

First Record of the *Pseudogekko brevipes* Complex from the Northern Philippines, with Description of a New Species

CAMERON D. SILER^{1,2,9}, DREW R. DAVIS³, JESSA L. WATTERS¹, ELYSE S. FREITAS^{1,2}, OLIVER W. GRIFFITH⁴, JAKE WILSON B. BINADAY⁵, ATHENA HEART T. LOBOS⁶, ACE KEVIN S. AMARGA⁷, AND RAFAE M. BROWN⁸

¹ Sam Noble Oklahoma Museum of Natural History, University of Oklahoma, 2401 Chautauqua Avenue, Norman, OK 73072, USA

² Department of Biology, University of Oklahoma, 2401 Chautauqua Avenue, Norman, OK 73072, USA

³ Department of Biology, University of South Dakota, 414 East Clark Street, Vermillion, SD 57069, USA

⁴ Department of Ecology and Evolutionary Biology, Yale University, 850 West Campus Drive, West Haven, CT 06516, USA

⁵ Matagbac, Tabaco City, Albay, Philippines

⁶ Cullat, Daraga, Albay, Philippines

⁷ Crop Protection Cluster, College of Agriculture, University of the Philippines Los Banos, Laguna, Philippines

⁸ Biodiversity Institute and Department of Ecology and Evolutionary Biology, University of Kansas, 1345 Jayhawk Boulevard, Lawrence, KS 66045, USA

ABSTRACT: The Philippines possess a remarkable species diversity of amphibians and reptiles, much of which is endemic to this Southeast Asia island nation. Lizard diversity in the family Gekkonidae is no exception, with more than 80% of the country's gecko species endemic to the archipelago, including the entire genus of False Geckos (*Pseudogekko*). This small radiation of diminutive, slender, arboreal forest species has been the focus of several recent phylogenetic and systematic studies that have highlighted the prevalence of undocumented species concentrated in several geographical regions within the archipelago. Newly available genetic data have led to the revision of two species complexes in the genus *Pseudogekko*, one of which is the focus of this study. We describe a new member of the *Pseudogekko brevipes* complex, which represents the first population from this species group discovered in the Luzon Faunal Region. Because of the species' secretive nature, rarity, or restricted geographic range, it has gone undetected despite recent biodiversity surveys targeting the central and northern portions of the Bicol Peninsula. We evaluate both morphological and genetic data to support the recognition of the new species. All three members of the *P. brevipes* complex have allopatric distributions situated within three of the archipelago's distinct faunal regions. The recognition of the new species increases the total number of taxa in the genus *Pseudogekko* to nine species.

Key words: Bicol region; Endemism; Faunal region; Gekkonidae; Mt. Bulusan; Mt. Mayon; Obligate forest species; Rare species

THE PHILIPPINES is home to a remarkable diversity of gecko species. Currently, 57 species of the family Gekkonidae are recognized, 46 of which (nearly 83%) are endemic to the archipelago. This fauna represents seven distinct genera of geckos: *Cyrtodactylus* (eight endemic species; Welton et al. 2009, 2010a,b); *Gekko* (12 endemics; Rösler et al. 2006; Brown et al. 2008, 2009, 2011; Linkem et al. 2010); *Hemiphyllodactylus* (two endemics; Grismer et al. 2013); *Lepidodactylus* (seven endemics; Brown and Alcalá 1978; Siler et al. 2014a); *Luperosaurus* (eight endemics; Brown and Diesmos 2000; Brown et al. 2007, 2010, 2011, 2012a; Gaulke et al. 2007); *Pseudogekko* (eight endemics; Taylor 1922; Siler et al. 2014a,b, 2016a; Davis et al. 2015); and *Ptychozoon* (one endemic; Brown et al. 1997, 2012b). The number of recognized endemic gecko species has increased substantially over the last decade as more vouchered specimens have become available in museum collections and as molecular phylogenetic investigations have aided in the identification of divergent genetic lineages (i.e., Siler et al. 2014b). Many new taxonomic discoveries have resulted from efforts to survey biodiversity, with scrutiny of insular allopatric populations of putatively widespread species (Welton et al. 2009, 2010a,b; Siler et al. 2014a,c, 2016b; Davis et al. 2014, 2016; Geheber et al. 2016). Often these widespread taxa, recognized historically to span multiple faunal regions, or Pleistocene Aggregate Island Complexes (PAICs; Brown and Guttman 2002; Brown and Diesmos 2009), have been shown to constitute complexes of multiple

species, each of which is restricted to a specific faunal region, island group, or isolated geographic area within a single island (i.e., Sierra Madre versus Cordillera mountain ranges, Luzon Island; Brown et al. 2012c, 2013).

False Geckos (genus *Pseudogekko*) represent a phenotypically distinctive clade of small, slender, arboreal lizards found exclusively in the Philippines (excluding Palawan and Mindoro PAICs; Siler et al. 2014a,b, 2016a; Davis et al. 2015). All eight species are obligate primary forest taxa (Brown and Alcalá 1978). Unfortunately, most species are represented globally by only a few vouchered specimens in museums, which might be artifacts of their rarity, highly specialized microhabitat preferences, cryptic coloration and morphology, secretive behavior, or any combination thereof. Despite few available vouchered genetic samples, recent studies still have managed to highlight potential cryptic species diversity, particularly among populations sampled for two species historically recognized as widespread in the Philippines: *Pseudogekko compresicarpus* and *Pseudogekko brevipes* (Siler et al. 2014a,b, 2016a; Davis et al. 2015). In fact, the results of studies on both species indicate that each lineage might represent species complexes. For example, a recent taxonomic study of *P. brevipes* resulted in the identification of two lineages: *P. brevipes* and *Pseudogekko atiorum* (Davis et al. 2015). The extent of distribution of *P. brevipes* was defined as Bohol, Leyte, and Samar islands of the Mindanao PAIC and a new species, *Pseudogekko atiorum*, was recognized from Negros and Siquijor islands of the West Visayan PAIC (Davis et al. 2015: fig. 1). To date, no members of this species complex have been documented from the Luzon PAIC of the northern Philippines (Fig. 1).

