Phylogeny of *Gekko* from the Northern Philippines, and Description of a New Species from Calayan Island

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ABSTRACT.—We use mitochondrial gene sequences to estimate relationships among *Gekko* populations from the northern Philippines. These data, plus morphological and biogeographical evidence, suggest that the Babuyan and Batanes island groups (north of Luzon Island) are inhabited by a minimum of six distinct evolutionary lineages, only two of which (*Gekko porosus* Taylor from the Batanes and *Gekko crombota* from Babuyan Claro) have been formally recognized as distinct species. In this paper, we provide a description of another new species, the endemic *Gekko* from Calayan Island. This geographically isolated species is diagnosed on the basis of a distinct color pattern, body size, scalation, and significant divergence in mitochondrial gene sequences. The new species has been found on rocky outcrops and limestone caves in forested areas and on trunks of mature forest trees ≤500 m above sea level, away from the island's coast. Given the history of geological isolation of Calayan Island and the distinctiveness of the endemic *Gekko* populations there, we are confident in diagnosing this gecko as a unique evolutionary lineage; it is unlikely that this species will be found on neighboring land masses. The remaining major islands of the Babuyans group (Camiguin Norte, Fuga, and Dalupiri islands) each contain similarly distinct endemic species that await description; additional surveys throughout the Batanes and Babuyan islands will be necessary to arrive at an estimate of total species diversity for this isolated gekkonid radiation.

The Philippine gekkonid lizard fauna consists of 10 genera and 40 described species: *Cyrtodactylus* (5 species); *Gekko* (10 or 11); *Gehyra* (1); *Hemidactylus* (5; including *platyurus*, a species formerly assigned to *Cosymbotus*); *Hemiphyllodactylus* (1); *Lepidodactylus* (6); *Luperosaurus* (7); *Pseudogekko* (4); and *Ptychozoon* (1) (Taylor, 1922a,b; Brown and Alcala, 1978; Brown et al., 1997, 2007, 2008, in press; Brown, 1999; Gaulke et al., 2007; Welton et al., in press).

Philippine species of the genus *Gekko* include three taxa shared with neighboring countries (*Gekko gecko*, *Gekko monarchus,* and *G. hokouensis*; Taylor, 1922a,b; Brown and Alcala, 1978; Ota et al., 1989). Although *G. gecko* and *G. monarchus* are common in collections, *Gekko hokouensis* has been represented in the country's gekkonid fauna by only a single specimen originally described by Taylor as *Luperosaurus amissus* (Taylor, 1922a,b), later considered to be *Gekko japonicus* (Brown and Alcala, 1978) and eventually determined to be *G. hokouensis* (Ota et al., 1989). The specimen was apparently collected from Tablas Island (Taylor, 1962), and no

specimens matching its description or the holotype have been collected since Taylor, suggesting erroneous attribution to the archipelago (Brown and Alcala, 1978; Ota et al., 1989).

Eight species of *Gekko* are confidently considered endemic to the Philippines; these include *Gekko athymus, Gekko gigante, Gekko mindorensis, Gekko palawanensis, Gekko porosus, Gekko romblon* (Taylor, 1922a; Brown and Alcala, 1978), *Gekko ernstkelleri* (Roesler et al., 2006), and *Gekko crombota* (Brown et al., 2008). All endemic Philippine *Gekko* share (1) moderate body size and longer, slender limbs; (2) near complete absence of interdigital webbing or cutaneous body expansions; (3) enlarged dorsal tubercles arranged in longitudinal rows on the dorsum (except *G. athymus*, dorsal tubercles absent); (4) scales of dorsum between tubercle rows minute, nonimbricate; (5) scales of venter enlarged, flat, imbricate; (6) differentiated postmentals elongate and slender; and (7) subcaudals enlarged, platelike (Brown and Alcala, 1978; Brown et al., 2007, 2008).

During recent biological inventories of the Babuyan Islands (Fig. 1), we obtained new specimens and tissues, allowing for a study of the genetic variation exhibited by isolated

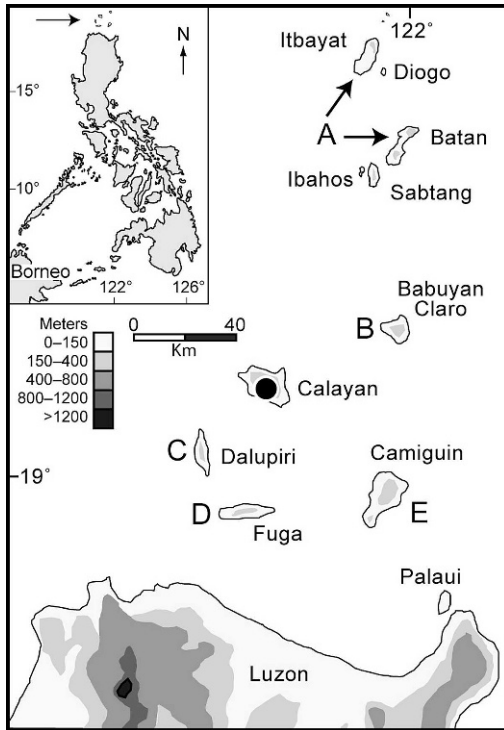[2]Corresponding Author. E-mail: rafe@ku.edu
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FIG. 1. Map of the most northern islands of the Philippines (inset) showing the type locality of *Gekko rossi* on Calayan Island (shaded circle) in relation to other landmasses discussed in the text. Additional northern Philippine lineages include *Gekko porosus* (A), *Gekko crombota* (B), and three undescribed species on Dalupiri, Fuga, and Camiguin Norte islands (C–E).

northern Philippine *Gekko* populations. In this paper, we present a phylogenetic analysis of the northern Philippine *Gekko* and a description of a new species from Calayan Island.

MATERIALS AND METHODS

Specimens and tissues were collected by the authors between 2004 and 2008. Specimens were initially preserved in 10% buffered formalin and then transferred to 70% ethanol 1–3 months later. Tissues were preserved in 95% ethanol. Voucher specimens are deposited in U.S. and Philippine museum collections (institutional abbreviations follow Leviton et al., 1985).

Morphological Data.—We (CO, CDS, and RMB) collected data from fluid-preserved specimens (Appendix 1). Sex was determined by eversion of hemipenes during preservation (males) and confirmed by noting prominent secondary sexual characteristics such as the presence of precloacofemoral pores and en-

larged cloacal spurs in males (both absent in females; Brown, 1999; Brown et al., 1997, 2007). Gonadal inspection was performed whenever possible. Measurements (to the nearest 0.1 mm) were taken with digital calipers following character definitions by Ota and Crombie (1989), Brown et al. (1997, 2007, 2008) and Brown (1999). Character abbreviations include: snout–vent length (SVL); tail length (TL); tail width (TW); tail depth (TD); head length (HL); head width (HW); head depth (HD); snout length (SNL); eye diameter (ED); eye–narial distance (END); auricular opening diameter (AO); internarial distance (IND); interorbital distance (IOD); axilla–groin distance (AGD); femur length (FL); tibia length (TBL); Toe I length (TIL); Toe IV length (TIVL); number of supralabials (SUL); infralabials (IFL; counted both to the center of the eye and posteriorly to the point at which labials were no longer differentiated); enlarged circumorbitals dorsoanterior to orbit (CO); modified spiny circumorbitals (cilaria) dorsoposterior to orbit; differentiated precloacal pore-bearing scales (PS); femoral pore-bearing scales (FPS); differentiated subdigital scansors on Fingers I–V (FS I–V); subdigital scansors on Toes I–V (TS I–V); midbody ventral transverse scale rows (MBVS); midbody dorsal transverse scale rows (MBDS); midbody transverse tubercle rows (MBTR); paravertebrals in AGD (PVS; counted along middorsum between limb insertions); ventrals (VS; counted midventrally between limb insertion); tail annuli (TA); and subcaudals (SC).

