

A New *Gekko* from Sibuyan Island, Central Philippines

Author(s) :Rafe M. Brown, Cameron D. Siler, Carl H. Oliveros, Arvin C. Diesmos, and Angel C. Alcala

Source: *Herpetologica*, 67(4):460-476. 2011.

Published By: The Herpetologists' League

DOI: 10.1655/HERPETOLOGICA-D-11-00025.1

URL: <http://www.bioone.org/doi/full/10.1655/HERPETOLOGICA-D-11-00025.1>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

A NEW GEKKO FROM SIBUYAN ISLAND, CENTRAL PHILIPPINES

RAFE M. BROWN^{1,5}, CAMERON D. SILER¹, CARL H. OLIVEROS^{1,2}, ARVIN C. DIESMOS³, AND
ANGEL C. ALCALA⁴

¹Natural History Museum, Biodiversity Institute & Department of Ecology and Evolutionary Biology, The University of Kansas, Lawrence, KS 66045, USA

²Isla Biodiversity Conservation, 9 Bougainvillea Street, Manuela Subdivision, Las Piñas City 1741, Philippines

³National Museum of the Philippines, Rizal Park, Padre Burgos Avenue, Ermita 1000, Manila, Philippines

⁴Angelo King Center for Research and Environmental Management, Silliman University, Dumaguete City 6200, Philippines

ABSTRACT: We describe a new species of lizard in the genus *Gekko* from Sibuyan Island in the Romblon Island group of the central Philippines. Although the new species is diagnosed from other Philippine *Gekko* by body size and shape, coloration, and multiple characteristics of external morphology, additional support for the recognition of the Sibuyan *Gekko* population as a distinct evolutionary lineage is garnered from DNA sequence data and biogeographical inference. The new species has been collected on trunks of trees or on granitic rocks along rivers in mature, lowland forest, and on vegetation at forest edges bordering agricultural areas. It is known only from Sibuyan Island and is undoubtedly endemic to this single small, isolated landmass. Although the larger, topographically complex islands of the Philippines have been the targets of numerous recent efforts to estimate vertebrate species diversity, smaller islands of the archipelago have received comparatively less attention and may support significant levels of underappreciated vertebrate diversity.

Key words: Gekkonidae; New species; Philippines; Romblon Island Group; Sibuyan Island

RECENTLY, enhanced survey efforts, careful scrutiny of widespread species, and use of molecular sequence data in combination with traditional morphological characters, have resulted in a dramatic increase in the diversity of gekkonid lizards in the Philippines. The archipelago is now known to support 10 genera and at least 48 gekkonid species assigned to the genera *Cyrtodactylus* (9 species), *Gekko* (12–13), *Gehyra* (1), *Hemidactylus* (5; including *platyurus*, a species formerly assigned to *Cosymbotus*), *Hemiphyllodactylus* (2), *Lepidodactylus* (6), *Lupeirosaurus* (8), *Pseudogekko* (4), and *Ptychozoon* (1) (Brown, 1999; Brown and Alcala, 1978; Brown and Diesmos, 2000; Brown et al., 1997, 2007, 2008, 2009, 2011; Gaulke et al., 2007; Linkem et al., 2010; Taylor, 1922a,b; Welton et al., 2009, 2010a,b; Zug, 2010).

Ten species of *Gekko* are considered endemic to the archipelago (Brown et al., 2009; Linkem et al., 2010) and two additional species with broad geographic distributions (*G. gekko*, *G. monarchus*) are also known from the country (Brown and Alcala, 1978; Ota et al., 1989; Taylor, 1922a,b). Although past treatments have included *G. hokouensis* as part of the Philippine

gekkonid fauna (Brown and Alcala, 1978), Ota et al. (1989) demonstrated that this taxon's inclusion in Philippine faunal accounts is likely in error. Similarly, the single Mindanao Island record for *Perochirus ateles* (Boulenger, 1885; Brown and Alcala, 1978; Duméril, 1856; Taylor, 1922a) has not been confirmed in the last 150 yr despite our recent field surveys in and around the type locality (Zamboanga), suggesting that it too may be in error (Bauer and Henle, 1994; Brown, 1976; Welton et al., 2010a).

The 10 endemic Philippine species of *Gekko* are *G. athymus* (Brown and Alcala, 1962), *G. carusadensis* (Linkem et al., 2010), *G. crombota* (Brown et al., 2008), *G. ernstkelleri* (Rösler et al., 2006), *G. gigante* (Brown and Alcala, 1978), *G. mindorensis* (Taylor, 1919), *G. palawanensis* (Taylor, 1925), *G. porosus* (Taylor, 1922b), *G. romblon* (Brown and Alcala, 1978), and *G. rossi* (Brown et al., 2009). These species represent a considerable range in body size, general appearance, and ecological attributes, but all possess the following combination of morphological traits: (1) body size moderate, with relatively long, slender limbs; (2) near complete absence of interdigital webbing or cutaneous body expansions; (3) dorsal tubercles arranged in longitudinal rows (except for *G. athymus*,

⁵ CORRESPONDENCE: e-mail, rafe@ku.edu

in which dorsal tuberculation is absent); (4) scales of dorsum between tubercle rows minute, nonimbricate; (5) scales of venter enlarged, imbricate, flat; (6) differentiated postmentals longitudinally elongate; and (7) subcaudals transversely enlarged, platelike (Brown and Alcalá, 1978; Brown et al., 2007, 2008, 2009).

Our survey work in the Romblon Island Group of central Philippines has resulted in the discovery of a new species of morphologically and genetically distinct *Gekko* related to *G. romblon*. In this article we use a combination of body size and shape information, meristic data of external morphology (scale counts), genetic sequence data, and inferences from the geological history of the archipelago to demonstrate that the Sibuyan Island *Gekko* population represents a distinct evolutionary lineage (de Queiroz, 1998, 1999; Wiley, 1978), worthy of specific rank.

MATERIALS AND METHODS

Morphology

We (RMB and CO) collected data from fluid-preserved specimens deposited in US and Philippine collections (see Appendix; institutional abbreviations follow Leviton et al., 1985). Sex was determined by inspection of gonads or by scoring of prominent secondary sexual characteristics (Brown, 1999; Brown et al., 1997, 2008, 2009, 2010) when dissection was not possible. Measurements (to the nearest 0.1 mm) were taken with digital calipers following character definitions by Brown (1999), and Brown et al. (2008, 2009). Characters include: snout-vent length, tail length, head length; head width, head depth, snout length, eye diameter, eye-narial distance, internarial distance, interorbital distance, axilla-groin distance, femur length, tibia length, upper arm length, forearm length, Toe I length, Toe IV length, tail width, tail depth, number of supralabials and infralabials posteriorly to the point at which point labials are no longer differentiated, enlarged prelocofemoral pore-bearing (males) or dimpled (females) scales, differentiated subdigital scensors beneath Finger III and Toe IV, midbody dorsal and ventral transverse scale rows between lateral body folds, midbody dorsal transverse

tubercle rows between dorsolateral body folds, undifferentiated paravertebrals and tubercle rows between midpoints of limb insertions, and midventrals between limb insertion.

Molecular Data

Because our primary goal was to estimate phylogenetic relationships among the island populations of *Gekko* in the Romblon Island group, we sequenced only 2–4 exemplars per species and selected only three outgroup taxa (*G. gekko*, *G. mindorensis*, and *G. monarchus*) based on relationships presented in a recent phylogenetic analysis of northern Philippine gekkonid lizards (Brown et al., 2009). A total of seven ingroup samples were used to estimate phylogenetic relationships of the Romblon Province *Gekko* populations.

Genomic DNA was extracted from liver tissues stored in 95–100% ethanol following the guanidine thiocyanate protocol of Esselstyn et al. (2008). For all 12 samples, the mitochondrial gene NADH Dehydrogenase Subunit 2 (ND2) and components of three flanking transfer RNA genes (tRNA^{trp}, tRNA^{ala}, tRNA^{asn}) were sequenced by the primers, thermal profiles, and purification and sequencing protocols of Brown et al. (2009) and Macey et al. (1999). Purified product was analyzed with an ABI Prism 3130×1 Genetic Analyzer (Applied Biosystems). Newly sequenced data were deposited in GenBank under accession numbers JN710488–506. Gene sequence contigs were assembled and edited with the use of Sequencher 4.8 (Gene Codes Corp., Ann Arbor, MI). Initial sequence alignments were produced in Muscle (Edgar, 2004), and manual adjustments were made in MacClade 4.08 (Maddison and Maddison, 2005).

Phylogenetic Analysis

Partitioned Bayesian analyses were conducted in MrBayes v3.1.2 (Ronquist and Huelsenbeck, 2003) for the combined data set. The mitochondrial data set was partitioned by codon position for the protein-coding region of ND2, and the three flanking tRNAs (tRNA^{trp}, tRNA^{ala}, tRNA^{asn}) were analyzed as a single subset. The Akaike Information Criterion (AIC), as implemented in jModeltest v0.1.1 (Guindon and Gascuel, 2003; Posada, 2008), was used to select the best model of nucleotide substitution for each

TABLE 1.—Models of evolution selected by Akaike Information Criterion for partitioned, model-based phylogenetic analyses. General time reversible (GTR) model with a gamma-distributed rate variation among sites (Γ) was applied for all data partitions in partitioned maximum-likelihood analyses.

Partition	AIC model	Number of characters
NADH 2, first codon position	GTR + Γ	346
NADH 2, second codon position	GTR + Γ	346
NADH 2, third codon position	GTR + Γ	346
tRNAs Trp, Ala, Asn	HKY + Γ	223

partition (Table 1). The best-fit models for each codon position of ND2, and for the combined tRNA data, were the general time reversible (GTR) model with a gamma-distributed rate variation among sites (Γ) and the Hasegawa, Kishino, and Yano (HKY) model with a gamma-distributed rate variation among sites (Γ), respectively. 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 four independent Metropolis-coupled MCMC analyses, each with four chains and an incremental heating temperature of 0.05, and an unconstrained branch length prior with an exponential distribution of 25 (Marshall, 2010; Marshall et al., 2006; Siler et al. 2010, 2011). All analyses were run for 25 million generations, sampling every 5000 generations. To assess stationarity, all sampled parameter values and log-likelihood scores from the cold Markov chain were plotted against generation time and compared among independent runs using Tracer v1.4 (Rambaut and Drummond, 2007). Finally, we plotted the cumulative and nonoverlapping split frequencies of the 20 most variable nodes, and compared split frequencies among independent runs with the use of Are We There Yet? (AWTY; Wilgenbusch et al., 2004). Although all samples showed patterns consistent with stationarity after 2.5 million generations (i.e.,

the first 10.0%), we conservatively discarded the first 20% of samples as burn-in.