⁹ CORRESPONDENCE: e-mail, camsiler@ou.edu

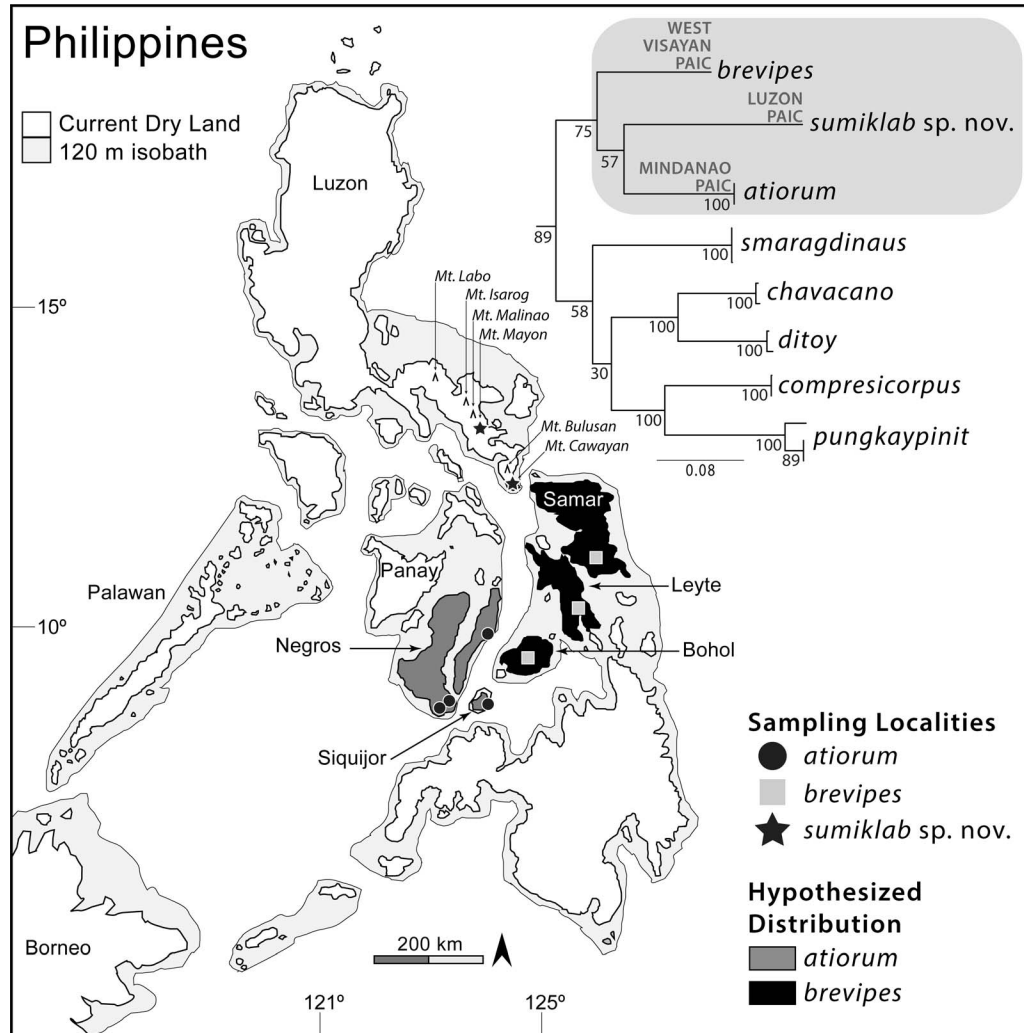


FIG. 1.—Map of the Philippine Islands showing the collection localities of the holotype and paratype, and predicted–potential geographic range of congener species (see shading key; additional data from Brown and Alcalá 1978; Ferner et al. 2000; Davis et al. 2015; Supsup et al. 2016), and localities where members of the *Pseudogekko brevipes* complex have been sampled. Topology in upper right depicts hypothesized relationships among species of *Pseudogekko* based on results of maximum likelihood analyses (support at each node represented by maximum likelihood bootstrap values).

During recent faunal surveys, two unique *Pseudogekko* specimens were captured along streams at low elevations in the foothills of two volcanoes, Mts. Mayon and Cawayan, of the southern Bicol Peninsula of Luzon Island. The two adult female specimens represent a new species, possessing a suite of molecular markers and diagnostic morphological features that readily differentiate them from all congeners from the Luzon PAIC (*P. compresicorpus* and *Pseudogekko smaragdinus*) and from other, more-closely related congeners of the *P. brevipes* complex (sensu Davis et al. 2015).

In this paper, we use a combination of body size and shape, meristic data (scale counts), and color pattern to demonstrate that the southern Bicol Peninsula *Pseudogekko* population represents a distinct evolutionary lineage (Wiley 1978; de Queiroz 1998, 1999) worthy of taxonomic recognition. Our findings are bolstered by phylogenetic analyses of a multilocus molecular dataset which confirms the new lineage's affinities and genetic divergence from currently recognized species. Here we describe this new

species, provide technical illustrations of key diagnostic traits, and discuss its natural history, ecology, and geographic distribution.