Molecular Data.—Samples from 21 specimens representing nine species of *Gekko* were included in phylogenetic analyses. These include five of the northern Philippine species, *G. monarchus* (a species shared with Sulawesi Island of Indonesia; Appendices 1 and 2) and outgroup species *G. gecko* and *Gekko smithi*. For all 21 samples, we sequenced the mitochondrial gene NADH Dehydrogenase Subunit 2 (ND2) and components of four flanking transfer RNA genes (tRNA[met], tRNA[trp], tRNA[ala], tRNA[asn]). All sequences were deposited in GenBank (Appendix 2).

Genomic DNA was extracted from liver tissue following the guanidine thiocyanate method of Esselstyn et al. (2008). The external primers Metf6 (5′-AAGCTTTCGGGCCCA-TACC-3′) and CO1H (5′-AGRGTGCCAATG-TCTTTGTGRTT-3′) (Macey et al., 1999) were used to amplify the target fragment using the polymerase chain reaction (PCR). Cycle sequencing reactions were performed with combinations of nested and internal primers designed for this study to collect complete double stranded sequences. We used two nested primers, GekND2.NestF1 (5′-CCATACCCCGA-

CAATGTTGGWAC-3') and GekND2.NestR1 (5'-AGCTGTAGACTYATRTACGGRGG-3'), and two internal primers, GekND2.IntF1 (5'-TCW-TAGCYTWYTCATCAATYGC-3') and GekND2.IntR4 (5'-GATGARWARGCTAWGATTTTTCG-GG-3').

We used the following thermal cycler profile: 4 min at 94°, followed by 35 cycles of 94° for 30 sec, 52–53° for 30 sec, and 72° for 1 min 30 sec, and a final extension phase at 72° for 7 min. Amplified products were visualized on 1.5% agarose gels. Clean single bands of the target product were purified with 1 µL of a 20% diluted solution of ExoSAP-IT (US78201, Amersham Biosciences, Piscataway, NJ) on the following thermal cycler profile: 31 min at 37°, followed by 15 min at 80°. Cycle sequencing reactions were run using ABI Prism BigDye Terminator chemistry (Vers. 3.1; Applied Biosystems, Foster City, CA), and purified with Sephadex Medium (NC9406038, Amersham Biosciences, Piscataway, NJ) in Centri-Sep 96 spin plates (CS-961, Princeton Separations, Princeton, NJ). Purified product was analyzed with an ABI Prism 3130xl Genetic Analyzer (Applied Biosystems). Gene sequence contigs were assembled and initially edited using Sequencher 4.8 (Gene Codes Corp., Ann Arbor, MI).

Alignment and Phylogenetic Analysis.—An initial alignment was produced in Muscle (Edgar, 2004), and manual adjustments were made in MacClade 4.08 (D. R. Maddison and W. P. Maddison, MacClade: Analysis of Phylogeny and Character Evolution, Sinauer, Sunderland, MA, 2005). Phylogenetic analyses were conducted using both parsimony and likelihood optimality criteria. Parsimony analyses were conducted in PAUP* 4.0 (D. L. Swofford, PAUP*. Phylogenetic Analysis Using Parsimony [*and Other Methods], Sinauer, Sunderland, MA, 2002) with gaps treated as missing data and all characters weighted equally. Most parsimonious trees were estimated using heuristic searches with 1,000 random addition-sequence replicates and tree bisection and reconnection (TBR) branch swapping. To assess nodal support, nonparametric bootstrapping was conducted using 1,000 bootstrap replicates, each with 100 random addition-sequence replicates and TBR branch swapping.

Partitioned maximum likelihood (ML) analyses were conducted in RAxMLHPC v7.0 (Stamatakis, 2006). The data set was partitioned by codon position for the protein-coding region of ND2, and each of the four flanking tRNAs (tRNA^{met}, tRNA^{trp}, tRNA^{ala}, tRNA^{asn}) were analyzed as separate partitions. The Akaike Information Criterion (AIC) as implemented in Modeltest v3.7 (Posada and Crandall, 1998) was used to find appropriate models of evolution for our data. The best-fit model for each of the seven partitions was the general time reversible (GTR) model, with a proportion of invariable sites (I) and a parameter for variation in rates among sites (Γ). Partitioned ML analyses were then run under the same model (GTR + I + Γ) with RAxMLHPC v7.0, with 100 replicate best tree inferences. Each inference was performed with the options ''–d'' to start each search with a random starting tree, and ''–f d'' to run each analysis with the rapid hill-climbing algorithm implemented in the new version of RAxML. Nodal support was assessed with 1,000 bootstrap pseudoreplicates.

Taxonomic Decisions.—We adopted the General Lineage Species Concept (GLC) of de Queiroz (1998, 1999) as the natural extension of the Evolutionary Species Concept (Simpson, 1961; Wiley, 1978; Frost and Hillis, 1990). Application of lineage-based species concepts to recognition of island taxa is straightforward because of the high probability of a history of isolation (Brown et al., 2000, 2008; Brown and Diesmos, 2002; Brown and Guttman, 2002) of these distinct lineages (McDermott et al., 1993; Yang et al., 1996; Marini et al., 2005). We consider as new species morphologically and genetically diagnosable allopatric populations for which the hypothesis of a distinct evolutionary lineage cannot be rejected.

RESULTS

Phylogeny.—The aligned dataset contained 1,282 total characters, of which 659 were variable, and 503 were parsimony-informative. The maximum parsimony analysis recovered a single most parsimonious tree (length = 1,114). The 100 inferences from the maximum likelihood analysis showed an average likelihood score of −ln L 6077.327465, with a single tree having the highest likelihood score of −ln L 6077.326765 (inferred by RAxML). The trees recovered from the two methods had a nearly identical topology (Fig. 2), differing only by the position of short terminal branches within species. Most Batanes and Babuyans populations are separated by substantial genetic divergences (9.3–14.6% uncorrected pairwise genetic sequence divergence; only 2.6% difference between Dalupiri and Camiguin Norte lineages), and no instances of multiple sympatric lineages per island were detected (5–10 individuals per island were sequenced, but only 2–3 are included in the presented analysis for computational simplicity, following confirmation that these were genetically identical). All relationships were highly supported with the
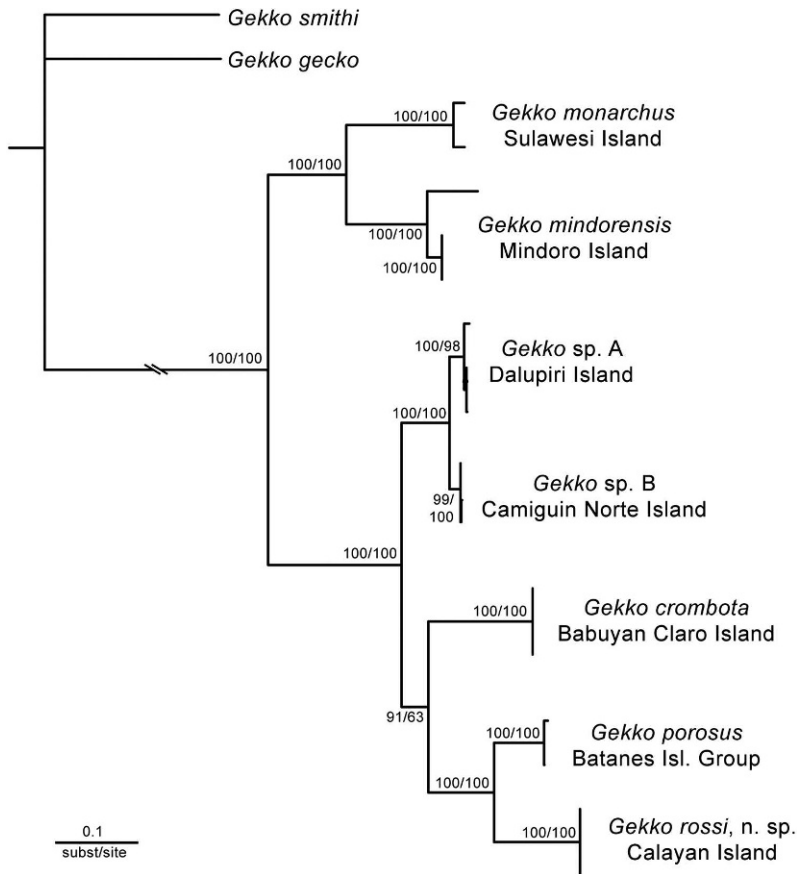
F<small>IG</small>. 2. The preferred topology, inferred in both partitioned likelihood and equally weighted parsimony analyses of ND2 sequence data (1282 nucleotide positions). Numbers adjacent to nodes are likelihood/parsimony bootstrap support values.