Partitioned maximum-likelihood (ML) analyses were conducted in RAxMLHPC v7.0 (Stamatakis, 2006) for all three data sets under the same partitioning strategy as for Bayesian analysis. The more complex model (GTR + Γ) was used for all subsets, and 100 replicate ML inferences were performed for each analysis. Each inference was initiated with a random starting tree, and employed a rapid hill-climbing algorithm (Stamatakis et al., 2007). Clade support was assessed with 1000 bootstrap pseudoreplicates, employing a rapid bootstrapping algorithm (Stamatakis et al., 2008).

Species Concept

For the recognition of the new species, we adopted the general lineage species concept of de Queiroz (1998, 1999) as the natural extension of the evolutionary species concept (Wiley, 1978). Application of lineage-based species concepts to central Philippine island endemics is nonproblematic (Brown and Diesmos, 2002; Brown and Guttman, 2002) because of the known history of isolation of island populations (Hall, 1998, 2002; Voris, 2000; Yumul et al., 2003, 2009). We consider as new species morphologically diagnosable lineage segments (either in isolation or sympatry) in which the hypothesis of conspecificity can be confidently rejected by

TABLE 2.—Uncorrected pairwise sequence divergence (%) for molecular data for *Gekko coi*, *G. romblon*, *G. mindorensis*, *G. monarchus*, and *G. gecko* (Fig. 1). Percentages on the diagonal represent intraspecific genetic diversity (bolded for emphasis).

	<i>Gekko coi</i>	<i>G. romblon</i>	<i>G. mindorensis</i>	<i>G. monarchus</i>
<i>G. romblon</i>	7.0–7.4	0.0–3.9		
<i>G. mindorensis</i>	19.1	19.1–19.3	0.2	
<i>G. monarchus</i>	19.0	18.8–19.1	14.7–14.8	0.0
<i>G. gecko</i>	28.6	28.7–28.8	28.1–28.2	28.3

discrete character differences, especially when taxonomic decisions are bolstered by genetic data and biogeographic information.

RESULTS

Morphology

Our surveys of mensural and meristic data recover instances of discrete, nonoverlapping ranges of variation in multiple characters of external morphology (Table 3) between Romblon + Tablas island populations (*G. romblon*) and the population of *Gekko* from Sibuyan Island (*Gekko* sp. nov.). The putative new species from Sibuyan is readily diagnosed from all Philippine congeners (see below) on the basis of body size and shape, coloration, and numerous characteristics of external morphology. The new species is easily diagnosed from its closest relative *G. romblon* on the basis of body shape, coloration, and discrete, diagnostic, characteristics of scalation (Table 3).

Phylogeny and Genetic Divergence

The ML analysis resulted in a single optimal tree ($-\ln L = 4129.152041$; Fig. 1). Trees estimated from ML and Bayesian analyses are consistent with respect to support for two unique species of *Gekko* distributed in the Romblon Island group. All analyses recover the Sibuyan Island population of *Gekko* as a lineage distinct from (but sister to) a clade consisting of the Tablas and Romblon island populations (e.g., *G. romblon* sensu stricto; Fig. 1). Uncorrected pairwise sequence divergences are low within *G. romblon* and include a moderately shallow ($\leq 3.9\%$) genetic divergence between Romblon and Tablas island populations. In contrast, these island populations exhibit relatively higher genetic divergence (7.0–7.4%) from the Sibuyan Island lineage (Table 2; Fig. 1).

SYSTEMATICS

Gekko coi sp. nov.

Figs. 2–5

Holotype.—PNM 9765 (Field no. RMB 2961; formerly KU 326208), an adult male collected by ACD at 2330 h on 2 January 2001 on a large stream-side boulder near sea level in mixed second growth and primary forest at Barangay

Tampayan, Municipality of Magdiwang, Romblon Province, northeast coast of Sibuyan Island, Philippines (12.486°N, 122.516°E; datum = WGS84).

Paratypes.—FMNH 251114–15, adult females, collected 17 and 18 March, 1992, by N. Ingle and S. Goodman on Mt. Guiting-guiting, Barangay Tampayan, Municipality of Magdiwang; CAS 139180, adult male collected by L. C. Alcala and party on 9 May 1972 at Taclobo Barrio, Municipality of San Fernando (paratype of *G. romblon*); CAS 139181, a juvenile, same collection data, but 12 May 1972 (paratype of *G. romblon*); CAS139182 (paratype of *G. romblon*) and CAS 155896, adult male, collected by L. C. Alcala and party on 13 May 1972, at Cansampay River, Taclobo Barrio, Municipality of San Fernando.

Diagnosis.—*Gekko coi* differs from all other species of Philippine *Gekko* (i.e., *G. athymus*, *G. carusadensis*, *G. crombota*, *G. ernstkelleri*, *G. gekko*, *G. gigante*, *G. mindorensis*, *G. monarchus*, *G. palawanensis*, *G. porosus*, *G. romblon*, and *G. rossi*) in having the following combination of diagnostic traits: (1) moderately large body size (snout–vent length [SVL] 65.2–84.0 for adult males, 72.1–77.1 mm for females); (2) dorsum medium brown to gray, with single row of alternating light (cream) and dark (dark brown) vertebral blotches; (3) high numbers of dorsal body scales (107–132 transverse midbody scales, 192–226 paravertebrals); (4) relatively few rows of conical body tubercles (13–15 midbody, 25–28 paravertebrally); (5) precloacofemorals in a continuous series (precloacals and femoral pore-bearing scale series distinctly differentiated but abutting with no undifferentiated scales interrupting the two series) of 86–92 differentiated, greatly enlarged (precloacals) to only slightly enlarged (femorals) scales.

Comparison with similar species.—*Gekko coi* differs from its phenotypically most similar and geographically most proximate Philippine congener (*G. romblon*) by its relatively elongate, slender body, and narrow head (versus more robust body, wide head, characterized by distinctly hypertrophied adductor musculature; Fig. 2), possession of 86–92 (versus 64–79 in *G. romblon*) differentiated precloacofemoral pore-bearing scales, 34–43 (versus 43–53) midbody ventrals, and by

TABLE 3.—Distribution of selected diagnostic characters in *Gekko coi* and other Philippine species of *Gekko*. Entries are presented in millimeters; all specimens are considered adults (data from juveniles excluded). Characters (following Linkem et al., 2010, and Brown et al., 2009) include (1) dorsal body coloration, (2) dorsal tail coloration, the numbers of (3) supralabials, (4) differentiated preacromiolar pore-bearing scales, (5) scensors below Toe IV, (6) white postorbital spots (+, present; -, absent), (7) midbody dorsals, (8) midbody ventrals, (9) midbody dorsal tubercle rows, (10) paravertebral tubercle rows, (11) ventrals, and (12) paravertebrals.

	N	Male snout-vent length	Female snout-vent length	1	2	3	4	5	6	7	8	9	10	11	12
<i>Gekko coi</i>	3 males; 3 females	65.2–84.0	72.1–77.1	Light and dark vertebral blotches	Alternating light and dark bands	12–15	85–92	16–18 +	99–106	39–43	13–15	25–28	77–88	178–185	
<i>G. romblon</i>	8 males; 4 females	78.7–87.1	71.0–81.0	Light and dark vertebral blotches	Gray-brown with thin white bands	12–14	66–79	14–18 +	102–129	43–53	12–16	22–34	84–94	193–231	
<i>G. athymus</i>	3 males; 2 females	99.2–119.9	88.2–117.1	Light and dark inverted V-shaped bands	Dark brown with yellow bands	11–13	20–24	18–22 –	92–104	30–36	–	–	66–72	66–72	
<i>G. carusardus</i>	6 males; 2 females	83.4–97.2	79.9–87.5	Small dark mottling	Alternating light and dark bands	12–14	46–50	18–20 –	90–106	38–47	14–17	25–28	–	179–190	
<i>G. crombota</i>	4 males; 9 females	85.5–117.9	85.1–106.9	Light trilobed bars	Alternating light and dark bands	13–15	58–74	15–18 –	107–132	38–42	18–22	29–33	67–85	192–226	
<i>G. ernstkelleri</i>	4 males; 6 females	82.0–92.1	78.0–88.0	White circular spots	Dark gray with bold white bands	15, 16	36–42	17–19 +	112–127	42–48	10–16	17–25	58–62	178–200	
<i>G. gekko</i>	6 males; 7 females	120.1–166.1	119.2–144.1	Rust-colored spots	Alternating light and dark bands	12–14	12–20	17–20 –	94–106	30–35	10–12	18–22	60–64	91–102	
<i>G. gigante</i>	5 males; 3 females	89.7–104.7	79.7–87.9	Dark paired blotches	Light brown with white bands	11–13	52–66	16–19 –	123–135	41–50	12–18	19–28	65–74	175–207	
<i>G. mindorensis</i>	22 males; 13 females	55.0–88.2	68.2–70.9	Dark thin transverse bands	Alternating light and dark bands	11–13	52–66	12–14 –	102–125	40–47	16–20	17–26	58–63	180–195	
<i>G. monarchus</i>	13 males; 10 females	56.2–80.7	40.6–69.7	Dark transverse spot rows	Dark gray with light gray bands	11–13	31–40	13–15 –	96–112	38–44	16–20	18–23	57–61	171–203	
<i>G. palawanensis</i>	3 males; 4 females	57.2–65.7	44.5–61.8	Dark paired spots	Alternating light and dark bands	12–14	64–70	16–19 –	114–121	38–43	10–20	23–27	54–58	155–170	
<i>G. porosus</i>	3 males	91.0–96.7	91.0–96.7	Indistinct transverse dark bands	Alternating light and dark bands	12, 13	74–80	14–16 –	88–103	35–40	15–17	17–24	64–74	173–191, 173–191	
<i>G. rossi</i>	8 males; 8 females	95.5–108.2	86.8–100.0	Dark transverse bars and light spots	Alternating light and dark bands	13–16	77–88	10–16 –	125–170	33–41	16–18	31–37	74–104	251–281	

