact medially between enlarged, first chin shield pair (vs. no contact).

Description of holotype.—Adult male; hemipenes everted, visible; body small, slender, SVL = 69.0 mm; head weakly differentiated from neck and roughly equal in width to body, HW 6.8% SVL, 88.4% HL; snout rounded in dorsal and lateral profile, SNL 48.8% HL; ear opening small; eyes small, ED 26.9% HL, 79.4% END; body moderately depressed, nearly uniform in thickness, MBW 137.4% MBD; scales smooth, glossy, imbricate; MBSRC 26; PVSRC 110; AGSRC 89; limbs short, diminutive, pentadactyl; F3lam five, T4lam seven (Fig. 4); FLL 6.5% AGD, 4.6% SVL; HLL 9.0% AGD, 6.4% SVL; tail nearly as wide as body, gradually tapered towards end, TW 80.0% MBW, TL 89.9% 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 posterodorsal portion of single nasal, longer axis directed posterodorsally and anteroventrally; supranasals present; postnasals absent; prefrontals small, widely separated, right prefrontal fused partially to frontonasal; frontal roughly diamond shaped, its anterior margin in broad contact with frontonasal, in contact with first two anterior supraoculars, 3.5× larger than anterior supraocular; supraoculars four; frontoparietals fused into single large scale, in contact with supraoculars two, three, and four; interparietal small, shorter than frontoparietal, longer than wide, triangular shaped, wider anteriorly, pineal eyespot circular, visible in posterior portion of interparietal; parietals in broad contact behind interparietal; enlarged nuchals absent; loreals two, posterior loreal slightly longer and higher than anterior loreal; preocular two; presubocular one; supraciliaries five, the anteriormost contacting prefrontal and separating posterior loreal from first supraocular, posteriormost extending to posterior edge of fourth supraocular; subocular scale row complete, in contact with supralabials; lower eyelid with one complete row of scales; supralabials six, first 1.5× width of others, fourth and fifth subocular; infralabials five (Fig. 3).

Mental wider than long, in contact with first infralabial; postmental single, enlarged, its width greater than width of mental; followed by two pairs of enlarged chin shields, first pair in contact, second pair moderately separated by single medial scale, second pair larger than first pair (Fig. 3). Scales on limbs smaller than body scales.

Measurements of holotype (mm).—SVL 69.0; AGD 49.0; MBW 4.8; MBD 3.5; TL 62.0; TW 3.9; TD 3.2; HL 5.3; HW 4.7; HD 3.3; ED 1.4; END 1.8; SNL 2.6; IND 1.5; FLL 3.2; HLL 4.4. MBSRC 26; AGSRC 89; PVSRC 110; F3lam 5; T4lam 7; SL 6; IFL 5; SO 4; SC 5.

Coloration of holotype in preservative (Fig. 5).—The dorsal, lateral, and ventral portions of the trunk are a light brown with darker speckling, and ventral surfaces are lighter than the dorsal and lateral regions. Under magnification, speckles are composed of clusters of many small, milky darker pigment spots bordering each scale. The supralabials are a slightly darker shade than the trunk of the body. Supraoculars have a darker fuscous shade than the trunk of the body. Coloration in life is unrecorded.

Variation.—Among the 13 specimens examined, we observed variation in the numbers of supralabials, infralabials, supraciliaries, and nuchal presence. The number of SL varied between six (CAS 157345, PNM 9820) and seven (CAS 28465, 152030, 152032; MCZ 26514, 26521, 26523, 26525, 183651; PNM 9821, 9824, 9825); IFL varied between five (CAS 157345, PNM 9820, 9821) and six (CAS 28465, 152030, 152032; MCZ 26514, 26521, 26523, 26525, 183651; PNM 9824, 9825); and SC varied between five (MCZ 26521, 26523, 26525; PNM 9820) and six (CAS 28465, 152030, 152032, 157345; MCZ 26514, 183651; PNM 9821, 9824, 9825). The enlarged, differentiated nuchal is present in some specimens (CAS 152030, 152032; MCZ 26514, 26521, 26523, 26525 183651; PNM 9824, 9825), but absent in others (CAS 28465, 157345; PNM 9820, 9821).

Etymology.—We derived the new species' name in reference to the modern human (*Homo sapiens*) population that inhabited central Palawan Island, at the Municipality of Quezon, 24,000–22,000 yr before present (Fox 1970, 1978). Constituting the celebrated "Tabon Man," Palawan human remains formerly were believed to represent the earliest documented evidence of human habitation in the archipelago. Although other northern Philippine localities are now recognized to possess the most ancient *H. sapiens* fossils, human paleontology and the search for "The first Filipino" had its inception in the Tabon Caves complex with the work of the National Museum of the Philippines in the late 1960s (Fox 1970, 1978). The specific epithet is masculine and plural, referring to the population of humans that inhabited the Tabon Caves complex. Suggested common name: Palawan Supple Skinks.

Distribution.—*Lygosoma tabonorum* is known only from Palawan and Cuyo islands in the Palawan PAIC of the Philippines (Fig. 2).