exception of moderate support (91 ML/63 MP) inferred for the relationship between *G. crombota* (Babuyan Claro Island) and the sister species couplet consisting of *Gekko porosus* (Batan Island) and *Gekko rossi* (Calayan Island). The southern Babuyans lineages (Dalupiri and Camiguin Norte Islands) form a strongly supported clade, to the exclusion of the lineages from the Northern Batanes and Babuyans (Calayan and Babuyan Claro). Other *Gekko* species *Gekko mindorensis* (Mindoro Island) and *G. monarchus* (represented here with samples from Sulawesi Island) cluster together and are sister to the northern Philippine lineages to the exclusion of outgroups *G. gecko* and *G. smithi* (Fig. 2). In summary, genetic data support the recognition of the Calayan Island population as a distinct and endemic lineage that is highly divergent from other described Babuyan and Batanes island populations (*G. porosus* and *Gekko crombota*).

T<small>AXONOMY</small>

Gekko rossi sp. nov.
Figures 3–5

Gekko monarchus Part (Calayan Island) Stejneger, L. 1907. Proc. U.S. Nat. Mus. 33:545–546

Holotype.—PNM 9543 (Field number RMB 5998; formerly KU 304877), an adult male collected at 2245 h 2 m from the ground on the trunk of a large (1.2 m dbh) tree by RMB at an area known locally as ''Macarra,'' Barangay Magsidel, Municipality of Calayan, Cagayan Province, Calayan Island, Philippines (19.294°N, 121.409°E; 245 m above sea level), on 15 March 2006.

Paratopotypes.—KU 304919, 304927, 304931, 304885, and PNM 9538, 9540 (formerly KU 304935, 304938) adult males; KU 304916–304918, 304923–304924, PNM 9542, 9539, 9537 (formerly KU 304934, 304936, 304937), gravid adult females; PNM 9541 (formerly KU 304939) and KU 304876, juveniles of undetermined sex,
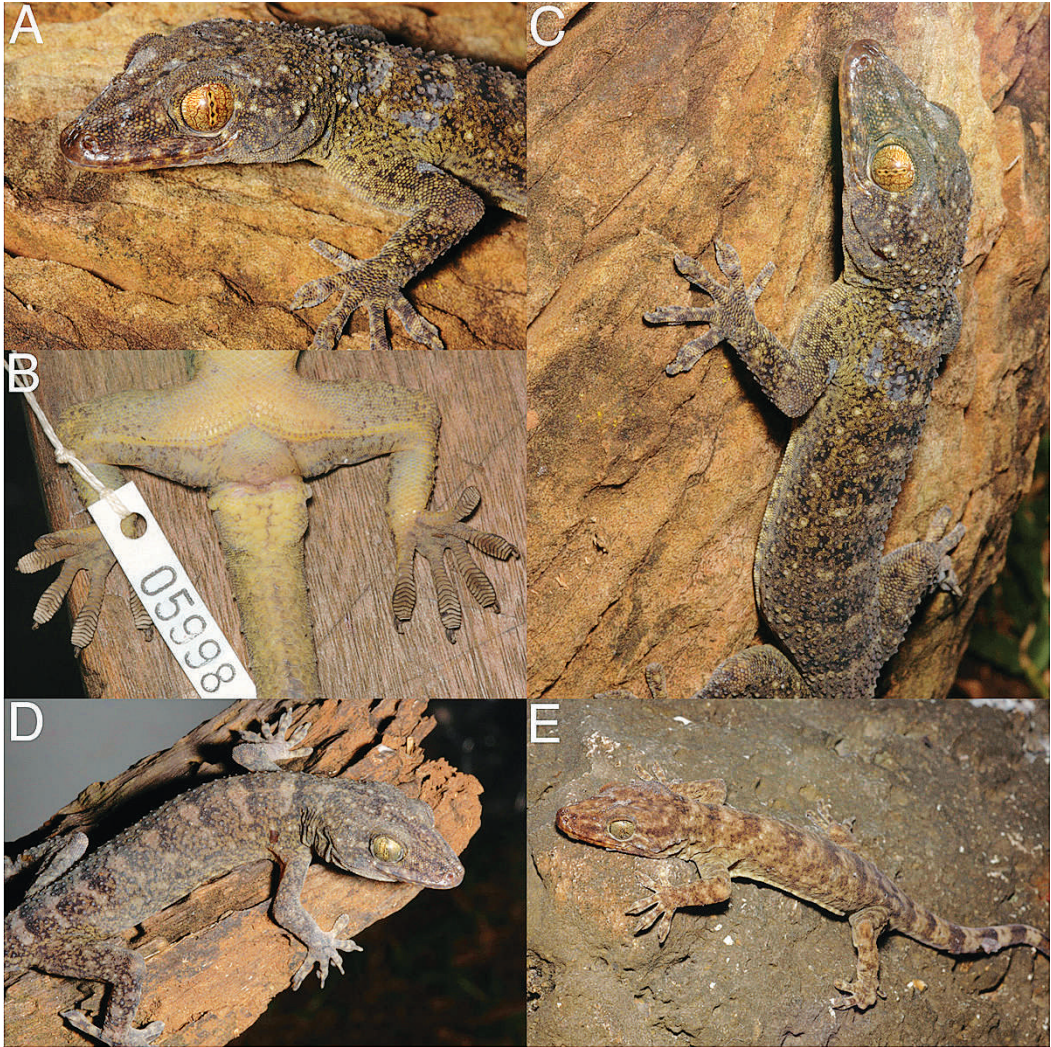
FIG. 3. (A–C) Adult male *Gekko rossi* holotype in life (PNM 9543; SVL = 98.4 mm); (D) *Gekko crombota* from Babuyan Claro Island (KU 304849); and (E) *Gekko porosus* from Batan Island (specimen not collected).

collected by RMB, C. Oliveros, and J. Fernandez; 15–17 March 2006, same locality, microhabitat, and circumstances of capture (tree trunks, < 3 m; 1830–2330 h) as holotype.

Other Paratype.—PNM 9091 (Field No. MGDP 129), adult male; collected by C. Oliveros and M. Pedregosa on large limestone boulders in second growth forest, 12 May 2004 at Sitio Longog, Municipality of Calayan, Cagayan Province, Calayan Island.

Diagnosis.—*Gekko rossi* differs from all other species of Philippine *Gekko* (i.e., *G. athymus, G. crombota, G. ernstkelleri, G. gecko, G. gigante, G. mindorensis, G. monarchus, G. palawanensis, G. porosus*, and *G. romblon*) by the following combination of characters (1) larger body size (SVL 95.5–108.2 mm for adult males; 86.8–100.0

for females); (2) dorsum brown with six diffuse transverse black bars adjacent to six transverse series of two or three cream spots; (3) high numbers of dorsal body scales (125–170 transverse midbody scales; 251–281 paravertebrals); (4) high number of sharply conical dorsal body tubercle rows (16–18 midbody; 31–37 paravertebrally); (5) 77–88 enlarged precloacal-femorals arranged in a continuous, uninterrupted series (pore bearing in males; lacking pores in females).