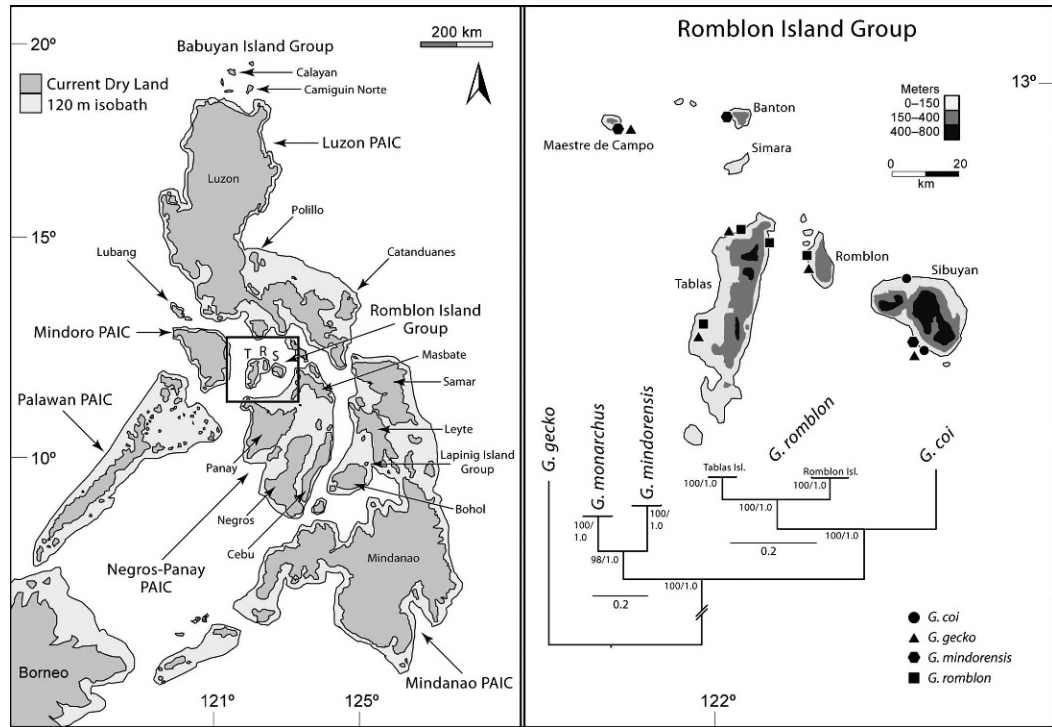


FIG. 1.—Map of Romblon Province (right panel) in relation to the remainder of the Philippines (left). Known distribution of *Gekko* species in the province is indicated with symbols (key, lower right) plotted at collection localities. A maximum-likelihood estimate of phylogeny (with ML bootstraps/Bayesian posterior probabilities included on internodes) is presented on right. Scale bars = substitutions/site.

178–185 (versus 193–231) paravertebrals. Enlarged rows of chin shields ventral to the infralabials are smaller on *G. coi* such that three enlarged subinfralabials contact infralabials 2–4 (versus only two scales contacting infralabials 2–4 in most specimens of *G. romblon*). Additionally, dorsal tail coloration of the *G. romblon* holotype (CAS 139190) and 70% of the remaining specimens from Romblon and Tablas islands is flat gray with thin white transverse lines (versus 100% of specimens with thick caudal bars of contrasting light and dark in *G. coi*). Finally, *G. coi* is distinguished from *G. romblon* by the presence (versus absence) of distinct, bold, black, irregularly shaped markings throughout the dorsal surfaces of the body, limbs, and head (Fig. 2).

Body size separates *G. coi* from the larger species *G. athymus*, *G. gecko*, *G. crombota*, *G. porosus*, and *G. rossi*, and the smaller species *G. palawanensis* (Table 3); dark reddish-brown dorsum with light and dark vertebral

spots and a large, prominent, postorbital spot distinguishes *G. coi* from all Philippine congeners except *G. romblon*; the number of precloacofemorals distinguishes *G. coi* from *G. athymus*, *G. carusadensis*, *G. crombota*, *G. ernstkelleri*, *G. gecko*, *G. gigante*, *G. mindorensis*, *G. monarchus*, *G. palawanensis*, and *G. porosus*. Midbody ventrals distinguish *G. coi* from *G. athymus*, *G. carusadensis*, *G. crombota*, *G. ernstkelleri*, *G. gecko*, *G. gigante*. Midbody dorsal tubercle rows distinguish *G. coi* from *G. crombota*, *G. mindorensis*, *G. monarchus*, and *G. rossi*, and paravertebral tubercle rows distinguish *G. coi* from *G. ernstkelleri*, *G. crombota*, *G. gecko*, *G. monarchus*, *G. porosus*, and *G. rossi*. Finally, the number of ventrals distinguishes *G. coi* from *G. athymus*, *G. ernstkelleri*, *G. gecko*, *G. gigante*, *G. mindorensis*, *G. monarchus*, *G. palawanensis*, and *G. porosus*, paravertebral separate *G. coi* from *G. athymus*, *G. crombota*, *G. gecko*, *G. palawanensis*,



FIG. 2.—*Gekko coi* male holotype (PNM 9765; A, B) in life; adult male *G. romblon* (KU 303978) from Romblon Island (C, D). (For interpretation color in this figure, see the online version of this article.)

and *G. rossi*. These and other differences among Philippine *Gekko* species are summarized in Table 3.

Description of holotype.—Adult male in excellent condition (Figs. 2A,B, 3A,B), with a small incision in the sternal region (portion of liver removed for genetic sample), and hemipenes fully everted. SVL 84.1 mm; habitus slender, limbs well developed, relatively slender; tail relatively long; margins of limbs smooth, lacking cutaneous flaps or dermal

folds; a thin adipose line (cutaneous fold) running along ventrolateral margin of trunk.

Head moderate, differentiated from neck, characterized by only slightly hypertrophied temporal and adductor musculature; noticeably broader (1.2 times) body at widest point; snout subtriangular, rounded at tip in dorsal and lateral aspect (Fig. 4A); head width 76.3% head length, 18.8% snout–vent length; snout length 63.3% head width and 48.3% head length; dorsal surfaces of head relatively

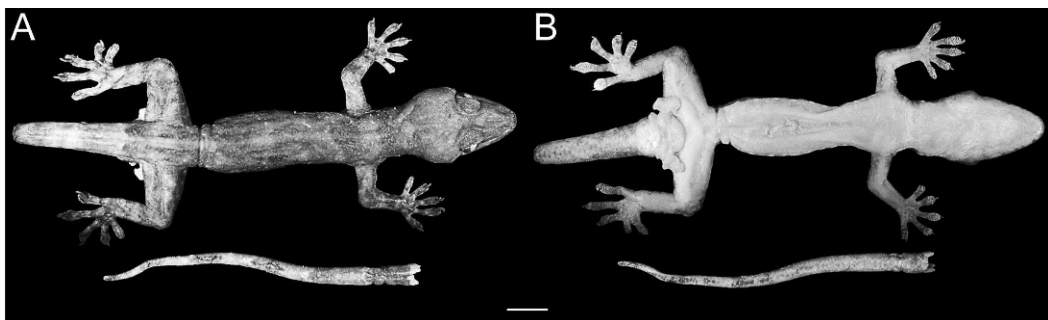


FIG. 3.—Dorsal (A) and ventral (B) view of the adult male *Gekko coi* holotype (PNM 9765; snout–vent length 84.0 mm). Scale bar = 10 mm.

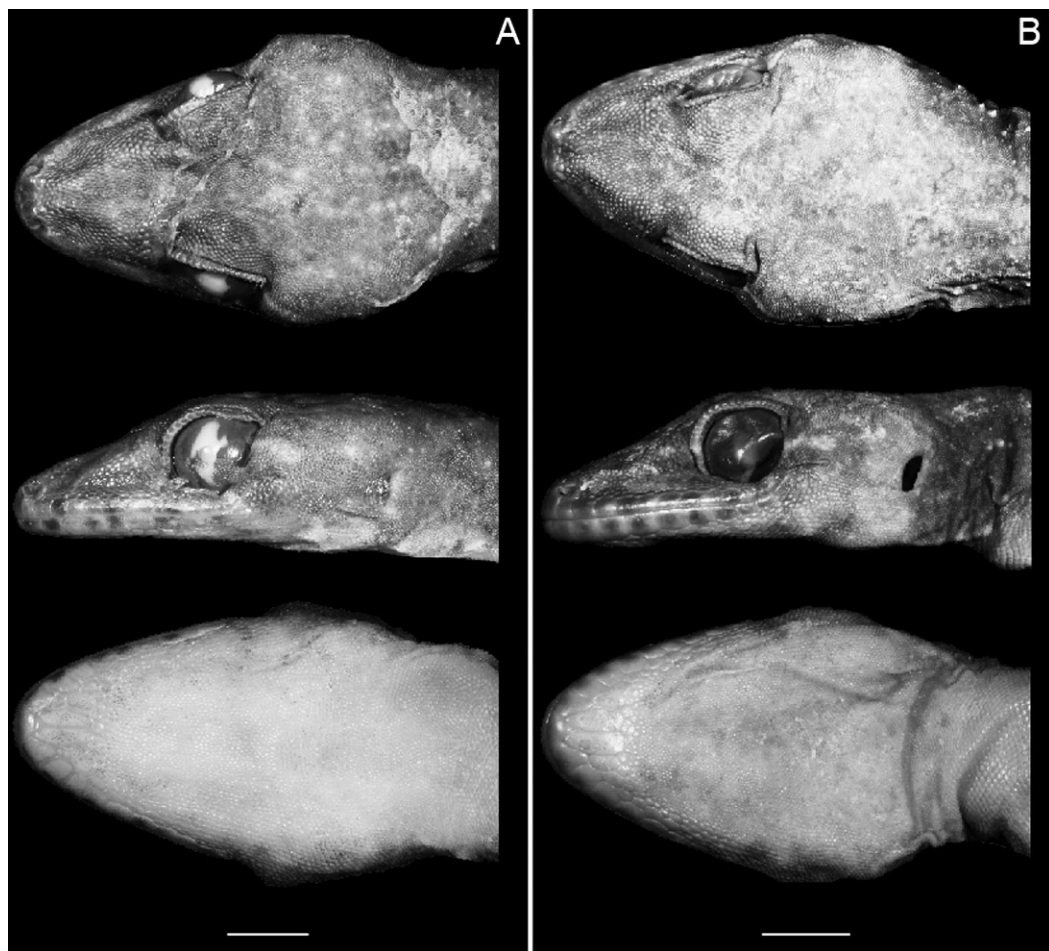


FIG. 4.—Dorsal, lateral, and ventral views of the heads of the adult male holotypes of *Gekko coi* (A: PNM 9765) and *G. romblon* (B: CAS 139190). Scale bars = 5 mm.