MATERIALS AND METHODS

Field Work and Specimen Preservation

We conducted fieldwork on Luzon Island in the Philippines (Fig. 1) in February and March 2016 and January and February 2017. Two specimens of the new species were collected during nocturnal surveys along streams at low elevation in the foothills of Mts. Mayon and Cawayan, Albay and Sorsogon provinces, southern Luzon. We euthanized specimens with aqueous chloretone, dissected genetic material (liver, preserved in 95% ethanol), fixed vouchers in 10% formalin, and eventually (<2 mo) transferred specimens to 70% ethanol. Museum abbreviations for specimens examined (Appendix II) or sequenced in this study follow those of Sabaj (2016).

TABLE 1.—Best-fit models of evolution, inferred by Akaike information criteria and applied in partitioned, model-based phylogenetic analyses of the multilocus phylogenetic dataset. The combined dataset consisted of 15 ingroup samples representing the new species and seven of the eight congeners (vouchered genetic material remains unavailable for *Pseudogekko isapa*) and four outgroup samples representing the genera *Cyrtodactylus* and *Luperosaurus*.

Partition	Best-fit model	AIC model applied	Number of characters
NADH 2, 1st codon position	GTR+ Γ	GTR+ Γ	337
NADH 2, 2nd codon position	GTR+ Γ	GTR+ Γ	337
NADH 2, 3rd codon position	GTR+ Γ	GTR+ Γ	337
16S	GTR+ Γ	GTR+ Γ	589
PTGER4, 1st codon position	HKY	GTR+ Γ	163
PTGER4, 2nd codon position	HKY	GTR+ Γ	163
PTGER4, 3rd codon position	HKY+ Γ	GTR+ Γ	162

Morphological Data

We examined fluid-preserved specimens for morphometric and meristic characters and compared these measurements with those published in our recent work on the genus (Siler et al. 2014a, 2016a; Davis et al. 2015). Sex was determined by visual confirmation of two eggs within the body of the holotype specimen and gonadal inspection in the paratype, measurements were taken with digital calipers (± 0.1 mm), and scale counts were made by CDS and RMB using a microscope. Character selection and methods for scoring were based on Siler et al. (2014a): snout–vent length (SVL); tail length; total length; tail width; tail depth; absolute and relative head length; head width; head depth; midbody width; snout length; eye diameter; eye–nares distance; internarial distance; interorbital distance; axilla–groin distance; femur length; tibia length; supralabials; infralabials; circumorbitals; preloacal pore series; Finger-III scensors; Toe-IV scensors; paravertebrals; and ventrals.

Taxon Sampling and DNA Analysis

We extracted total genomic DNA from the newly collected tissue using Fujita's modified guanidine thiocyanate extraction method (Esselstyn et al. 2008) and used available genomic extractions for congener species from our recent work on the genus (Siler et al. 2014a,b; Davis et al. 2015). We sequenced the 16S ribosomal RNA mitochondrial gene for 15 ingroup samples representing the new species and seven of the eight congeners (vouchered genetic material remains unavailable for *Pseudogekko isapa*; Siler et al. 2016a), and we amplified and sequenced the nuclear locus prostaglandin E receptor 4 (PTGER4) from the holotype to render our data compatible with previously published datasets. Four individuals were chosen as outgroup taxa, representing the genera *Cyrtodactylus* (*C.*

annulatus, *C. philippinicus*) and *Luperosaurus* (*L. cumingii*, *L. angliit*), based on Brown et al. (2012a) and Siler et al. (2014a,b). Primers and protocols for all novel polymerase chain reaction and sequencing efforts for PTGER4 followed Siler et al. (2014b) and for 16S followed Palumbi et al. (1991). Previously published sequence data for the mitochondrial NADH dehydrogenase subunit 2 (ND2) gene and PTGER4 for members of the genus *Pseudogekko* were available on GenBank (Appendix I; Siler et al. 2014a,b). Numerous attempts to amplify ND2 for the new species were unsuccessful. Novel sequence data were deposited in GenBank (Appendix I).

Alignment and Phylogenetic Analysis

Initial alignments were produced in MUSCLE (Edgar 2004) with minimal manual adjustments. The ND2 and PTGER4 datasets were partitioned by codon position for protein-coding regions, and 16S was treated as a single partition. We employed the Akaike information criterion (AIC), as implemented in jModelTest v2.1.10 (Posada 2008), to explore best-fit models of nucleotide substitutions for each partition (Table 1). Following observed absence of well-supported incongruence between datasets (PTGER4, 16S, ND2), we combined and concatenated our data and performed partitioned maximum likelihood (ML) analyses in RAxML-VI-HPC v7.0 (Stamatakis 2006). The more complex model (GTR+ Γ) was used for all subsets (Table 1), and 100 replicate ML inferences were performed for each analysis. Each inference was initiated with a random starting tree, and nodal support was assessed with 100 bootstrap pseudoreplicates (Stamatakis et al. 2008). We calculated percent uncorrected pairwise distances separately for mitochondrial (mtDNA) and nuclear (nuDNA) datasets using PAUP* v4.0 (Swofford 2002; Table 2).

TABLE 2.—Mean uncorrected pairwise sequence divergence (%) for mitochondrial data (16S ribosomal RNA, below diagonal) and nuclear data (prostaglandin E receptor 4, above diagonal) for the eight major lineages of *Pseudogekko* recovered in phylogenetic analyses (Fig. 1). Genetic samples from *P. isapa* are unavailable. Percentages on the diagonal represent intraspecific genetic diversity for mitochondrial data, when sampling permitted (bolded for emphasis). (—) = information on intraspecific genetic variation not available.