Comparison with Similar Species.—*Gekko rossi* differs from its phenotypically most similar Philippine congener, *Gekko porosus* (Batan and Itbayat islands, of the Batanes Island group, Fig. 1) by having dorsum brown with six diffuse transverse black bars adjacent to six
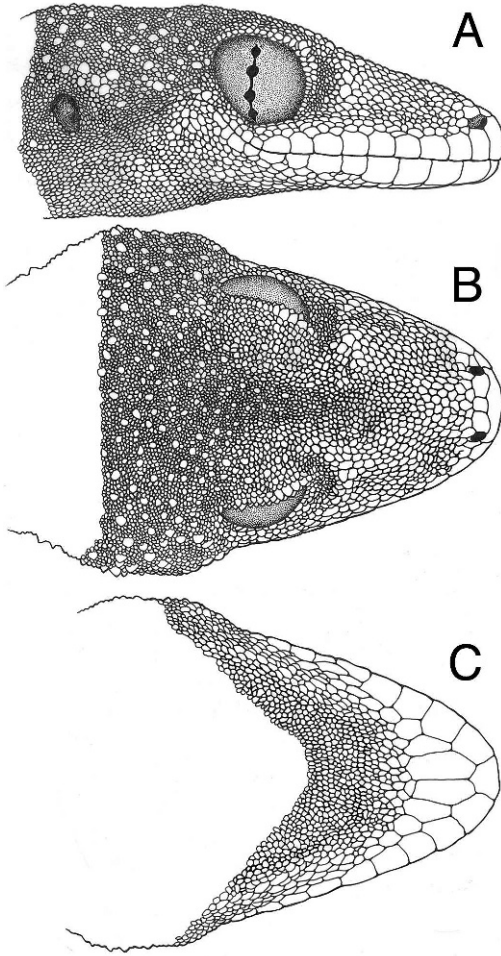
FIG. 4. Lateral (A), dorsal (B), and ventral (C) scalation of head of holotype of *Gekko rossi* (male PNM 9543). Scale bar = 5 mm.

FIG. 5. (A) Ventral view of left hand and (B) left side of precloacal-femoral pore-bearing scale series of holotype of *Gekko rossi* holotype, hemipenes excluded for simplicity (male PNM 9543). Scale bars = 5 mm.

transverse series of three cream spots (Fig. 3; vs. dark transverse bands and circular vertebral blotches in *G. porosus*, light spots absent), a greater number (125–170) of transverse midbody dorsal scales (vs. 88–103), a greater number (251–281) of paravertebral scales (vs. 173–191), the presence of sharply protuberant (vs. merely convex or slightly raised) dorsal tubercles, a greater number (31–37) of paravertebral tubercle rows (vs. 17–24), and by the absence of a modified distal femoral pore-bearing patch (vs. present, composed of a short series of 2 or 3 rows of pore-bearing scales [Brown et al., 2008:fig. 4C]). Finally, although body sizes of these two species overlap, adult males of *G. rossi* (SVL 95.5–108.2 mm) tend to be larger than *G. porosus* (91.0–96.7).

The new species differs from the morphologically similar *G. crombota* (Brown et al., 2008) by
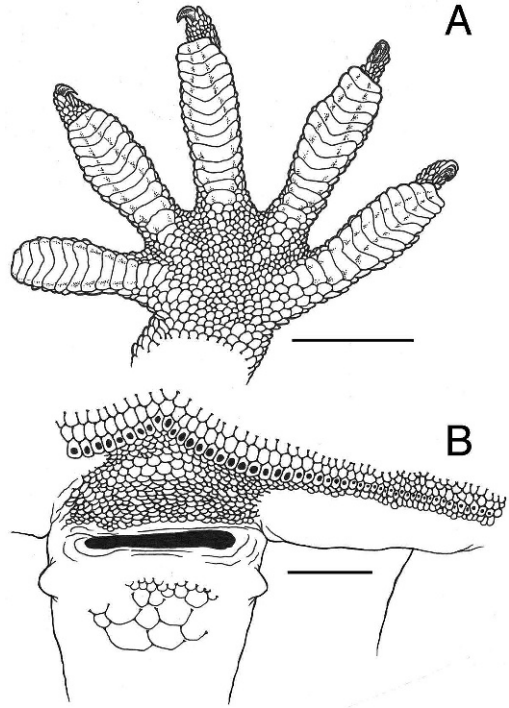
three longitudinal paravertebral rows of cream spots adjacent to diffuse transverse black bars (vs. presence of trilobed cream bars) on the body trunk; a tendency toward higher midbody dorsal scale counts (125–170 vs. 107–132); a greater number (251–281) of paravertebral scales (vs. 192–226); fewer (16–18) midbody dorsal tubercle rows (vs. 18–22); precloacal-femorals arranged in a continuous series (vs. 1 or 2 scale separation between precloacals and femorals; Brown et al., 2008:fig 4B); and a greater number (77–88) of precloacal-femoral pore-bearing scales (vs. 58–74).

The new species differs from *G. monarchus, G. mindorensis, G. romblon, G. ernstkelleri,* and *G. palawanensis* by larger male body size (95.5–108.2 mm SVL; Table 1); the only remaining Philippine species overlapping the body size of *G. rossi* are *G. gecko* (SVL 120.0–153.8 mm), *G, gigante* (89.7–104.7), and *G. athymus* (99.2–119.9). The number of precloacals distinguished *G. rossi* from *G. monarchus, G. mindorensis, G. romblon, G. gigante, G. ernstkelleri, G. palawanensis, G. athymus,* and *G. gecko* (Table 1). The absence of separated precloacal and femoral pore-bearing scales is shared (Table 1) with *G. porosus, G. monarchus, G. mindorensis, G. ernstkelleri, G. athymus,* and *G. gecko.* The new species has

fewer Toe IV scansors than *G. gigante, G. ernstkelleri, G. palawanensis,* and *G. athymus.* The new species has fewer (33–41) midbody ventrals than *G. gigante* (41–50) and *G. ernstkelleri* (42–48), more midbody dorsals than *G. monarchus* (96–112), *G. mindorensis* (102–125), *G. romblon* (102–108), *G. palawanensis* (114–121), and *G. athymus* (92–104). The new species has the highest paravertebral count (251–281) of any Philippine *Gekko* (Table 1) and more ventrals than all Philippine species except *G. crombota* (Table 1). Additionally, the new species has more paravertebral tubercle rows in the axilla-groin region than all Philippine species except *G. crombota* (Table 1) and is further distinguished from *G. athymus* by the presence (vs. absence) of dorsal body tubercles. Finally, dorsal coloration (dorsum brown with six diffuse transverse black bars adjacent to six transverse series of two or three cream spots) distinguishes *G. rossi* from the highly variable range of patterns exhibited by other Philippine *Gekko.* These and other differences are summarized in Table 1.

Description of Holotype.—Adult male (PNM 9543, formerly KU 304877; field No. RMB 5998; Figs. 3–5). SVL 98.4 mm; habitus robust, limbs well developed, relatively slender (but with femoral segments of hind limbs hypertrophied); TBL 16.7% SVL, 72.6% FL; 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 large, characterized by lightly hypertrophied temporal and adductor musculature, as wide as body at widest point; snout subtriangular, rounded at tip in dorsal and lateral aspect (Fig. 4A, B, C); HW 69.2% HL and 18.3% SVL; HL, 26.4% SVL; SNL 59.4% HW and 41.2% of HL; dorsal surfaces of head relatively smooth, with pronounced concave postnasal, prefrontal, interoribital, and parietal depressions; auricular opening large, round, oriented slightly lateroposteriorly from beneath temporal swellings on either side of head; tympanum very deeply sunken; orbits large, bordered by slightly distinct supraorbital crests; eye large, pupil vertical, its margin wavy (Fig. 3A); AO 59.6% ED, IOD 23.8% HW.

Rostral large, subrectangular, nearly twice as broad as high, with two dorsomedial depressions between raised posterodorsal projections that form the anterolaterally projecting edge of the nares and suture anteriorly with the supranasals; nostril surrounded by rostral, the first labial, and an enlarged, round, convex supranasal, an enlarged posterosupranasal, and two small postnasals; supranasals separated on either side by a single large internasal.