homogeneous, with only slightly pronounced concave postnasal, prefrontal, and interorbital concavities; auricular opening large, ovoid, angled slightly anteroposteriorly from beneath temporal swellings on either side of head; tympanum deeply sunken; orbit large, bordered by only moderately distinct supraorbital crest and sharply prominent preorbital crest; eye large, pupil vertical, margin wavy (Fig. 4A); auricular opening 50.5% eye diameter; limbs and digits relatively long and slender; femoral segments of hind limbs thick, bulky compared to humeral segments of forelimbs; tibia length 15.2% SVL, 76.6% femur length.

Rostral large, rectangular in anterior view, twice as broad as high, with two dorsomedial

fissures between raised posterodorsal projections that form the anteriormost projecting edge of the nares, and sutured anteriorly with the supranasals; nostril surrounded by rostral, first labial, an enlarged lower postnasal, a smaller upper postnasal, and an enlarged, round to octagonal, convex supranasal; supranasals separated by a single enlarged, elongate internasal; supranasals and internasal followed posteriorly by a pair of slightly enlarged posterosupranasals, separated by three slightly enlarged median scales; scales immediately posterior to posterosupranasals only slightly enlarged.

Total number of differentiated supralabials 15/15 (L/R; 11/10 to center of eye), bordered dorsally by several rows of nondifferentiated,

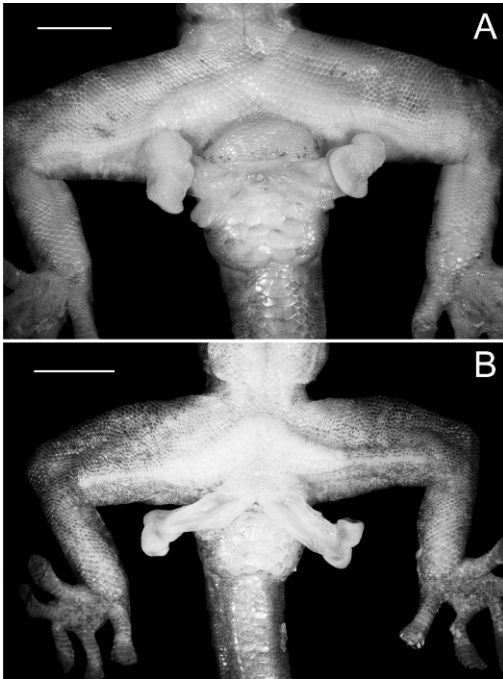


FIG. 5.—Inferior view of the prelocoacofemoral region of the male *Gekko coi* holotype (A: PNM 9765) and a specimen of *G. romblon* from type locality on Tablas Island (B: KU 315347). Scale bars = 5 mm.

nonenlarged snout scales; total number of differentiated infralabials 13/12 (L/R; 9/9 to center of eye), bordered ventrally by two rows of enlarged scales and three rows of only slightly differentiated chin scales; mental triangular; mental and first four infralabials greatly enlarged and wrapping onto ventral surfaces of chin, nearly twice the size of individual infralabials 4–12; mental followed posteriorly by a pair of slender, highly elongate medial postmentals; postmentals bordered posterolaterally by a secondary pair, approximately one-sixth or one-seventh the length of first pair; postmental scale series bordered posteriorly by a single series of only slightly enlarged scales; followed immediately by a sharp transition to undifferentiated chin and gular scales; posttricial scales undifferentiated; remaining undifferentiated gulars very small, round, nonimbricate, juxtaposed (Fig. 4A).

Dorsal cephalic scales fairly homogeneous in size, shape, disposition, and distribution; cephalic scalation varies from large, convex, round to oval scales of rostrum to minute (approximately one-third to one-fifth size of

rostrals), granular scales of posterior regions of head and neck; postnasal, prefrontal, and interorbital depressions with slightly smaller scales; palpebral scales heterogeneous, with some scales as small as adjacent interorbital region and others as large and raised as rostral scales; undifferentiated posterior head scales granular, convex, reducing in size posteriorly, interspersed with increasingly dense enlarged rounded to slightly conical tubercles; throat and chin scales small, juxtaposed and nonimbricate, making a sharp transition to gular and pectoral region scalation, with enlarged cycloid, imbricate scales continuing to increase in size through abdomen, becoming very enlarged and strongly imbricate.

Ornamental cephalic scalation limited to convex tubercles on posterolateral portions of head (temporal, supratympanic, and posttricial regions) and a slightly differentiated series of 2–3 enlarged, weakly conical unkeeled preorbital scales (Fig. 4A); 27/25 circumorbitals in total, differentiated into the following distinct regions: (1) several minute precircumorbitals, (2) enlarged, flat, squarelike circumorbitals dorsoanterior to orbit (13/11), (3) several smaller, undifferentiated supraorbital scaled (4/6), (4) transverse elongation and modification into fringe-like points (spiny cilia, 10/8) across dorsoposterior margin of orbit, gradually reducing to (5) several smaller to minute postcircumorbitals, a total of 47 interorbital scales (straight line distance from center of each eye, across both eyelids).

Axilla–groin distance 44.0% SVL; undifferentiated dorsal body scales round, convex, juxtaposed, relatively homogeneous in size; each dorsal scale surrounded by six interstitial granules, giving the appearance of a “Star of David” configuration under high magnification; dorsals interspersed with 15 irregularly transverse rows (25 paravertebral rows) of enlarged, slightly conical dorsal body tubercles; tubercles surrounded by undifferentiated adjacent dorsal scalation; dorsals sharply transition to imbricate ventrals along the ventrolateral adipose fold; transverse midbody dorsals 109; paravertebrals between midpoints of limb insertions 185; midbody dorsals in 106 rows; midbody ventrals in 43 transverse rows; scales on dorsal surfaces of limbs larger and more imbricate than dorsals, interspersed

with enlarged, flat to slightly conical tubercles on the radioulnar segment of the limb but absent on the humeral segment, and terminating at the dorsal surfaces of hands and feet; enlarged patches of distinct imbricate scales present on wrist, anterior (preaxial) surface of upper arm and thigh, on knee, and on distal ventral surface of hind limb; scales on dorsal surfaces of hands and feet similar to dorsal limb scales (but lacking tubercles); ventral body scales flat, cycloid, strongly imbricate, much larger than lateral or dorsal body scales, largest at midventral line.

Seventy-four pore-bearing or dimpled scales (Fig. 5A) in continuous precloacofemoral series, each punctured by pore bearing dark orange exudate, arranged in a wavy, widely obtuse, inverted-V formation and continuing to just beyond the patellar region; precloacal pores 3–4 times diameter of femoral pores; precloacals (14/14) situated atop a substantial precloacal bulge that is folded over into the precloacal region in preserved type but was erect and protuberant in life; precloacals preceded by five similarly enlarged but nondimpled scale rows; precloacals followed by a gap of undifferentiated scales, followed by five enlarged-scales rows, forming a triangular patch of scales anterior to the vent; femoral series lacks preceding or following enlarged scale rows; scales latero-posterior to precloacofemoral series (i.e., along ventroposterior surfaces of hind limb) reduce in size sharply to minute scales of the posterior edge of the hind limb.

Digits moderately expanded and covered on palmar/plantar surfaces by bowed, unnotched, undivided scansors (Fig. 4A); digits with minute vestiges of interdigital webbing; subdigital scansors of manus: 9/10, 11/12, 13/14, 15/16, and 11/12 on left/right digits I–V respectively; pes: 11/11, 12/12, 15/15, 17/16, and 14/13 on left/right digits I–V respectively; subdigital scansors of manus and pes bordered proximally (on palmar and plantar surfaces) by 1–4 slightly enlarged scales that form a near-continuous series with enlarged scansors; all digits clawed, but first (inner) claw greatly reduced; remaining terminal claw-bearing phalanges compressed, with large recurved claws, not rising free at distal end until they extend beyond dilated hyperextensible portion of digit.

Tail base bordered by a pair of moderately enlarged conical postcloacal spurs on each side of vent; postcloacal swellings pronounced; hemipenes completely everted; tail long, 105 mm, 1.25% snout–vent length; tail not depressed, subcylindrical, divided into indistinct fracture planes/autotomy grooves, with whorls (or annulations) clearly visible in basal portions of the tail (with slightly enlarged scales along the caudal margin of each annulation) but becoming less distinct toward distal portion; an estimated 25–27 annuli total; tail depth (not including basal postcloacal swelling) 60.6% tail width; dorsal tail with only a few enlarged caudal tubercles; caudals similar in size to dorsals; subcaudals a single enlarged medial row of platelike scales, flanked laterally by one slightly enlarged row; subcaudals widely expanded to cover majority of ventral surface of tail.