	<i>sumiklab</i>	<i>atiorum</i>	<i>brevipes</i>	<i>chavacano</i>	<i>compresicorpus</i>	<i>ditoy</i>	<i>pungkaupinit</i>	<i>smaragdinus</i>
<i>sumiklab</i>	—	0.8	1.0	2.0	1.8	1.8	1.6	2.0
<i>atiorum</i>	11.0	0.0	0.4	1.2	1.0	1.0	1.0	1.2
<i>brevipes</i>	11.1	10.8	—	1.2	1.0	1.8	0.8	1.2
<i>chavacano</i>	13.1	12.1	11.3	0.4	0.6	0.6	1.0	1.6
<i>compresicorpus</i>	13.2	13.4	12.2	8.9	0.2	0.4	0.8	1.4
<i>ditoy</i>	13.8	13.4	12.7	9.1	12.3	0.0	0.6	1.4
<i>pungkaupinit</i>	12.6	12.7	12.4	12.0	9.6	13.7	0.0	1.8
<i>smaragdinus</i>	12.0	11.2	12.0	11.2	12.8	12.4	12.7	0.0

TABLE 3.—Summary of mensural characters in all known species of *Pseudogekko*. Sample size, body length, and total length among males and females, and general geographical distribution are included for reference. Characters summarized for adult specimens only. SVL, axilla–groin distance, total length, midbody width, head length, head width, and snout length given as a range (mm) over mean \pm 1 standard deviation (SD); all body proportions given as a range (percentage) over mean \pm 1 SD. See Appendix II for listing of specimens examined. (—) = data unavailable due to vouchered specimens being female only; N/A = tail of one of the two examined specimens is short and regenerated, and therefore not included in the total length range reported.

Character	<i>sumiklab</i> (2 female)	<i>atorum</i> (8 male, 7 female)	<i>brevipes</i> (1 male, 3 female)	<i>characano</i> (1 male, 1 female)	<i>compressicornis</i> (3 male, 5 female)	<i>ditoy</i> (1 male, 1 female)	<i>isapa</i> (1 male, 2 female)	<i>pingkaypinit</i> (4 male, 2 female)	<i>smaragdinus</i> (16 male, 17 female)
Range	Luzon Faunal Region	Western Visayan Faunal Region	Mindanao Faunal Region	Western Mindanao Island	Luzon Faunal Region	Samar and Leyte islands	Romblon Island Group	Mindanao Faunal Region	Polillo Island and Bicol Peninsula (Luzon Island)
SVL (male)	41.8, 46.6	41.1–52.5 (47.0 \pm 4.5)	39.0	55.9	55.9–58.8 (57.6 \pm 1.5)	49.4	63.4	66.6–76.8 (71.8 \pm 5.1)	54.2–64.3 (59.4 \pm 2.5)
SVL (female)	23.6, 25.8	19.4–28.4 (24.8 \pm 2.4)	34.5–42.4 (38.6 \pm 4.0)	54.7	54.9–59.7 (57.1 \pm 2.6)	52.6	62.1	75.2–75.3	50.2–61.7 (57.4 \pm 3.5)
Axilla–groin distance	87.8, 91.0	80.2–113.5 (97.3 \pm 13.0)	72.0–87.5 (77.3 \pm 7.3)	26.7–30.0	27.0–32.6 (30.4 \pm 1.8)	25.1–29.7	32.1–33.0	37.2–41.2 (39.6 \pm 1.8)	26.2–35.5 (31.5 \pm 2.2)
Total length	5.8, 5.8	7.4–9.4 (8.5 \pm 0.6)	6.2–9.5 (7.4 \pm 1.5)	95.8 ^a	105.9–117.3 (111.7 \pm 5.7)	N/A	N/A	125.3–141.2 (135.2 \pm 8.6)	103.6–129.7 (119.4 \pm 6.4)
Head length	14.0, 12.4	16.0–19.8 (18.3 \pm 0.9)	16.7–24.4 (19.2 \pm 3.6)	10.4	9.2–11.3 (9.7 \pm 0.3)	9.3–9.6	11.7–11.8	11.4–13.6 (12.6 \pm 0.9)	7.8–10.7 (9.5 \pm 0.7)
Head length/SVL	5.7, 6.7	5.9–8.3 (7.1 \pm 0.7)	5.6–6.5 (5.9 \pm 0.5)	18.6–19.1	16.1–18.1 (17.1 \pm 0.7)	18.2–18.9	18.6–18.9	16.0–18.3 (17.2 \pm 0.8)	14.9–17.4 (16.3 \pm 0.6)
Head width	13.6, 14.4	14.3–16.4 (15.3 \pm 0.6)	14.2–16.8 (15.2 \pm 1.2)	7.8–8.5	7.5–10.1 (8.2 \pm 0.8)	7.7–7.9	7.4–10.1	9.3–11.2 (10.6 \pm 0.9)	7.1–9.8 (8.6 \pm 0.6)
Head width/SVL	4.0, 4.0	4.3–5.8 (5.1 \pm 0.4)	3.8–4.4 (4.1 \pm 0.2)	14.3–15.2	13.0–16.3 (14.2 \pm 1.0)	14.7–15.9	15.2–16.0	14.0–15.2 (14.7 \pm 0.4)	13.8–16.0 (14.8 \pm 0.6)
Snout length	69.2, 69.0	55.1–69.1 (59.5 \pm 3.7)	44.4–62.3 (56.5 \pm 8.3)	55.2–58.0	56.1–64.6 (59.6 \pm 3.0)	5.4–5.7	7.2–7.5	6.7–7.5 (7.2 \pm 0.4)	4.9–6.5 (5.7 \pm 0.4)
Snout length/head length						57.4–59.3	61.9–64.1	53.6–68.4 (60.0 \pm 4.8)	50.7–67.9 (60.3 \pm 2.9)

^a Tail of one of the two examined specimens is short and regenerated and therefore not included in the total length range reported.