Total number of differentiated supralabials 13/14 (L/R; 10/11 to center of eye), bordered dorsally by one row of slightly differentiated snout scales; total number of differentiated infralabials 12/12 (9/9 to center of eye), bordered ventrally by one row of enlarged scales and four rows of only slightly differentiated chin scales; mental triangular; mental and first five infralabials greatly enlarged and wrapping onto ventral surfaces of chin, at least twice the size of individual infralabials 6–13; mental followed by a pair of slender, elongate postmentals; postmentals bordered posterolaterally by a secondary pair, more than one-half the length of first pair, and a tertiary pair of nonelongate, hexagonal lateral postmentals, not more than one-quarter the length of primary postmentals; postmental bordered posteriorly by 2 or 3 scale rows of slightly enlarged, irregular scales; followed immediately by a sharp transition to nondifferentiated chin and gular scales; postrictal scales slightly enlarged, 2 or 3 times the size of gular scales; remainder of undifferentiated gular scales very small, round, juxtaposed (Fig. 4C).

Dorsal cephalic scales highly heterogeneous and varied in shape and disposition; scales of rostrum somewhat enlarged, round, oval to subrectangular, and convex; postnasal, prefrontal, and interorbital depressions with noticeably smaller scales; palpebral scales heterogeneous, with some scales as small as adjacent interorbital region and others as large and raised as rostral scales; undifferentiated temporal region scales granular, flat to irregularly convex, reducing in size posteriorly, interspersed with numerous highly enlarged, protuberant and conical tubercles; nuchal region with small, juxtaposed, flat trunk scales interspersed with enlarged sharply conical body tubercles; throat and chin scales small, juxtaposed; gular and pectoral regions with enlarged cycloid, imbricate scales, increasing posteriorly through venter, becoming very enlarged and strongly imbricate.

Ornamental occiput scalation includes numerous conical tubercles on posterolateral portions of head (temporal, supratympanic, and postrictal regions; Figs. 3, 4) and a short curved series of 4–5 enlarged, bluntly conical preorbital scales (Figs. 3B, 4A, B); 45/41 total circumorbitals, differentiated into the following distinct regions: (1) 17/15 minute precircumorbitals, (2) 7/8 enlarged, flat, squarish circumoribtals dorsoanterior to orbit, (3) 9/8 transversely elongated fringe-like spiny ciliaria across dorsoposterior margin of orbit, gradually reducing to (4) 12/10 minute postcircumorbitals; a total of 45 interorbital scales (straight line distance from center of each eye, across both eyelids).

TABLE 1. Distribution of selected diagnostic characters in *Gekko rossi* and other Philippine species of *Gekko* (exclusive of the widespread *Gekko gekko* and *Gekko hokouensis* [a Japanese species probably erroneously included in the Philippine herpetofauna]). Measurements are presented in millimeters and all specimens (with the exception of the *Gekko porosus* holotype) are considered adults. Data from two juvenile paratypes of *G. rossi* were also excluded.

	rossi	crombota	porosus holotype	porosus adults	monarchus	mindorensis	romblon	gigante	ernstkelleri	palawanensis	athymus
N =	8m; 8f	4m; 9f	1f (juv)	3m	2m; 1f	22m; 13f	4m; 6f	5m; 3f	4m; 6f	3m; 5f	3m; 2f
Male SVL	95.5–108.2	85.5–117.9		91.0–96.7	56.2–80.7	55.0–88.2	62.7–89.2	89.7–104.7	82.0–92.1	57.2–65.7	99.2–119.9
Female SVL	86.8–100.0	85.1–106.9	49.3	91.0–96.7	40.6–69.7	68.2–70.9	58.6–72.5	79.7–87.9	78.0–88.0	44.5–61.8	88.2–117.1
Vertebral coloration	dark transverse bars & light spots	light tri-lobed bars	light circular blotches	indistinct transverse dark bands	dark transverse spot rows	dark thin transverse bands	light + dark vertebral blotches	dark paired blotches	white circular spots	dark paired spots	light + dark inverted V-shaped
Supralabials[a]	13–16	13–15	12	12, 13	11–13	11–13	11–14	11–13	15, 16	12–14	11–13
Preanofemorals	77–88	58–74	82[b]	74–80	31–40	52–66	71–84	52–66	36–42	64–70	20–24
Preanal and femoral series interrupted	–	+ (75%)	?[c]	–	–	–	+ (33%)	+ (28%)	–	+ (39%)	–
Distal femoral pore-bearing patch present	–	–	?[c]	+	–	–	–	–	–	–	–
Toe IV scansors	10–16	15–18	16	14–16	13–15	12–14	12, 13	16–19	17–19	16–19	18–22
Dorsal tubercles	protuberant	protuberant	convex	convex	protuberant to conical	protuberant	convex	protuberant	protuberant to conical	conical	absent
Internasals contacting rostral	1, 2	1	1	1	1, 2	1	1, 2	1	1	1	1
Scales contacting nostril	5	5	5	5	5	5	5	5	5, 6	5	5
Midbody ventrals	33–41	38–42	40	35–40	38–44	40–47	37–42	41–50	42–48	38–43	30–36
Midbody dorsals	125–170	107–132	100	88–103	96–112	102–125	102–108	123–135	112–127	114–121	92–104
Midbody tubercle rows	16–18	18–22	15	15–17	16–20	16–20	12–15	12–18	10–16	10–20	—
Vertebral tubercles in AGD	31–37	29–33	18	17–24	18–23	17–26	18–24	19–28	17–25	23–27	—
Paravertebrals in AGD	251–281	192–226	175	173–191	171–203	180–195	175–195	175–207	178–200	155–170	158–179
Ventrals in AGD	74–104	67–85	64	64–74	57–61	58–63	63–66	65–74	58–62	54–58	66–72

[a] Defined as all supralabials counted posteriorly to the point at which scales were no longer differentiated.
[b] Taylor (1922a,b) reported 80 preanofemorals; Brown and Alcala (1978) reported 70–72; we count 82 enlarged scales in the pore-bearing series.
[c] This character is impossible to assess in the immature female holotype (CAS 60526) because of the absence of pores in females.

Axilla–groin distance 46.9% SVL; undifferentiated dorsal body scales round to irregularly octagonal, convex, nonimbricate, relatively homogeneous; dorsals sharply transition to imbricate ventrals along the ventrolateral adipose fold; dorsals lack interstitial granules but interspersed with 18 irregularly transverse rows (36 paravertebral rows) of highly enlarged and protuberant, to strongly conical dorsal body tubercles; each dorsal tubercle with a raised, thornlike point; 144 transverse midbody dorsals; 250 paravertebrals between midpoints of limb insertions; 38 transversely arranged ventrals; scales on dorsal surfaces of limbs larger than dorsals, with interspersed enlarged tubercles extending down limbs, especially concentrated on radioulnar segment of forelimb (and covering entirety of hind limb), and terminating at the dorsal surfaces of hands and feet; enlarged patches of distinct imbricate scales present on wrist, anterior (prebrachial) surface of upper arm and thigh, on knee, and on distal ventral surface of hind limb, just before attachment of foot; scales on dorsal surfaces of hands and feet similar to dorsal limb scales; ventral body scales flat, cycloid, strongly imbricate, much larger than lateral or dorsal body scales, largest at midventral line.