Variation.—The type series consists of three adult males, three adult females, and a single juvenile specimen. Ranges of diagnostic meristic and mensural characters are presented in Table 3. We detected no sexual dimorphism in the type series and ranges of all meristic and mensural measurements broadly overlap between the sexes. With data for males and females combined, mean SVL (± 1 SD; range) was 76.0 (± 6.76 ; 65.2–84.0), nonregenerated tail length 81.5 (± 8.6 ; 75.4–81.6), axilla–groin distance 35.5 (± 1.9 ; 32.1–37.0), tail width 6.6 (± 0.9 ; 5.0–7.6), tail depth 5.0 (± 1.1 ; 4.3–6.0), head length 21.4 (± 1.4 ; 19.1–22.7), head width 14.7 (± 1.1 ; 13.3–15.8), head depth 8.1 (± 0.6 ; 6.9–8.6), snout length 9.5 (± 1.2 ; 7.4–10.4), eye–narial distance 7.5 (± 1.2 ; 5.1–8.2), inter-narial distance 2.8 (± 0.24 ; 2.5–3.1), interorbital distance 5.6 (± 0.7 ; 4.8–6.6), femur length 15.6 (± 1.0 ; 13.8–16.7), tibia length 13.2 (± 1.2 ; 11.0–14.2), upper arm 8.7 (± 0.5 ; 7.5–9.1), forearm length 9.9 (± 0.7 ; 9.7–10.5), Toe I length 4.0 (± 0.2 ; 3.9–4.4), Toe IV length 8.0 (± 0.3 ; 7.5–8.4), and Finger III length 6.2 (± 0.2 ; 5.9–6.5).

Scalation in the type series is remarkably uniform, with a few exceptions. Dorsal tuberculation ranges from sparse (CAS 139182) to dense (FMNH 251114, CAS 155896), and in relatively more tuberculate individuals, caudal annulations are discernable for nearly the entire length of the tail,

owing to the aggregation of enlarged, posteriorly projecting tubercles along the caudal edge of each tail segment. Intersupranasal configuration varies from a single scale (CAS 139181–82), to two scales equivalent in size (PNM 9765; CAS 139180, FMNH 251114–15) to a minute anterior scale, followed by a greatly enlarged posterior intersupranasal (CAS 155896).

Intersexual variation in scalation appears limited to the presence of pierced pores (with orange exudate) in the precloacofemoral pore-bearing series of males (whereas in females these scales are enlarged and often dimpled, but lack pores) and the presence of two enlarged, protuberant postcloacal spurs in males (only a single enlarge scale present in females), on either side of the vent.

Coloration of holotype in ethanol.—Dorsal ground coloration of head, body, tail, and dorsal surfaces of limbs medium brown with irregular tan blotches, darker brown patches, and a vertebral region divided into alternating light and dark bands (Figs. 2A,B and 3A).

Dorsal and lateral surfaces of head similar to dorsal ground coloration; a light cream bar extends posteriorly from the orbit; palpebra dark gray, almost black; rostral and supralabials medium gray with dark gray spots; infralabials immaculate cream.

Limbs colored as torso, but with slightly more contrasting dark (black) and light (cream) patches; dorsal surfaces of hands and feet dark gray with cream spots; digits light gray with cream spots and black claws; tail medium gray with dark gray bands alternating with bold transverse white bands (not prominent distally).

Ventral head, neck, torso, and ventral surfaces of limbs light cream; ventral surfaces of digits (scansors) medium gray; preanofemoral region white with orange pore exudate; ventral surfaces of tail medium gray, fading to alternating blotches of dark gray and cream.

Coloration of holotype in life.—(From field notes of RMB and photographs of holotype before preservation; Fig. 2A,B.) Dorsal ground coloration dark purplish-gray to pinkish-brown, with alternating dark gray blotches interspersed broken vertebral stripe of medium cream; dorsum with five light-cream vertebral stripe segments in the axilla-groin region, each alternating with four dark, saddlelike blotches;

dorsolateral regions (flanks) more even brown, with rows of cream to bluish-white lateral midbody tubercle rows.

Dorsal nuchal region and posterior portions of head very similar to trunk coloration but with denser melanic pigmentation (forming distinct black spots) offset with cream-colored tubercles; postorbital and preorbital white bars radiate out from the orbit; postrictal region flat gray; labial scales purplish-gray with cream to yellow spots; darker black blotches congregate on snout in loreal, postnasal, interorbital, and parietal regions; infralabial region, chin, and gular regions yellowish white.

Dorsal surfaces of limbs purplish brown with white and dark cross bars; dorsal surfaces of digits purplish brown with white spots on digits; proximal dorsal surfaces of tail brown with dark blotches and thin transverse white lines, transitioning to banded alternating dark gray and cream on more distal portions of tail.

Ventral body and limbs cream, becoming yellowish with scattered dark flecks posteriorly and bright yellow in groin; precloacofemoral region bright yellow with dark orange pores; palmar and plantar surfaces of manus and pes yellowish tan with light gray subdigital scansors; ventral tail light gray with brown transverse bars.

Color variation.—Dorsal ground coloration ranges from relatively dark brown (females FMNH 251114–15) to medium orange-brown (juvenile CAS 139181 and adult male holotype PNM 9765) to nearly flat gray (males CAS 139180, 139182, and 155896). The darkest patterned individuals have a highly distinct light tan vertebral stripe, broken periodically by four or five dark brown to black, saddlelike blotches (male holotype PNM 9765, and females FMNH 251114–15). More darkly patterned individuals, exhibit a faint, nearly reticulate marbled pattern of dark brown ground color, accentuated with distinct white and black markings on the dorsal surfaces of the head (absent in more pale specimens [CAS 139180, 139182, 155896], possibly due to condition of specimen preservation and/or fading with time). All specimens possess the distinct bold white postorbital spot (most distinct in FMNH 251114–15). The nuchal region is particularly dark in some specimens (FMNH 251114–15, PNM 9765) and traversed

with bold white dorsal tubercle rows, or with tubercles matching the underlying ground coloration (CAS 139180, 139182, 155896). Ventral coloration is immaculate cream (CAS 139180–82, 155896, PNM 9765) to cream with light brown spots across the chin and throat, pectoral and pelvic regions, and ventral surfaces of hind limbs. The one juvenile (CAS 139181) is more boldly patterned than adults, with a distinctly barred tail with alternating tan and dark brown regions.

Distribution and natural history.—The new species is known only from Sibuyan Island in Romblon Province, central Philippines. Specimens have been collected close to the ground on tree trunks and from granitic rocks and boulders in riparian habitats in low-elevation primary forests along the southern border of Mt. Guiting-guiting Natural Park. Several additional specimens were collected from inside the axils of coconut palms in adjacent agricultural areas. Other than house geckos (*Gehyra mutilata*, *Hemidactylus frenatus*, *H. platyurus*) the new species is only known to be sympatric with *G. gecko* and *G. mindorensis*. Its sister species, *G. romblon*, co-occurs with *G. gecko* on the islands of Tablas and Romblon.

Etymology.—We name this distinctive new species for our colleague and friend Leonardo L. Co, a widely respected botanist and conservation biologist who passed away prematurely in November 2010 while conducting fieldwork on Leyte Island. The specific epithet *coi* is a patronym in the genitive singular. Suggested common name: Leonard's Forest Gecko.

DISCUSSION

We are especially confident in making the current taxonomic decision because the new species' status as a cohesive and morphologically distinct evolutionary lineage is bolstered by genetic data (indicating high levels of genetic differentiation from its most closely related congener) and biogeographic information (lineage isolation on an ancient oceanic island), both of which strongly support our conclusions. Geological evidence suggests that Sibuyan Island was never connected to any other landmasses (Dimalanta et al., 2009; Hall, 2002; Yumul et al., 2003) and has remained isolated through Pleistocene climat-

ic oscillations that resulted in the formation of enlarged aggregate island complexes in other parts of the archipelago (Brown and Diesmos, 2002, 2009; Clark and Mix, 2000; Thomas et al., 2009; Voris, 2000). In contrast to Sibuyan Island, which remained isolated, we know that Tablas and Romblon islands became conjoined as a single aggregate island as many as 10 times during the mid- to late-Pleistocene (Brown and Diesmos, 2009; Inger, 1954; Rohling et al., 1998; Voris, 2000), an observation consistent with our consideration of the populations of *G. romblon* on these two islands as a single evolutionary entity (*G. romblon*). And although we found some evidence of shallow genetic divergence between Romblon Island and Tablas Island populations of *G. romblon* (Table 2), we failed to find character differences that would allow us to diagnose these two potentially diverging lineages (currently isolated island populations) as separate species. Thus, genetic and biogeographic data are in perfect accordance with the hypothesis of two evolutionary lineages of geckos in the Romblon Island group: *G. romblon* (from Tablas and Romblon islands) and *G. coi* (from Sibuyan Island). The presence of additional species of endemic vertebrates on Sibuyan additionally emphasizes the importance of this island as an important center of biological endemism (Esselstyn and Goodman, 2010; Goodman et al., 1995; Rickart et al., 2005).

The conservation status of *G. romblon* and *G. coi* requires comment. Although the IUCN conservation status of *G. romblon* has recently been formally assessed as "Least Concern" (Brown et al., 2007), part of that decision was based on its relatively wide distribution on three islands (Romblon, Tablas, and Sibuyan). With the current revision in taxonomy, the geographic range of *G. romblon* is now limited to Romblon and Tablas, whereas that of *G. coi* is limited to the single landmass of Sibuyan Island. The range-restricted nature of these taxa suggests that future evaluators of their conservation status may wish to consider elevation to a higher threat category if clear threats to their continued survival are identified.

Our subjective impression (bolstered by relative numbers of specimens in museum collections; see Appendix) is that *G. romblon* is much more common on Tablas and Romblon

Islands than *G. coi* is on Sibuyan. Although this simplistic observation might suggest that *G. coi* is less abundant, rare, or in decline, we note that the new species occurs on a large landmass (~460 km²), much of which is protected as part of Mt. Guiting-guiting Natural Park (Goodman and Ingle, 1993; Goodman et al., 1995), where it is sufficiently protected. In contrast, the more abundant, but possibly disturbance-tolerant *G. romblon* has been collected in a variety of heavily impacted habitats, from tertiary growth scrub on limestone outcrops, to heavily mined (for bat guano) caves, to contour-mined marble quarries (R. Brown and C. Siler, personal observations). Our suspicion is simply that *G. coi* is a more secretive, rarely encountered species, and that biologists have not yet learned to observe it in its preferred microhabitat or period of activity. For this reason we recommend the conservation status assessment of "Data Deficient" pending actual field-based studies of distribution, abundance, and conservation status of the new species.