Species Concept

In this and past taxonomic treatments of Philippine gekkonid lizards (e.g., Brown et al. 2008, 2009; Siler et al. 2014a, 2016a; Davis et al. 2015), we have applied the general lineage concept of species (de Queiroz 1998, 1999) as an extension of the evolutionary species concept (Simpson 1961; Wiley 1978; Frost and Hillis 1990; de Queiroz 2005) to serve as a framework for lineage-based species recognition. We employ an integrative approach to species delimitation that considers a suite of disparate lines of evidence including: (1) diagnostic, fixed morphological character differences (discrete states, or ranges of states of nonoverlapping with closely related congeners); (2) phylogenetic evidence in support of divergent lineages; and (3) species boundaries that might be expected based on other sources of information present (i.e., habitat differences, allopatric geographic distributions confined to separate PAICs, etc.). Although we consider a species position in the phylogeny to be informative (Brown et al. 2008, 2009, 2010; Welton et al. 2010a), we do not use genetic distances alone to diagnose taxa.

TAXONOMIC ACCOUNT

Pseudogekko sumiklab sp. nov. (Tables 2–4; Figs. 1–5)

Holotype.—PNM 9843 (DRD Field No. 2700, formerly OMNH 44874), adult female, collected between 1900 and 2200 h on 5 March 2016, on the foothills of Mt. Mayon, Sitio Nagsipit, Barangay Mariroc, Municipality of Tabaco, Albay Province, Luzon Island, Philippines (13.30558°N, 123.68898°E; in all cases, datum = WGS84; 399 m elev.), by CDS, DRD, OWG, N. Huron, J. Fernandez, J. Bulalacao, W. Bulalacao, and B. Gurobat.

Paratype.—KU 343847 (RMB 22872), adult female, collected 2040 h on 27 January 2017, on Mt. Cawayan, Municipality of Irosin, Sorsogon Province, Luzon Island, Philippines (12.70141°N, 124.07820°E; 280 m elev.), by JWBB, J. Fernandez, and RMB.

Diagnosis.—*Pseudogekko sumiklab* can be distinguished from congeners by the following combination of characters: (1) body size small (SVL 41.8, 46.6 mm [holotype, paratype]); (2) axilla–groin distance short (23.6, 25.8 mm); (3) head length short (5.8, 7.1 mm); (4) absolute snout length short (4.0, 5.1 mm); (5) relative snout length long (64.7, 69.2% HL); (6) Finger-III scansors 11, 12; (7) Toe-IV scansors 13, 14; (8) supralabials 14; (9) infralabials 13, 14; (10) circumorbitals 39, 46; (11) paravertebrals 220, 224; (12) ventrals 106, 109; (13) enlarged preloicals 13; (14) femoral pore-bearing scales absent; (15) cephalic spots present, black and cream; (16) dorsolateral trunk spots present; (17) black vertebral spots present; (18) limb spots absent; (19) transverse tail bands absent; (20) trunk stripes absent; (21) interorbital band absent; (22) iris ring coloration absent; and (23) significant genetic divergence (Tables 2–4; Figs. 2–4).

Comparisons.—Several characters distinguish *Pseudogekko sumiklab* from all other species of *Pseudogekko* (Tables 3, 4). *Pseudogekko sumiklab* most closely resembles *P. atiorum* and *P. brevipes*; however, it differs from these species in several important characters. *Pseudogekko sumiklab* can be distinguished from *P. atiorum* by having a

TABLE 4.—Summary of qualitative diagnostic characters (meristic; present, absent) in all known species of *Pseudogekko*. In cases of scale count variation within species, numbers of individuals showing specific counts are given in parentheses. Characters are summarized for adult specimens only. When coloration in life of characters is not documented, characters are listed as unknown. See Appendix II for listing of specimens examined. (+, –) = presence, absence.

Character	<i>sumiklab</i> (2 female)	<i>attorum</i> (8 male, 7 female)	<i>brevipes</i> (1 male, 3 female)	<i>chavacano</i> (1 male, 1 female)	<i>compresicorpus</i> (3 male, 4 female)
Finger-III scansors	11, 12	12 (3) 13 (9) 14 (3)	12 (4)	15 (1) 16 (1)	15 (4) 16 (2) 17 (1)
Toe-IV scansors	13, 14	14 (1) 15 (2) 16 (2) 17 (10)	15 (4)	17 (1) 20 (1)	18 (5) 19 (2)
Supralabials	14, 14	15 (7) 16 (4) 17 (4)	13 (2) 14 (2)	15 (1) 16 (1)	16 (1) 17 (1) 18 (3) 19 (1) 20 (1)
Infralabial	13, 14	12 (1) 13 (4) 14 (9) 15 (1)	14 (1) 15 (3)	16 (1) 17 (1)	13 (1) 15 (2) 16 (4)
Circumorbitals	46, 39	35–38	33–35	46	39–45
Paravertebral scales	220, 224	226–240	211–218	195–197	226–234
Ventral scales	106, 109	119–129	96–117	122–123	127–130
Enlarged pore series	13, 13 (precloacal) ^a	13–15 (precloacal)	12 (precloacal)	16 (precloacal)	10–14 (precloacal)
Femoral pores	–	–	–	–	–
Dominant body coloration	Medium brown to tan	Dark brown	Unknown	Light brown	Dark brown to tan
Cephalic spots	+, sparse, black and cream	+, sparse, cream	Unknown	+, dense, neon green	+, dense, neon green
Dorsolateral spots	+, cream	+, cream	+	+, neon green	+, faint, neon green
Vertebral spots	+, black	–	–	–	–
Limb spots	–	–	–	+, dense, neon green	+, faint, neon green
Transverse caudal bands	–	–	–	+	–
Black subcaudal stripe	+ or –	–	–	–	–
Body stripes	–	–	–	–	–
Interorbital band	–	+, light brown	+	–	–
Iris ring coloration	–	–	Unknown	–	+, light blue