Seventy-nine dimpled pore-bearing scales (Fig. 5B) in a continuous precloacal-femoral series (42 on L/37 on R) each punctured with pore bearing dark orange exudates; precloacal-femorals arranged in a wavy, obtuse, inverted ''V'' and continuing to the ends of the knee; inferred ''precloacal'' pores 2–3 times the diameter of inferred ''femoral'' pores (Fig. 5B); precloacals situated atop a substantial precloacal bulge that folds over into precloacal region in preserved specimen but was erect and protuberant in life (Fig. 5B); precloacal-femorals preceded by five similarly enlarged but nondimpled scale rows; precloacals followed by minute scales and two enlarged scales rows (absent following femorals); femoral series lacks preceding or following enlarged scale rows; scales lateroposterior to precloacal-femoral 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. 5A); no interdigital webbing; scansors of manus: 13/13, 12/12, 14/15, 13/15, and 13/14 on left/right digits I–V, respectively; pes: 10/13, 12/13, 15/16, 15/12, and 15/14 on left/right digits I–V, respectively; scansors of manus and pes bordered basally (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 to a conical nail; other terminal claw-bearing phalanges compressed, with large recurved claws, not free until beyond dilated portion of digit.

Tail base bordered by a single, greatly enlarged conical postcloacal spur on each side of vent; postcloacal swellings pronounced; hemipenes completely everted; regenerated portion long, 122% SVL; TD (not including basal postcloacal swelling) 93.7% TW; tail not depressed, nearly cylindrical, divided into distinct fracture planes/autotomy grooves (= whorls or annulations); dorsal surface heavily adorned with spinose, posteriorly raised tubercles, concentrated along posterior edge of annulations, caudals similar in size to dorsals; subcaudals enlarged, platelike, 3–5 rows per annulus, widely expanded to cover most of ventral surface or split into a pair of subcaudals along posterior margin of each annulus; distal portions regenerated; tail with clear autotomy scar and distally regenerated portion, 15 annuli before autotomy scar (80 mm), 7–8 annulations estimated in autotomized portion based on length (39 mm), for an approximate total of 22 or 23 annuli.

Variation.—The type series contains eight large adult males with hemipenes everted, two presumably juvenile females, and eight mature females (all gravid, with a pair of large white subovate eggs visible through skin of posteroventral body wall). Ranges of selected diagnostic meristic characters are presented in Table 1.

Coloration of Holotype in Ethanol.—Dorsal ground coloration of head, body, tail, and dorsal surfaces of limbs medium gray with scattered indistinct light and dark (almost black) gray blotches; six diffuse black bars traverse the axilla–groin distance, with two more above both the fore- and hind-limb insertions; accompanying each bar are three light gray spots, one vertebral and a pair of paravertebral ones on each side of the dorsal midline, bars and spots of consistent intensity throughout trunk.

Dorsal and lateral surfaces of head similar to dorsal ground color; temporal and nuchal region with small, distinct cream spots; palpebra darker gray than surrounding occiput; rostral and supralabial regions medium gray with cream spots on supralabials; infralabials very light gray; infra-auricular region light gray, contrasting with dark gray supra-auricular region.

Limbs colored as torso, lacking transverse banding; dorsal surfaces of hands and feet light gray; digits medium gray with cream spots; tail medium gray with dark gray bands every two or three caudal annuli; regenerated portion dark gray.

Ventral head, neck, and torso light cream; ventral surfaces of limbs slightly darker with black flecks; ventral surfaces of digits (scansors) dark gray; palmar and plantar surfaces medium gray; precloacofemoral region white with orange pores; ventral surfaces of tail medium gray, not banded.

Coloration of Holotype in Life.—From photographs by RMB (Fig. 3A–C). Dorsal ground coloration dark yellowish-brown (laterally) to dark brown (dorsally), with indistinct, irregularly scattered light gray and black blotches and small spots; dorsum with six diffuse bars light cream trilobed bars traversing the axilla-groin region, each bordered posteriorly by an accompanying set of three cream spots, one situated vertebrally, and flanked by a paravertebral pair on either side.

Dorsal nuchal region and posterior portions of head similar to trunk coloration but darker and with distinct, subcircular, cream spots and black blotches; similar cream spots span a line between the orbit and auricular opening; postrictal region flat purplish gray; labial scales purplish gray with cream spots on every third labial scale; rostral and circumnasal scales dark purplish gray; interorbital region, and parietal region medium gray with white spots; infralabial region and chin gray to light gray; gular region light gray to brownish-tan.

Dorsal surfaces of limbs light gray with numerous dark brown, black, and yellowish-cream spots; knees and elbows flat gray; dorsal surfaces of digits dark gray, with cream spots; dorsal and lateral portions of tail banded alternating dark gray and cream (corresponding to every third or fourth tail annulus); distal autotomy regrowth dark brown to dark gray, nonbanded.

Ventral body and limbs yellowish-cream with scattered gray and dark brown flecks, especially on chin and ventral surfaces of limbs; precloacalfemoral region yellow with dark orange pores, contrasting distinctly with posterior surfaces of thighs; limbs gray, fading to yellow at wrists and ankles; palmar and plantar surfaces of manus and pes yellowish with light gray distal portions and darker subdigital scansors; ventral tail yellowish, fading to cream distally, lacking transverse bars, regenerated portion solid brown; eye gold, with radiating purple lines surrounding crenulated black pupil.

Color Variation.—Dorsal color pattern is somewhat variable in the type series. In some specimens, transverse banding is relatively complete and continuous (KU 304876, PNM 9538, 9539, 9541) and in others (KU 304917, 304918; PNM 9540), the diffuse black transverse banding is more or less discontinuous and irregularly broken into transverse blotches. In others (KU 304885, 304924, 304927, 304931; PNM 9091), bands are distinctly interrupted vertebrally and dorsolaterally, with paired black squarish spots on either side of the vertebral line (accompanying the transverse series of three paravertebral cream spots). In three specimens (KU 304916, 304919, 304923), dark transverse banding is faint or absent and dorsal coloration is limited to paired cream paravertebral spots on a brown background.

Juveniles (KU 304876, PNM 9541) are patterned more brightly than adults, with more intensely contrasting light and dark dorsal coloration with tail banding nearly black and white. In the place of paired paravertebral cream spots, juveniles possess trilobed cream bars, reminiscent of adult coloration in *G. crombota*.

Ventral coloration nearly invariant: ventral body surfaces are cream to light gray (yellowish in life); subcaudal coloration is light to dark gray. Only in the two juveniles does the black and white transverse banded caudal pigmentation wrap around to the ventral surface of the tail. In life, males had a more brightly colored yellow (nearly orange in some specimens) congregation of pigment in the precloacal region, along the line of femoral scales, overlying the hemipenal bulge, and on wrists and ankles. Eye coloration was consistently gold in adults, but silvery in juveniles.

Distribution and Natural History.—The new species is known only from Calayan Island where it was collected low (<5 m) on trunks and buttresses of trees or on the faces of rocky outcrops and in limestone caves in primary dipterocarp forest at moderate elevations (300–400 m) far from the island's coast (Fig. 6). Given the island's geological history of isolation (McDermott et al., 1993; Yang et al., 1996; Marini et al., 2005), we consider it extremely unlikely that *G. rossi* will be encountered on other islands in the Babuyan island group, the Batanes island group, or mainland Luzon.

Our impression is that the new species is very common in internal forested regions at the type locality, but we note that we did not find it near the island's denuded coast. It is possible that only the forested areas of Calayan Island (Fig. 6) are optimal habitat for this species.