The description of *G. coi* brings the total number of Philippine *Gekko* to 12 taxa, including 10 endemic species. We are certain that this number continues to represent an underestimate of true species diversity and we would not be surprised if Philippine species numbers in the genus were to substantially increase in coming years. Unexpected and surprisingly distinct species are still being described from the archipelago's larger islands on isolated karst formations (Linkem et al., 2010; Rösler et al., 2006); accordingly, special attention is being paid to these isolated limestone outcrops. Caves in particular may soon produce additional species discoveries of the kind now commonly observed on the Asian mainland (Grismer et al., 2009; Ngo, 2008; Ngo et al., 2008; Ngo and Grismer, 2010; Ngo and Pauwels, 2010; Nguyen et al., 2006, 2010; Pauwels et al., 2004). Small isolated islands undoubtedly hold additional species diversity in the archipelago; we are aware of at least two morphologically and genetically distinct species in the Babuyan islands that await description (Brown et al., 2009). We suspect that other, smaller landmasses in the Babuyan-Batanes island banks may harbor additional undescribed species (Oliveros et al., 2011). Additionally, isolated mountain ranges on

larger islands (Luzon, Mindoro, Samar-Leyte, Palawan, Mindanao) will likely be shown to support additional species diversity. Recent discoveries of distinct gekkonids from the mountains of Luzon (Brown et al., 2007, 2011), Palawan (Brown et al., 2010; Welton et al., 2009) and Mindanao (Welton et al., 2010a,b) suggest that the separate, isolated mountainous regions of the large islands all warrant comprehensive faunal survey efforts if we are to conclude that their biodiversity is reasonably well known.

More subtle or possibly morphologically cryptic species diversity most likely resides in the widespread species *G. mindorensis* and *G. monarchus*. Preliminary molecular sequence data (C. Siler, A. Diesmos, and R. Brown, personal observations) indicate that these taxa contain highly divergent lineages with geographical distributions corresponding to geological components of the archipelago (Brown and Diesmos, 2002, 2009; Hall, 1998; Yumul et al., 2009). Although these populations have not yet been assessed for morphological character differences, we are confident that additional species await description. Finally, many smaller, deep-water islands (e.g., not connected to adjacent islands during the last glaciations; Brown and Diesmos, 2009) and some land-bridge islands (those hypothesized to have been connected to adjacent islands during the last glaciations; Brown and Diesmos, 2009) have not been surveyed adequately for herpetofauna and, as such, are good possibilities for the potential discovery of additional *Gekko* species. These include the islands of Lubang, Marinduque, Masbate, Siquijor, Dinagat, Siargao, Sarangani, Coron, Busuanga, Burias, Ticao, Semira, Semirara, Maestre de Campo, Cuyo, Basilan, Jolo, Tawi-Tawi, and many other similarly small, isolated landmasses. One such example is the Gigante Island group species, *G. gigante* (Brown and Alcala, 1978; Brown and Alcala, 2000). The existence of endemic species on these small limestone islands convinces us that isolation on landmasses separated by deep water may not be necessary to promote gekkonid diversification if limestone habitats have been isolated over geological time scales (Hall, 1998, 2002; Yumul et al., 2003, 2009).

Poorly developed knowledge of biodiversity contributes to destructive exploitation of Southeast Asian forests (Clements et al., 2006; Collins et al., 1991; Whitmore and Sayer, 1992) whereas knowledge of endemic biodiversity helps provide fuel for conservation of natural resources (Sodhi and Ehrlich, 2010; Sodhi et al., 2008). As such, it is critical that faunal inventories continue to be undertaken throughout the country in a wide variety of habitats and forest types. We are certain that Philippine gekkonid lizard diversity remains substantially underestimated and that continued biodiversity survey work will continue to provide compelling opportunities for targeted, taxon-specific conservation efforts.

Acknowledgments.—We thank the following individuals and their respective institutions for the loans of specimens or assistance while we were working in museum collections (museum abbreviations follow Leviton et al., 1985): A. Resetar, R. F. Inger, and H. Voris (FMNH); J. Vindum, R. Drewes, and A. Leviton (CAS); A. Campbell and L. Trueb (KU); A. Wynn, R. Heyer, and K. de Queiroz (USNM); A. Resetar, J. Hanken, and J. Losos (MCZ); and V. Palpalatoc and J. Barns (PNM). The Stearns Fellowship of the California Academy of Sciences provided support that allowed RMB, CDS, and ACD to undertake multiple visits to CAS. Financial support for fieldwork for CDS was provided by a Panorama Fund grant from University of Kansas Biodiversity Institute, a Fulbright Fellowship, a Fulbright-Hayes Fellowship, and NSF DEB 0804115. Financial support for RMB and ACD was provided by NSF EF 0334952, DEB 073199, and 0743491 funds to RMB. University of Kansas IACUC approved research protocols and the Department of the Environment and Natural Resources Protected Areas and Wildlife Bureau facilitated research and export permits necessary for this and related studies. We thank J. Fernandez, M. Diesmos, and G. Gee-Das for various forms of assistance in the field, and C. Linkem for assistance with specimen photography. We are particularly grateful to T. M. Lim, C. Custodio, and A. Tagtag for their unceasing support for our field research program. Critical review of the manuscript was provided by L. Welton, B. L. Stuart, and an anonymous reviewer.

LITERATURE CITED

- BAUER, A. M., AND K. HENLE. 1994. Gekkonidae (Reptilia, Sauria) Part I Australia and Oceania. *Das Tierreich* 109, de Gruyter & Co., Berlin, Germany.
- BOULENGER, G. A. 1885. Catalogue of the Lizards in the British Museum (Natural History). Second edition. Vol. I. Gekkonidae, Eublepharidae, Uroplatidae, Pygopodidae, Agamidae. British Museum (Natural History), London, UK.
- BROWN, R. M. 1999. New species of parachute gecko (Squamata; Gekkonidae; Genus *Ptychozoon*) from northeastern Thailand and Central Vietnam. *Copeia* 1999:990–1001.
- BROWN, R. M., AND A. C. ALCALA. 2000. Geckos, cave frogs, and small land-bridge islands in the Visayan sea. *Haring Ibon* 2:19–22.
- BROWN, R. M., AND A. C. DIESMOS. 2000. The lizard genus *Luperosaurus*: taxonomy, history, and conservation prospects for some of the world's rarest lizards. *Sylvatrop: Technical Journal of Philippine Ecosystems and Natural Resources* 10:107–124.
- BROWN, R. M., AND A. C. DIESMOS. 2002. Application of lineage-based species concepts to oceanic island frog populations: The effects of differing taxonomic philosophies on the estimation of Philippine biodiversity. *Silliman Journal* 42:133–162.
- BROWN, R. M., AND A. C. DIESMOS. 2009. Philippines, biology. Pp. 723–732. *In* R. Gillespie and D. Clague (Eds.), *Encyclopedia of Islands*. University of California Press, Berkeley, California, USA.
- BROWN, R. M., AND S. I. GUTTMAN. 2002. Phylogenetic systematics of the *Rana signata* complex of Philippine and Bornean stream frogs: Reconsideration of Huxley's modification of Wallace's Line at the Oriental-Australian faunal zone interface. *Biological Journal of the Linnean Society* 76:393–461.
- BROWN, R. M., J. W. FERNER, AND A. C. DIESMOS. 1997. Definition of the Philippine Parachute Gecko, *Ptychozoon intermedium* Taylor 1915 (Reptilia: Lacertilia: Gekkonidae): redescription, designation of a neotype, and comparisons with related species. *Herpetologica* 53:357–373.
- BROWN, R. M., A. C. DIESMOS, AND M. V. DUYA. 2007. A new *Luperosaurus* (Squamata: Gekkonidae) from the Sierra Madre of Luzon Island, Philippines. *Raffles Bulletin of Zoology* 55:167–174.
- BROWN, R. M., M. GAULKE, AND J. C. GONZALEZ. 2007. *Gekko romblon*. *In*: IUCN 2010. IUCN Red List of Threatened Species. Version 2010.4. Available at <http://www.iucnredlist.org>.
- BROWN, R. M., C. OLIVEROS, C. D. SILER, AND A. C. DIESMOS. 2008. A new *Gekko* from the Babuyan Islands, northern Philippines. *Herpetologica* 64:305–320.
- BROWN, R. M., C. OLIVEROS, C. D. SILER, AND A. C. DIESMOS. 2009. Phylogeny of *Gekko* from the northern Philippines, and description of a new species from Calayan Island. *Journal of Herpetology* 43:620–635.
- BROWN, R. M., A. C. DIESMOS, M. V. DUYA, H. J. D. GARCIA, AND E. L. RICO. 2010. A new forest gecko (Squamata; Gekkonidae; Genus *Luperosaurus*) from Mt. Mantalingajan, southern Palawan Island, Philippines. *Journal of Herpetology* 44:37–48.
- BROWN, R. M., A. C. DIESMOS, AND C. OLIVEROS. 2011. A new flap-legged forest gecko (Genus *Luperosaurus*) from the northeastern Philippines. *Journal of Herpetology* 45:202–210.
- BROWN, W. C. 1976. Review of the genus *Perochirus* (Gekkonidae). *Occasional Papers of the California Academy of Sciences* 126:1–14.
- BROWN, W. C., AND A. C. ALCALA. 1962. A new lizard of the genus *Gekko* from the Philippine Islands. *Proceedings of the Biological Society of Washington* 75:67–70.
- BROWN, W. C., AND A. C. ALCALA. 1978. *Philippine Lizards of the Family Gekkonidae*. Silliman University Press, Dumaguete City, Philippines.
- CLARK, P. U., AND A. C. MIX. 2000. Ice sheets by the volume. *Nature* 406:689–690.