^a Number of enlarged scales in precloacal region reported for adult female holotype.

shorter absolute head length (5.8, 7.1 mm vs. 7.4–9.4 mm) and head width (5.6, 5.7 mm vs. 5.9–8.3 mm) and fewer supralabials (14 vs. 15–17), paravertebrals (220, 224 vs. 226–240), and ventrals (106, 109 vs. 119–129). The new species further differs from this taxon by a greater number of circumorbitals (39, 46 vs. 35–38), the presence (vs. absence) of vertebral spots, the absence (vs. presence) of an interorbital band, and the presence (vs. absence) of a subcaudal stripe. From *P. brevipes* the new species differs by having a greater total length (87.8, 91.0 mm vs. 72.0–87.5 mm), fewer infralabials (13, 14 vs. 14, 15), more circumorbitals (39, 46 vs. 33–35), paravertebrals (220, 224 vs. 211–218), and enlarged precloacal pore-bearing scales (13 vs. 12) and the absence (vs. presence) of an interorbital band and presence (vs. absence) of a subcaudal stripe.

Pseudogekko sumiklab can be distinguished from *P. chavacano* by having a smaller body size (SVL ≤ 46.6 mm vs. 54.7 mm), axilla–groin distance (≤ 25.8 mm vs. 26.7–30.0 mm), head length (≤ 7.8 mm vs. 10.4 mm), head width (≤ 6.7 mm vs. 7.8–8.5 mm), and snout length (4.0 mm vs. 5.8–6.0 mm), and fewer Finger-III scansors (11, 12 vs. 15, 16), Toe-IV scansors (13, 14 vs. 17, 20), supralabials (14 vs. 15, 16),

infralabials (13, 14 vs. 16, 17), ventrals (106, 109 vs. 122, 123), and numbers of enlarged, precloacal pore-bearing scales (13 vs. 16). Additionally, the new species has more paravertebrals (220, 224 vs. 195, 197) and is further distinguished by the presence of black and cream (vs. dense neon green) cephalic spots, presence of cream (vs. neon green) dorsolateral spots, presence (vs. absence) of black vertebral spots, absence (vs. presence) of dense neon green limb spots, and absence (vs. presence) of transverse tail bands. From *P. compresicorpus*, the new species differs by having a smaller body size (SVL ≤ 46.6 mm vs. 54.9–59.7 mm), axilla–groin distance (≤ 25.8 mm vs. 27.0–32.6 mm), total length (≤ 91.0 mm vs. 105.9–117.3 mm), head length (≤ 7.8 mm vs. 9.2–11.3 mm), head width (≤ 6.7 mm vs. 7.5–10.1 mm), and snout length (4.0 mm vs. 5.3–7.4 mm), and fewer Finger-III scansors (11, 12 vs. 15–17), Toe-IV scansors (13, 14 vs. 18, 19), supralabials (14 vs. 16–20), paravertebrals (220, 224 vs. 226–234), and ventrals (106, 109 vs. 127–130), and by the presence of sparse black and cream (vs. dense neon green) cephalic spots, presence of cream (vs. faint neon green) dorsolateral spots, presence (vs. absence) of black vertebral spots, absence (vs. presence) of faint neon green

TABLE 4.—Extended.

<i>ditoy</i> (1 male, 1 female)	<i>isapa</i> (1 male, 1 female)	<i>pungkaypinit</i> (4 male, 2 female)	<i>smaragdinus</i> (16 male, 17 female)
14 (1)	13 (2)	15 (3)	15 (1)
15 (1)		16 (1)	16 (4)
		17 (2)	17 (9)
			18 (19)
16 (1)	17 (2)	17 (1)	16 (1)
17 (1)		18 (2)	18 (6)
		19 (2)	19 (8)
		21 (1)	20 (12)
			21 (5)
			22 (1)
17 (1)	20 (1)	16 (1)	16 (8)
20 (1)	21 (1)	18 (2)	17 (10)
		19 (2)	18 (11)
		20 (1)	19 (4)
16 (1)	17 (1)	17 (4)	14 (6)
17 (1)	19 (1)	18 (1)	15 (12)
		19 (1)	16 (10)
			17 (5)
40, 43	50 (1)	50–55	33–35
	54 (1)		
180, 185	240–246	265–280	241–252
111, 118	135–141	125–155	124–130
18 (precloacal)	15 (precloacal)	17–20 (precloacal)	32–41 (precloacofemoral)
–	–	–	+
Light brown	Brownish tan	Grayish brown	Bright neon yellow to orange (undisturbed) to neon green (disturbed)
–	+	–	+, dense black, sparse white
–	–	–	+, large black, small white
–	–	–	–
–	–	–	+, sparse black and white
–	Unknown	–	+, neon yellow, white, and neon orange
–	–	–	–
–	–	+, lateral body surface, slender, anterodorsal–posteroventral, light brown	–
–	+	–	–
–	Unknown	–	–