Other gekkonids encountered on Calayan Island include *Gehyra mutilata, Hemidactylus frenatus,* and *Lepidodactylus* sp. Calayan Island is the type locality of the rare *Luperosaurus macgregori*, although it has not been reported on this island since the original description (Stejneger, 1907) but has recently been rediscovered on Babuyan Claro Island (Brown and Diesmos, 2000; Brown et al., 2007, 2008).
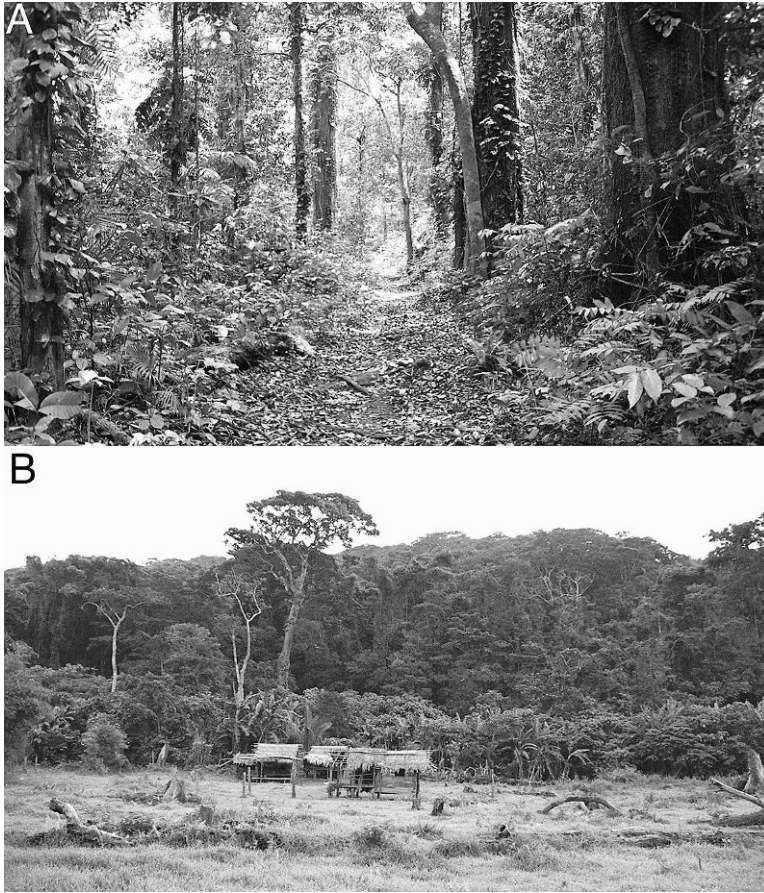
F<small>IG</small>. 6. *Gekko rossi* habitat at the type locality. Forest interior at 1,000 m (A); forest edge at 300 m (B). Photographs by M. Babon and A. Bajarias Jr.

Etymology.—We are pleased to name this new species of *Gekko* for Charles Andrew Ross in recognition of his numerous contributions to the systematics of reptiles and amphibians of the Philippines and his particular enthusiasm for the herpetofauna of the Babuyan islands. Suggested common name: Ross' Calayan Gecko.

D<small>ISCUSSION</small>

The description of *G. rossi* brings the total number of endemic Philippine species of the genus *Gekko* to nine (11 species when nonendemics *G. gecko* and *G. monarchus* are included and the single doubtful record of *G. hokouensis* is excluded). We are certain that this number underestimates actual species diversity, and we have previously noted (Brown et al., 2008) numerous taxonomic problems that must be addressed before a comprehensive understanding of Philippine gekkonid evolution can be

realized. With regard to the *Gekko* fauna of the northern Philippines, the Babuyans and Batanes island groups require additional survey work before we can be reasonably certain that the total gekkonid fauna is known. Endemism in both island groups (Ota and Crombie, 1989; Lazell, 1992a; Ota and Ross, 1994) is expected to be high because of their isolation (Yang et al., 1996; Marini et al., 2005; Brown et al., 2008). The Batanes support endemic populations of pit vipers (Leviton, 1964), gekkonid lizards (Taylor, 1922a; Ota and Crombie, 1989), agamid lizards (Lazell, 1992), and snakes of the genus *Lycodon* (Ota and Ross, 1994). The Babuyan Islands are home to endemic lizards of the genera *Luperosaurus* (Stejneger, 1907) and *Gekko* (Brown et al., 2008) and multiple species of snakes in the genus *Lycodon* (Ota and Ross, 1994).

We are aware of at least three additional, morphologically distinct, undescribed *Gekko* species in the Babuyans (Fuga, Dalupiri, and

Camiguin Norte island populations; H. Ota and R. Crombie, unpubl. data), and we suspect that several additional new species will be discovered if biologists are able to visit other Philippine islands isolated by deep water. In particular, northern populations (all currently considered *G. porosus*) require reevaluation with fresh specimens and genetic data once the Batanes Islands have been thoroughly surveyed. The endemic *Gekko* of Lanyu Island, south of Taiwan (*G. kikuchii*; Oshima, 1912) appears to be more closely related to Philippine taxa than to other Taiwanese and Ryukyu Archipelago species (e.g., *G. japonicus, G. hokouensis, G. yakuensis, G. shibatai, G. vertebralis*; Ota, 1989; Ota et al., 1989; Toda et al., 2001, 2008), but phylogenetic appraisal of this taxonomic expectation must await the availability of genetic samples. *Gekko kikuchii* has been phenotypically allied to *G. mindorensis* (Bauer, 1994; Ferner et al., 2001; R. Crombie and H. Ota, pers. comm.); it is not morphologically similar to the new species described here.

The unexpected relationships elucidated by our phylogenetic estimate of northern Philippine *Gekko* warrant comment. The southern Babuyans lineages (Dalupiri and Camiguin Norte Islands) form a strongly supported clade, whereas the *Gekko* of the northern Babuyans (Calayan and Babuyan Claro) and Batan Island appear to be closely related. This result is contrary to expectations based on previous discussions of species distributions that have emphasized longitudinal patterns of species endemism. Most studies to date have identified endemic species or species complexes on either the eastern Babuyan-Batanes Island bank or the western Babuyan-Batanes bank (Ota and Crombie, 1989; Lazell, 1992; Ota and Ross, 1994). We enthusiastically await the results of several additional phylogenetic studies involving other northern Philippine reptile lineages to determine whether the latitudinal (north–south divergence) or longitudinal (east–west divergence) pattern prevails.

Surprisingly, *G. rossi* appears to be most closely related to *G. porosus*, rather than to the more geographically proximate island lineages such as those on Dalupiri or Camiguin Norte (Fig. 2). Relationships supported by phylogenetic analysis of the ND2 locus were very well supported (likelihood and parsimony bootstraps of 99 to 100 throughout) with the exception of the node subtending the (*G. crombota* [*G. rossi* + *G. porosus*]) clade. Thus, we are unable to assert with complete confidence the systematic position of *G. crombota* from Babuyan Claro Island. However, we can state with a high degree of confidence that the combination of genetic + morphological data

support the recognition of a minimum of six evolutionary lineages (= species) that occur north of Luzon Island. With the exception of the two undescribed species on Dalupiri and Camiguin Norte, which are separated by only 2.6% uncorrected sequence divergence (but are morphologically highly distinct species; RMB and CO, pers. obs.), all taxa represented in our analysis show 9.3–14.6% divergence and all taxa are readily distinguishable on the basis of scalation, body size, and color pattern.

If island emergence is followed by colonization (with some necessary lag time as habitats become suitable to support terrestrial vertebrates), we might expect island age to be correlated with the level of genetic divergence exhibited by endemic lineages inhabiting those islands. If the processes of dispersal and establishment of populations is relatively constant, this expected correlation may be strong (Steppan et al., 2003). Alternatively, a lack of a correlation would support the presumption that historical contingency and chance may be responsible for establishment of lineages on oceanic islands. Finally, if a strong correlation is present and individual outliers can be identified, the identification of recent dispersal events may be possible.

There is no clear relationship between genetic divergence and estimated island age in northern Philippine *Gekko*. Radiometric ages of volcanic flows of Babuyan and Batanes Islands (Yang et al., 1996) provide a rough estimate or minimum date of the volcanic activity that forced these islands above sea level. Although some highly divergent lineages such as *G. porosus* and *G. rossi* are endemic to the relatively old islands of Batan (9.36–2.0 mya) and Calayan (6.50–4.37 mya), other highly divergent lineages such as *G. crombota* are found on extremely young islands such as Babuyan Claro (1.70–0.80 mya), suggesting error in radiometric dating techniques, recent dispersal from an unidentified source, or a combination of these and other factors. Finally, the close sister relationship (with a pairwise genetic distance of only 2.6%) between the lineages endemic to Dalupiri (*Gekko* sp. A) and Camiguin Norte (*Gekko* sp. B) cannot be explained by the estimated island ages (Dalupiri: 22.40 mya; Camiguin Norte: 2.82–0.40 mya) unless we assume recent dispersal from the former to the latter. Thus, in the absence of a straightforward correlation, we feel it more likely, at least for this relatively young group of islands and their endemic geckos, that colonization of the islands north of Luzon has not been a steady, constant process (see discussion in Lazell, 1992). Rather, we assume that dispersal to, and successful colonization of, islands north of Luzon is a stochastic process

that is dependent upon an array of abiotic factors (weather, wind, ocean current, and chance) and biotic components of the environment (e.g., numbers of colonists, competition from previously established gecko populations, etc.).