- CLEMENTS, R., N. SODHI, M. SCHILTHUIZEN, AND P. K. L. NG. 2006. Limestone karsts of Southeast Asia: Impaired arks of biodiversity. *Bioscience* 56:733–742.
- COLLINS, N. M., J. A. SAYER, AND T. C. WHITMORE. 1991. *The Conservation Atlas of Tropical Forests: Asia and the Pacific*. Simon and Schuster, New York, New York, USA.
- DE QUEIROZ, K. 1998. The general lineage concept of species, species criteria, and the process of speciation. Pp. 57–75. *In* D. J. Howard and S. H. Berlocher (Eds.), *Endless Forms: Species and Speciation*. Oxford University Press, New York, New York, USA.
- DE QUEIROZ, K. 1999. The general lineage concept of species and the defining properties of the species category. Pp. 49–89. *In* R. A. Wilson (Ed.), *Species: New Interdisciplinary Essays*. Massachusetts Institute of Technology Press, Cambridge, Massachusetts, USA.
- DIMALANTA, C. B., E. G. L. RAMOS, G. P. YUMUL, JR., AND H. BELLUM. 2009. New features from the Romblon Island Group: Key to understanding the arc–continent collision in Central Philippines. *Tectonophysics* 479: 120–129.
- DUMÉRIL, A. H. A. 1856. Description des reptiles nouveaux ou imparfaitement connus de la collection du Muséum d'Histoire Naturelle et remarques sur la classification et les caractères des reptiles. *Archives du Muséum Histoire Natural*, Paris 8:176.
- EDGAR, R. C. 2004. MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32:1792–1797.
- ESSELSTYN, J. A., AND S. M. GOODMAN. 2010. New species of shrew (Soricidae: *Crociodura*) from Sibuyan Island, Philippines. *Journal of Mammalogy* 91:1467–1472.
- ESSELSTYN, J. A., H. J. D. GARCIA, M. G. SAULOG, AND L. R. HEANEY. 2008. A new species of *Desmalopex* (Pteropodidae) from the Philippines, with a phylogenetic analysis of the Pteropodini. *Journal of Mammalogy* 89:815–825.
- GAULKE, M., H. RÖSLER, AND R. M. BROWN. 2007. A new species of *Luperosaurus* (Squamata: Gekkonidae) from Panay Island, Philippines, with comments on the taxonomic status of *Luperosaurus cumingii* (Gray, 1845). *Copeia* 2007:413–425.
- GOODMAN, S. M., AND S. R. INGLE. 1993. Sibuyan Island in the Philippines—Threatened and in need of conservation. *Oryx* 27:174–180.
- GOODMAN, S. M., D. WILLARD, AND P. GONZALES. 1995. The birds of Sibuyan Island, Romblon Province, Philippines, with particular reference to their elevational distribution and biogeographic affinities. *Fieldiana* 82:1–57.
- GRISMER, L. L., A. NORHAYAL, K. O. CHAN, D. BELABUT, M. A. MUIN, P. W. WOOD, JR., AND J. L. GRISMER. 2009. Two new diminutive species of *Cnemaspis* Strauch 1887 (Squamata: Gekkonidae) from Peninsular Malaysia. *Zootaxa* 2019:40–56.
- GUINDON, S., AND O. GASCUEL. 2003. A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood. *Systematic Biology* 52:696–704.
- HALL, R. 1998. The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. Pp. 99–131. *In* R. Hall and J. D. Holloway (Eds.), *Biogeography and Geological Evolution of SE Asia*. Backhuys Publishers, Leiden, The Netherlands.
- HALL, R. 2002. Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: Computer-based reconstructions and animations. *Journal of Asian Earth Sciences* 20:353–434.
- INGER, R. F. 1954. Systematics and zoogeography of Philippine Amphibia. *Fieldiana* 33:181–531.
- LEVITON, A. E., R. H. GIBBS, JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* 1985:802–821.
- LINKEM, C. W., C. D. SILER, A. C. DIEMOS, AND R. M. BROWN. 2010. A new species of *Gekko* (Squamata: Gekkonidae) from central Luzon Island, Philippines. *Zootaxa* 2396:37–94.
- MACEY, J. R., Y. WANG, N. B. ANANJEVA, A. LARSON, AND T. J. PAPPENFUSS. 1999. Vicariant patterns of fragmentation among gekkonid lizards of the genus *Teratoscincus* produced by the Indian collision: A molecular phylogenetic perspective and an area cladogram for central Asia. *Molecular Phylogenetics and Evolution* 12: 320–332.
- MADDISON, D. R., AND W. P. MADDISON. 2005. *MacClade: Analysis of phylogeny and character evolution*, Version 4.08. Sinauer, Sunderland, Massachusetts, USA.
- MARSHALL, D. C. 2010. Cryptic failure of partitioned Bayesian phylogenetic analyses: Lost in the land of long trees. *Systematic Biology* 59:108–117.
- MARSHALL, D. C., C. SIMON, AND T. R. BUCKLEY. 2006. Accurate branch length estimation in partitioned Bayesian analyses requires accommodation of among-partition rate variation and attention to branch length priors. *Systematic Biology* 55:993–1003.
- NGO, V. T. 2008. Two new cave-dwelling species of *Cyrtodactylus* Gray, 1827 (Squamata: Gekkonidae) from Southwestern Vietnam. *Zootaxa* 1909:37–51.
- NGO, V. T., AND L. LEE GRISMER. 2010. A new karst dwelling *Cyrtodactylus* (Squamata: Gekkonidae) from Son La Province, north-western Vietnam. *Hamadryad* 35:84–95.
- NGO, V. T., AND O. S. G. PAUWELS. 2010. A new cave-dwelling species of *Cyrtodactylus* Gray, 1827 (Squamata: Gekkonidae) from Khammouane Province, southern Laos. *Zootaxa* 2730:44–56.
- NGO, V. T., L. L. GRISMER, AND J. L. GRISMER. 2008. A new endemic cave dwelling species of *Cyrtodactylus* Gray, 1827 (Squamata: Gekkonidae) in Kien Giang Biosphere Reserve, Southwestern Vietnam. *Zootaxa* 1967:53–62.
- NGUYEN, S. N., N. L. ORLOV, AND I. S. DAREVSKY. 2006. Descriptions of two new species of the genus *Cyrtodactylus* Gray, 1827 (Squamata: Sauria: Gekkonidae) from southern Vietnam. *Russian Journal of Herpetology* 13:215–226.
- NGUYEN, T. Q., P. KINGSADA, H. RÖSLER, M. AUER, AND T. ZIEGLER. 2010. A new species of *Cyrtodactylus* (Squamata: Gekkonidae) from northern Laos. *Zootaxa* 2652:1–16.
- OLIVEROS, C. H., H. OTA, R. I. CROMBIE, AND R. M. BROWN. 2011. The Herpetofauna of the Babuyan group of islands, northern Philippines. *Scientific Papers of the Natural History Museum of the University of Kansas* 43:1–20.
- OTA, H., K. Y. LUE, S. H. CHEN, AND W. C. BROWN. 1989. Taxonomic status of the Taiwanese *Gekko*, with