limb spots, and absence (vs. presence) of light blue iris ring coloration; from *P. ditoy* and *P. isapa* by having a smaller body size (SVL \leq 46.6 mm vs. 52.6 mm [*P. ditoy*], 62.1 mm [*P. isapa*]), axilla–groin distance (\leq 25.8 mm vs. 25.1–29.7 mm [*P. ditoy*], 32.1–33.0 mm [*P. isapa*]), head length (\leq 7.8 mm vs. 9.3–9.6 mm [*P. ditoy*], 11.7–11.8 mm [*P. isapa*]), head width (\leq 6.7 mm vs. 7.7–7.9 mm [*P. ditoy*], 7.4–10.1 mm [*P. isapa*]), and snout length (4.0 mm vs. 5.4–5.7 mm [*P. ditoy*], 7.2–7.5 mm [*P. isapa*]), and fewer Finger-III scansors (11, 12 vs. 14, 15 [*P. ditoy*], 13 [*P. isapa*]), Toe-IV scansors (13 vs. 16, 17 [*P. ditoy*], 17 [*P. isapa*]), supralabials (14 vs. 17, 20 [*P. ditoy*], 20, 21 [*P. isapa*]), infralabials (13, 14 vs. 16, 17 [*P. ditoy*], 17–19 [*P. isapa*]), ventrals (106, 109 vs. 111–118 [*P. ditoy*], 135–141 [*P. isapa*]), and enlarged precloacal pores (13 vs. 18 [*P. ditoy*], 15 [*P. isapa*]), and by the presence (vs. absence) of dorsolateral and vertebral spots; additionally from *P. ditoy* by having more paravertebrals (220, 224 vs. 180–185) and by the presence (vs. absence) of cephalic spots; additionally from *P. isapa* the new species differs by having fewer circumorbitals (\leq 46 vs. 50–54) and paravertebrals (220, 224 vs. 240–246), and by the absence (vs. presence) of an interorbital band; from *P. pungkaypinit* and *P. smar-*

agdinus by having a smaller body size (SVL \leq 46.6 mm vs. 75.2–75.3 mm [*P. pungkaypinit*], 50.2–61.7 mm [*P. smaragdinus*]), axilla–groin distance (\leq 25.8 mm vs. 37.2–41.2 mm [*P. pungkaypinit*], 26.2–35.5 mm [*P. smaragdinus*]), total length (\leq 91.0 mm vs. 125.3–141.2 mm [*P. pungkaypinit*], 103.6–129.7 mm [*P. smaragdinus*]), head length (5.8 mm vs. 11.4–13.6 mm [*P. pungkaypinit*], 7.8–10.7 mm [*P. smaragdinus*]), head width (\leq 6.7 mm vs. 9.3–11.2 mm [*P. pungkaypinit*], 7.1–9.8 mm [*P. smaragdinus*]), and snout length (4.0 mm vs. 6.7–7.5 mm [*P. pungkaypinit*], 4.9–6.5 mm [*P. smaragdinus*]), and fewer Finger-III scansors (11, 12 vs. 15–17 [*P. pungkaypinit*], 15–18 [*P. smaragdinus*]), Toe-IV scansors (13, 14 vs. 17–21 [*P. pungkaypinit*], 16–22 [*P. smaragdinus*]), supralabials (14 vs. 16–20 [*P. pungkaypinit*], 16–19 [*P. smaragdinus*]), infralabials (13, 14 vs. 17–19 [*P. pungkaypinit*], 14–17 [*P. smaragdinus*]), paravertebrals (220, 224 vs. 265–280 [*P. pungkaypinit*], 241–252 [*P. smaragdinus*]), ventrals (106, 109 vs. 125–155 [*P. pungkaypinit*], 124–130 [*P. smaragdinus*]), enlarged pore-bearing scales (13 vs. 17–20 [*P. pungkaypinit*], 32–41 [*P. smaragdinus*]), and by the presence (vs. absence) of vertebral spots; additionally from *P. pungkaypinit* by having fewer circumorbitals (\leq 46 vs. 50–

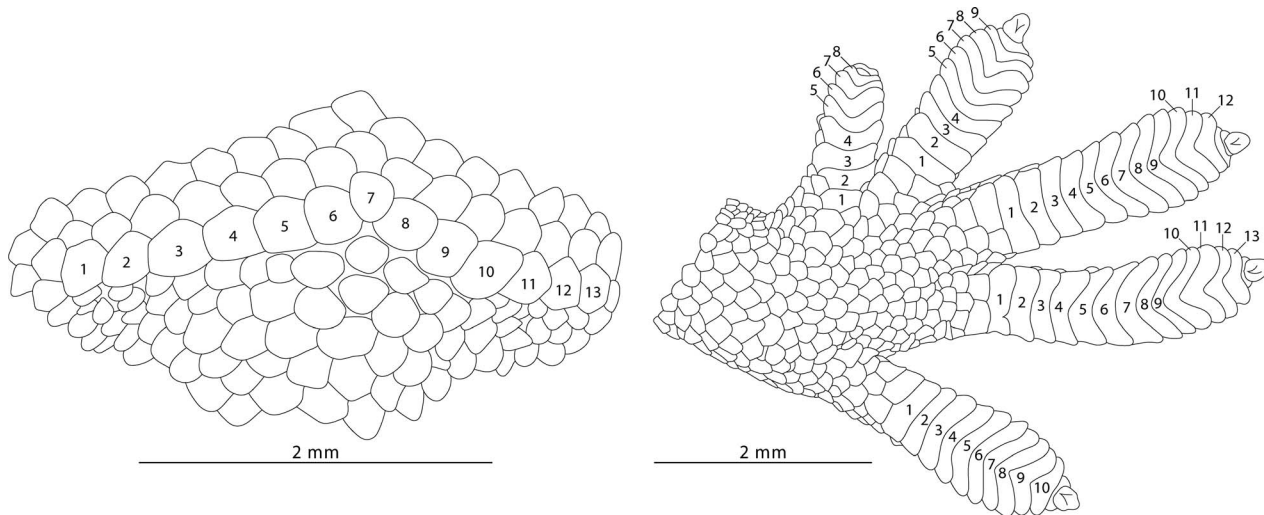


FIG. 2.—Illustrations of the series of enlarged precloacal scales and the underside of the left foot showing toe scansor counts of *Pseudogekko sumiklab* sp. nov. (PNM 9843; holotype). Scale bars = 2 mm. Illustrations by CDS.