Aside from the new species reported here, numerous Philippine gekkonid taxa await description, including several additional species of *Gekko* from the Babuyans and Batanes island groups, morphologically cryptic *Gekko* lineages masquerading in the taxonomy of ''widespread'' species complexes such as *G. mindoresis* (RMB, CDS, and ACD, unpubl. data), several undiagosed lineages of the genus *Cyrtodactylus* (Welton et al., in press), and undescribed species of the genus *Luperosaurus* (Brown et al., 2007; Gaulke et al., 2007; Brown et al., in press).

It is very clear that Philippine gekkonid diversity is substantially underestimated (Ota and Crombie, 1989; Brown et al., 2007, 2008; Gaulke et al., 2007). We expect the numbers of Philippine gekkonid taxa to minimally double in the near future, and we hope an improved understanding of the evolutionary diversity in this conspicuous group of Philippine vertebrates will contribute to conservation efforts aimed at preserving the remaining forested regions of the country.

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APPENDIX 1

Specimens Examined

All specimens examined are from the Philippines unless otherwise noted. Numbers in parentheses

indicate the number of specimens examined for each species.

Gekko athymus.—(7) PALAWAN ISLAND, PALAWAN PROVINCE, approximately 10 km west-southwest of Iwahig: CAS 137677; approximately 8–9 km south of Balico: CAS-SU 23119 (holotype); approximately 20 km southwest 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 crombota.—(21) 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) PANAY ISLAND, ANTIQUE PROVINCE, Municipality of Pandan, Barangay Duyong, Duyong Hillside (= ''Mt. Lihidian''), 300 m.a.sl.: PNM 9152–54; KU 300196–300202.

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

Gekko gigante.—(13) SOUTH GIGANTE ISLAND, ILOILO PROVINCE, Municipality of Carles, Tantangan: CAS 124315–124317 (paratypes); NORTH GIGANTE ISLAND, ILOILO PROVINCE, Municipality of Carles: CAS 124866–124867 (Paratypes); Barangay Asloman: KU 302716–302720, 305138–305140.

Gekko hokouensis.—(1) ''Tablas Island'' (presumably in error): FMNH 17812 (*Luperosaurus amissus* holotype*)*.

Gekko mindorensis.—(56) 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.—(6) PALAWAN ISLAND, PALAWAN PROVINCE, approximately 1.5 km west-southwest of Iwahig: CAS-SU 28416; approximately 5 km south-southeast of Iwahig: CAS-SU 28496; approximately 7 km west-northwest of Iwahig: CAS-SU 28554; Municipality of Brookes Point, Mt. Mantalingahan: KU 309362; INDONESIA, SULAWESI ISLAND: BSI 340, 819 (specimens deposited at Museum Zoologicum Bogoriense, Cibinong, Jakarta, Indonesia).

Gekko palawanensis.—(24) PALAWAN ISLAND, PALAWAN PROVINCE, 7 km west-northwest of Iwahig: CAS 17318; 8 km west of Iwahig: CAS 17319; approximately 9 km west of Iwahig: CAS 17320–17322; 19 currently uncataloged specimens at KU (RMB 7460, 7531, 7561–7562, 7589–7590, 7615, 7642. 7726–7727, 7780, 7878, 7922–7924, 7930–7931, 7937–7938).

Gekko porosus.—(8) BATAN ISLAND, BATANES PROVINCE, 3 km east-northeast of Basco Town: USNM 266519, 291387; Mahatao: USNM 266517; Municipality of Basco, outskirts of Basco Town, near airport: PNM 9532–9536; ITBAYAT ISLAND: CAS 60526 (holotype).

Gekko romblon.—(15) SIBUYAN ISLAND, ROMBLON PROVINCE, Taclobo Barrio: CAS 139180–139182 (paratypes); ROMBLON ISLAND, ROMBLON PROVINCE, Municipality of Romblon, Barangay Li-O: KU 302733–302742, 303977–303978.

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

Gekko sp. B.—(24) 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.

APPENDIX 2. Voucher specimens corresponding to DNA sequences used in this study.

Species	Source	GenBank accession numbers (ND2)	Locality
Gekko gecko	Macey et al. (1999)	AF114249	Kathu District, Phuket Province, Phuket Island, Thailand
Gekko smithi	JAM 1712 (tissue only)	FJ487868	Ulu Gombak Field Studies Center, Selangor, West Malaysia; deposited in the Forest Research Institute of Maysia (FRIM) reference collection
Gekko monarchus	BSI[a] 340	FJ487869	Tangkoko Nature Reserve, Kabupaten Minihasa, Sulawesi Utara Province, Sulawesi Island, Indonesia
Gekko monarchus	BSI 819	FJ487870	Bogani Nani Wartabone National Park, Desa Lombongo, Kabupaten Bone Bolango, Gorontalo Province, Sulawesi Island, Indonesia
Gekko mindorensis	KU 302667	FJ487887	Mindoro Island, Mindoro Oriental Province, Philippines
Gekko mindorensis	KU 303876	FJ487885	Mindoro Island, Mindoro Oriental Province, Philippines
Gekko mindorensis	KU 303959	FJ487886	Mindoro Island, Mindoro Oriental Province, Philippines
Gekko rossi	KU 304876	FJ487871	Calayan Island, Babuyan Island Group, Cagayan Province, Philippines
Gekko rossi	KU 304877	FJ487873	Calayan Island, Babuyan Island Group, Cagayan Province, Philippines
Gekko rossi	KU 304917	FJ487872	Calayan Island, Babuyan Island Group, Cagayan Province, Philippines
Gekko crombota	KU 304809	FJ487875	Babuyan Claro Island, Babuyan Island Group, Cagayan Province, Philippines
Gekko crombota	KU 304821	FJ487876	Babuyan Claro Island, Babuyan Island Group, Cagayan Province, Philippines
Gekko crombota	KU 304830	FJ487874	Babuyan Claro Island, Babuyan Island Group, Cagayan Province, Philippines
Gekko sp. A Dalupiri	KU 307023	FJ487883	Dalupiri Island, Babuyan Island Group, Cagayan Province, Philippines
Gekko sp. A Dalupiri	KU 307024	FJ487884	Dalupiri Island, Babuyan Island Group, Cagayan Province, Philippines
Gekko sp. A Dalupiri	KU 307054	FJ487882	Dalupiri Island, Babuyan Island Group, Cagayan Province, Philippines
Gekko sp. B Camiguin Norte	KU 304583	FJ487879	Camiguin Norte Island, Babuyan Island Group, Cagayan Province, Philippines
Gekko sp. B Camiguin Norte	KU 304585	FJ487877	Camiguin Norte Island, Babuyan Island Group, Cagayan Province, Philippines
Gekko sp. B Camiguin Norte	KU 304606	FJ487878	Camiguin Norte Island, Babuyan Island Group, Cagayan Province, Philippines
Gekko porosus	PNM 9532	FJ487880	Batan Island, Batanes Island Group, Philippines
Gekko porosus	PNM 9533	FJ487881	Batan Island, Batanes Island Group, Philippines

[a] BSI = Sulawesi Biotic Surveys and Inventories Project sample, deposited in Museum Zoologicum Bogoriense (National Museum of Indonesia, Cibinong, Java).