- comments on the synonymy of *Luperosaurus amissus* Taylor. *Journal of Herpetology* 23:76–78.
- PAUWELS, O. S. G., A. M. BAUER, M. SUMONTHA, AND L. CHANHOM. 2004. *Cyrtodactylus thirakhupti* (Squamata: Gekkonidae), a new cave-dwelling gecko from southern Thailand. *Zootaxa* 772:1–11.
- POSADA, D. 2008. jModelTest: Phylogenetic Model Averaging. *Molecular Biology and Evolution*, 25:1253–1256
- RAMBAUT, A., AND A. J. DRUMMOND. 2007. Tracer v1.4. Available at: <http://beast.bio.ed.ac.uk/Tracer>.
- RICKART, E. A., L. R. HEANEY, S. M. GOODMAN, AND S. A. JANS. 2005. Review of the Philippine genera *Chrotomys* and *Celaenomys* (Murinae) and description of a new species. *Journal of Mammalogy* 86:415–428.
- ROHLING, E. J., M. FENTON, F. J. JORISSEN, G. BERTRAND, G. GANSSSEN, AND J. P. CAULET. 1998. Magnitude of sea level lowstands of the last 500,000 years. *Nature* 394:162–165.
- RONQUIST, F., AND J. P. HUELSENBECK. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574.
- RÖSLER, H., C. D. SILER, R. M. BROWN, A. D. DEMEGILLO, AND M. GAULKE. 2006. *Gekko ernstkelleri* sp. n.—A new gekkonid lizard from Panay Island, Philippines. *Salamandra* 42:197–211.
- SILER, C. D., J. R. OAKS, J. A. ESSELSTYN, A. C. DIESMOS, AND R. M. BROWN. 2010. Phylogeny and biogeography of Philippine bent-toed geckos (Gekkonidae: *Cyrtodactylus*) contradict a prevailing model of Pleistocene diversification. *Molecular Phylogenetics and Evolution* 55:699–710.
- SILER, C. D., A. C. DIESMOS, A. C. ALCALA, AND R. M. BROWN. 2011. Phylogeny of Philippine slender skinks (Scincidae: *Brachymeles*) reveals underestimated species diversity, complex biogeographical relationships, and cryptic patterns of lineage diversification. *Molecular Phylogenetics and Evolution* 59:53–65.
- SODHI, N. S., AND P. R. EHRLICH. 2010. *Conservation Biology for All*. Oxford University Press, Oxford, UK.
- SODHI, N. S., G. ACCIAIOLI, M. ERB, AND A. K. J. TAN. 2008. *Biodiversity and Human Livelihoods in Protected Areas: Case Studies from the Malay Archipelago*. Cambridge University Press, Cambridge, UK.
- STAMATAKIS, A. 2006. RAXML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22:2688–2690.
- STAMATAKIS, A., F. BLAGOJEVIC, D. NIKOLOPOULOS, AND C. ANTONOPOULOS. 2007. Exploring new search algorithms and hardware for phylogenetics: RAXML meets the IBM cell. *J. VLSI Signal Processing* 48:271–286.
- STAMATAKIS, A., P. HOOVER, AND J. ROUGEMONT. 2008. A Rapid Bootstrap Algorithm for the RAXML Web Servers. *Systematic Biology* 57:758–771.
- TAYLOR, E. H. 1919. New or rare Philippine reptiles. *Philippine Journal of Science* 13:105–125.
- TAYLOR, E. H. 1922a. The lizards of the Philippine Islands. Philippine Bureau of Science, Manila, Philippines.
- TAYLOR, E. H. 1922b. Additions to the herpetological fauna of the Philippine Islands, I. *Philippine Journal of Science* 21:161–206.
- TAYLOR, E. H. 1925. Additions to the herpetological fauna of the Philippine Islands, IV. *Philippine Journal of Science* 21:97–111.
- THOMAS, A. L., G. M. HENDERSON, P. DESCHAMPS, Y. YOKOYAMA, A. J. MASON, E. BARD, B. HAMELIN, N. DURAND, AND G. CAMOIN. 2009. Penultimate deglacial sea-level timing from uranium-thorium dating of Tahitian corals. *Science* 324:1186–1189.
- VORIS, H. K. 2000. Maps of Pleistocene sea levels in Southeast Asia: Shorelines, river systems and time durations. *Journal of Biogeography* 27:1153–1167.
- WELTON, L. J., C. SILER, A. C. DIESMOS, AND R. M. BROWN. 2009. A new bent-toed gecko (Genus *Cyrtodactylus*) from southern Palawan Island, Philippines, and clarification of the taxonomic status of *C. annulatus*. *Herpetologica* 65:323–343.
- WELTON, L. J., C. SILER, A. C. DIESMOS, AND R. M. BROWN. 2010a. Phylogeny-based species delimitation of southern Philippine bent-toed geckos and a new species of *Cyrtodactylus* (Squamata: Gekkonidae) from western Mindanao and the Sulu Archipelago. *Zootaxa* 2390:49–68.
- WELTON, L. J., C. SILER, A. C. DIESMOS, AND R. M. BROWN. 2010b. Philippine bent-toed geckos of the *Cyrtodactylus agusanensis* complex: Multilocus phylogeny, morphological diversity, and description of three new species. *Herpetological Monographs* 24:55–85.
- WHITMORE, T. C., AND J. A. SAYER. 1992. *Tropical Deforestation and Species Extinction*. Chapman and Hall, London, UK.
- WILEY, E. O. 1978. The evolutionary species concept reconsidered. *Systematic Zoology* 21:17–26.
- WILGENBUSCH, J. C., D. L. WARREN, AND D. L. SWOFFORD. 2004. AWTY: A system for graphical exploration of MCMC convergence in Bayesian phylogenetic inference. Available at: <http://ceb.csit.fsu.edu/awty>.
- YUMUL, G. P., JR., C. B. DIMALANTA, R. A. TAMAYO, JR., AND R. C. MAURY. 2003. Collision, subduction and accretion events in the Philippines: A synthesis. *The Island Arc* 12:77–91.
- YUMUL, G., JR., C. DIMILANTA, K. QUEAÑO, AND E. MARQUEZ. 2009. Philippines, geology. Pp. 732–738. In R. Gillespie and D. Clague (Eds.), *Encyclopedia of Islands*. University of California Press, Berkeley, California, USA.
- ZUG, G. 2010. Speciation and dispersal in a low diversity taxon: The slender Geckos *Hemiphyllodactylus* (Reptilia, Gekkonidae). *Smithsonian Contribution to Zoology* Number 631, Smithsonian Institution Scholarly Press, Washington, District of Columbia, USA.

Accepted: 20 August 2011
Associate Editor: Bryan Stuart

APPENDIX I

Comparative Material Examined

All specimens examined are from the Philippines. Numbers in parentheses indicate the number of specimens examined for each species and museum abbreviations follow Leviton et al. (1985).

Gekko athymus (eight specimens): PALAWAN ISLAND, PALAWAN PROVINCE, ca. 10 km WSW of Iwahig: CAS 137677; ca. 8–9 km S of Balico: CAS-SU 23119 (holotype); ca. 20 km SW of Iwahig: CAS-SU 23121 (paratype); Municipality of Brooke's Point, Barangay Mainit: KU 309335; Barangay Samariñana; Mt. Mantalingahan, 900 m: KU 309331–309334.

Gekko carusadensis (eight specimens): LUZON ISLAND, BULACAN PROVINCE, Municipality of San Miguel and Doña Remedios Trinidad, Barangay Biak na Bato: PNM 9715 (holotype); PNM 9716–18, KU 319985, 320484, 320485, 319970 (paratypes).

Gekko crombota (21 specimens): BABUYAN CLARO ISLAND, CAGAYAN PROVINCE, Municipality of Calayan, Barangay Babuyan Claro: PNM 9280 (holotype); KU 304807–304809, 304814, 304821, 304825–304826, 3043830, 304836, 304845, 304848; PNM 9281–9284, PNM 9090, 9095–9098.

Gekko ernstkelleri (10 specimens): PANAY ISLAND, ANTIQUE PROVINCE, Municipality of Pandan, Barangay Duyong, Duyong Hillside (= Mt. Lihidian): PNM 9152–54; KU 300196–300202.

Gekko gekko (13 specimens): LUBANG ISLAND, OCCIDENTAL MINDORO PROVINCE, Municipality of Lubang, Barangay Paraiso: KU 303960–303972.

Gekko gigante (13 specimens): SOUTH GIGANTE ISLAND, ILOILO PROVINCE, Municipality of Carles, Barangay Tantaran: CAS 124315–17 (paratypes); NORTH GIGANTE ISLAND, ILOILO PROVINCE, Municipality of Carles: CAS 124866–124867 (Paratypes); Barangay Asloman: KU 302716–302720, 305138–305140.

Gekko hokouensis (1 specimen): Tablas, Philippines (presumably in error): FMNH 17812 (*Luperosaurus amissus* holotype).

Gekko mindorensis (56 specimens): NEGROS ISLAND, NEGROS ORIENTAL PROVINCE, Himangpangon Cave, Manjayod: CAS-SU 28656–28660; GUIMARAS ISLAND, GUIMARAS PROVINCE, Municipality of Buenavista, Barangay Old Poblacion: KU 302721, 302725; NEGROS ISLAND, NEGROS OCCIDENTAL PROVINCE, Municipality of Cauayan, Barangay Camalandaan: KU 302722–302724; MASBATE ISLAND, MASBATE PROVINCE, Municipality of Mandaon, Barangay Poblacion: KU 302726–302728; PANAY ISLAND, CAPIZ PROVINCE, Municipality of Pilar, Barangay Natividad: KU 302729–302732; LUBANG ISLAND: OCCIDENTAL MINDORO

PROVINCE, Municipality of Lubang, Barangay Vigo: KU 303913–303916, 303917–303951.

Gekko monarchus (23 specimens): PALAWAN ISLAND, PALAWAN PROVINCE, ca. 1.5 km WSW of Iwahig: CAS-SU 28416; ca. 5 km SSE of Iwahig: CAS-SU 28496; ca. 7 km WNW of Iwahig: CAS-SU 28554; Municipality of Brookes Point, Mt. Mantalingahan: KU 309362; Barangay Mainit, Mainit Falls: KU 309285–87, 326431–33; Municipality of Nara, Barangay Estrella, Estrella Falls: KU 326425, 326426; Municipality of Quezon, Poblacion Quezon, National Museum Complex: KU 309289–91; Municipality of Puerto Princesa, Barangay Irawan, Irawan Watershed: KU 309048, 309171, 309280–83; INDONESIA, SULAWESI ISLAND: BSI 340, 819 (uncatalogued specimens, deposited at Museum Zoologicum Bogoriense, Chibnong, Jakarta, Indonesia).

Gekko palawanensis (7 specimens): PALAWAN ISLAND, PALAWAN PROVINCE, 7 km WNW of Iwahig: CAS 17318; 8 km W of Iwahig: CAS 17319; ca. 9 km W of Iwahig: CAS 17320–17322; Municipality of Puerto Princesa, Barangay Irawan, Irawan Watershed: KU 309279, 309468.

Gekko porosus (21 specimens): BATAN ISLAND, BATANES PROVINCE, 3 km ENE of Basco Town: USNM 266519, 291387; Mahatao: USNM 266517; Municipality of Basco, outskirts of Basco Town, near airport: PNM 9532–36; ITBAYAT ISLAND: CAS 60526 (holotype); Municipality of Basco, Barangay San Antonio: KU 313972–76; Municipality of Ivana, Barangay Salagao: KU 313970–71; 313983–89.

Gekko romblon (15 specimens): ROMBLON ISLAND, ROMBLON PROVINCE, Municipality of Concepcion, Barangay San Vicente: KU 302733–35; Municipality of Romblon, Barangay Li-O: KU 302736–42, 303977–78; TABLAS ISLAND, ROMBLON PROVINCE, Municipality of San Agustin, Mt. Progreso: CAS 139190 (holotype); Dubduban Barrio: CAS 139189, MCZ R-146961 (paratypes); Municipality of Calatrava, Barangay Balogo, Sitio Piqueno: KU 315246–48.

Gekko rossi (19 specimens): CALAYAN ISLAND, CAGAYAN PROVINCE, Municipality of Calayan, Barangay Magsidel, Macarra: PNM 9543 (Holotype), 9542, 9537–42, KU 304876, 304885, 304916–304919, 304923–304924, 304927, 304931 (paratopotypes); Barangay Longog: PNM 9091 (paratype).

Gekko sp. A (35 specimens): DALUPIRI ISLAND, CAGAYAN PROVINCE, Municipality of Calayan, Nipa Creek: KU 307022–307039, 307040–307057.

Gekko sp. B (24 specimens): CAMIGUIN NORTE ISLAND, CAGAYAN PROVINCE, Municipality of Calayan, Barangay Balatubat: KU 304583, 304585, 304586, 304588, 304605–304611, 304617, 304673, 304728–304733, 304738, 307990, 308043; Magas-asok: PNM; 9099; Pomoctan Island (small island adjacent to Camiguin Norte Island): PNM 9100.