Genetic diversity.—Analysis of mitochondrial and nuclear sequences indicates the genetic distinctiveness of *L. tabonorum* from *L. quadrupes* of Java, Indonesia. Uncorrected pairwise sequence divergences observed are low within *L. tabonorum* (ND1, 0.3–1.6%; R35, 0.0%) and high between these two lineages (ND1, 8.9–9.8%; R35, 0.8%).

Natural history.—Relatively little primary forest remains on the islands of the Palawan PAIC. Although we suspect that *Lygosoma tabonorum* once occurred in low- to mid-elevation primary forest habitats, all recent observations of this species are from secondary growth forests. The species seems to be common in decaying logs and root networks around trees in forest fragments. Individuals of the species were observed during daytime surveys after rotting log microhabitats were overturned by raking efforts. Once disturbed, individuals would move quickly in a serpentine motion to burrow into loose organic material and soil substrate. Only a single additional species of *Lygosoma* is recognized from the Palawan PAIC, *L. bowringii*, with both species occurring in sympatry at several sites in central Palawan Island. Although the reproductive mode of the new species remains unrecorded, we assume that the species is oviparous like many members of the genus (Taylor 1963; Teynié et al. 2004; Grismer et al. 2007; Das 2010; Teynié and David 2010; Geissler et al. 2011).

This species does not qualify for Critically Endangered, Endangered, Vulnerable, or Near Threatened status based on the following criteria (IUCN 2015): (1) no data indicating there has been a reduction in population size for the species; (2) the area of occupancy for the species is estimated to be >2000 km^2; (3) the species is known to exist in multiple localities; (4) no evidence exists for population declines or fluctuations through time; and (5) the species was found to be quite common at the type locality; thus, populations are inferred to be healthy. Although *L. tabonorum* is only known from two islands in the Palawan PAIC, the species seems to be relatively common in secondary growth forests of Palawan Island. We suggest that it is more widespread than available data indicate and, until additional data are available, we classify this species as Least Concern, LC (IUCN 2015).

Discussion

The description of *Lygosoma tabonorum* from Palawan and Cuyo islands brings the total number of species in the genus to 30, of which 18 occur in Southeast Asia (Uetz and Hošek 2016). *Lygosoma tabonorum* is the first Philippine endemic species within the genus. Based on our current understanding of species-level diversity within the ecologically similar *Brachymeles* in the Philippines (Davis et al. 2014), we anticipate the description of additional cryptic species among the members of the *L. quadrupes* species complex, with additional study of molecular and morphological analyses.

Although both *Brachymeles* and *Lygosoma* occur in the Philippines, they are nearly allopatric in their distributions (Fig. 1). The one exception seems to be the presence of both *L. bowringii* and *B. vermis* on Tawi-tawi Island in the Sulu Archipelago. Interestingly, Huxley's Line (Huxley 1868), a modification of Wallace's Line (Wallace 1860, 1876, 1881), largely separates the diversity of both genera (Fig. 1). Only three species contradict this pattern: *B. apus* from northern Borneo; *B. miriamae* from Thailand; and *L. bowringii* from the Sulu Archipelago in the southern Philippines and Sulawesi, Indonesia. Species of both genera seem to occupy a similar ecological niche of dry, rotting, wooden material and leaf litter (Davis et al. 2014; personal observations). Studies that explore the ecology and species-level diversity of both genera will help clarify the biogeographic patterns observed in this region of the Old World tropics. Without robust, time-calibrated phylogenetic studies of either genus, it remains to be seen whether Philippine lineages were the result of ancient diversification events (Blackburn et al. 2010; Siler et al. 2012a), or represent more recent arrivals via recognized dispersal corridors to the Philippines (Brown et al. 2013).

The species richness of *Lygosoma* remains poorly understood, with uncertainty primarily among higher level relationships with closely allied genera (e.g., *Mochlus*, *Lepidothyris*; Datta-Roy et al. 2014), as well as the continued recognition of widespread species that likely represent complexes of multiple, distinct evolutionary lineages (e.g., *L. bowringii*, *L. quadrupes*). Increased survey work throughout the range of these species, and focused assessment of morphological variation among allopatric populations in disparate ecoregions of Southeast Asia, would improve our understanding of species boundaries and levels of undescribed diversity. For example, although populations of *L. quadrupes* occur in Cambodia, southern China, Indonesia, Laos, Peninsular Malaysia, Thailand, and Vietnam (Geissler et al. 2011; Fig. 1), it is peculiar that the species has yet to be documented on Borneo, despite observations of other members of *Lygosoma* on the island (e.g., *L. bampfyldei*, *L. bowringii*). As vouchered genetic data become available, inter- and intraspecies phylogenetic and population genetic studies will facilitate an understanding of the biodiversity patterns for this genus of burrowing skinks.

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Appendix

Specimens Examined

Numbers in parentheses indicate the number of specimens examined. Several sample sizes are greater than those observed in the description because of the examination of subadult specimens, which were excluded from morphometric analyses. Within the locality string for each specimen, countries are written in 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 albopunctata (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).

Lygsoma 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 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).

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