55), the presence (vs. absence) of cephalic spots, presence (vs. absence) of dorsolateral spots, and absence (vs. presence) of trunk stripes; additionally from *P. smaragdinus* by having a greater number of circumorbitals (≥ 39 vs. 33–35), the absence (vs. presence) of femoral pores, absence (vs. presence) of bright neon yellow to orange (undisturbed) to neon green (disturbed) body coloration, and absence (vs. presence) of transverse tail bands.

Description of holotype.—Adult female in excellent condition; small incision in the sternal region (portion of liver removed for genetic sample). Body small, slender, SVL 41.8 mm; limbs well developed, moderately slender; tail slender; margins of limbs smooth, cutaneous flaps or dermal folds absent.

Head size moderate, slightly differentiated from neck, characterized by only slightly hypertrophied temporal and adductor musculature; calcium deposits of endolymphatic sacs visible through skin in lateral nuchal region; snout broadly rounded in dorsal view, bluntly rounded in lateral view; head width 104.8% midbody width, 97.4% head length; head length 14.0% SVL; snout length 71.0% head width, 69.2% head length; dorsal surfaces of head relatively homogeneous, with slightly to moderately pronounced concavities in postnasal, internasal, prefrontal, and interorbital regions; auricular opening small, nearly round, beneath temporal swellings on either side of head; tympanum deeply sunken; orbit large; eye large, pupil vertical, margin wavy; limbs relatively short, hands and feet small, digits reduced; thighs thicker than upper arms; tibia length 10.2% SVL, 82.5% femur length.

Rostral size moderate, narrowly heart-shaped in anterodorsal view, nearly as broad as high, anterolaterally abutting anteriormost enlarged supralabials, projecting onto dorsal surface of head to point in line with anteriormost edge of nasal; nasal surrounded by first labial, rostral, two enlarged postnasals, and one enlarged supranasal; supranasals separated by three small median scales, larger than postnasals; circumorbitals 46 in total.

Total number of differentiated supralabials 14 (11 to center of eye), bordered dorsally by one row of differenti-

ated—enlarged snout scales; total number of differentiated infralabials 13 (10 to center of eye), bordered ventrally by one or two rows of slightly enlarged scales; two rows of chin scales enlarged; postriental scales undifferentiated; gulars small, round, slightly imbricate.

Dorsal cephalic scales relatively homogeneous in size, shape, and distribution, slightly convex, round to oval scales; postnasal, prefrontal, internasal, and interorbital depressions; undifferentiated posterior head scales granular, slightly convex.

Axilla–groin distance 55.1% SVL; undifferentiated dorsal body scales round to oval, moderately convex, juxtaposed, relatively homogeneous in size; each dorsal scale surrounded by 4–6 interstitial granules; dorsals gradually transition to imbricate ventrals along lateral body surface; paravertebrals between midpoints of limb insertions 220; ventrals between midpoints of limb insertions 106; scales on dorsal surfaces of limbs more imbricate than dorsals, with more-sharply raised edges; scales on dorsal surfaces of hands and feet similar to dorsal limb scales, imbricate; ventral body scales flat, cycloid, imbricate, rounder and much larger than lateral or dorsal body scales, relatively homogeneous in size. Thirteen enlarged, dimpled scales in continuous precloacal series (assumed to be pore-bearing in males) arranged in a widely obtuse, inverted “V”-formation.

Digits moderately expanded and subdigital surfaces covered by bowed, unnotched, undivided scansors; digits with minute vestiges of interdigital webbing; subdigital scansors of fingers (left, right) I (7,7), II (9,9), III (11,11), IV (14,13), V (10,10); subdigital scansors of toes (left, right) I (8,8), II (9,9), III (12,12), IV (13,13), V (10,10); subdigital scansors of hands and feet bordered laterally (on palmar and plantar surfaces) by two or three slightly enlarged scales that form a near-continuous series with enlarged scansors; palmar and plantar scaled small, homogeneous; all digits clawed, but first (inner) claw greatly reduced; remaining terminal claw-bearing phalanges compressed, with moderately sized recurved claws.

Tail relatively long compared to body, tail length 46.0 mm, 110.1% SVL; round, not heavily depressed; tail height 87.7%



FIG. 3.—Photographs in life of adult female holotype (PNM 9843; upper photographs by CDS) and paratype (KU 343847; lower photograph by J. Fernandez and RMB) from the Bicol Peninsula of Luzon Island, Philippines. A color version of this figure is available online.



FIG. 4.—Photographs of the preserved holotype of *Pseudogekko sumiklab* (PNM 9843) showing lateral view of the head and dorsal view of the body. Photographs by CDS and JLW. A color version of this figure is available online.

tail width; caudals similar in size to dorsals, subcaudals similar in size to ventrals.

Coloration of holotype in life (Fig. 3).—Color codes follow Köhler (2012). Dorsal base color on head, trunk, and tail is gray (code 293). Interspersed through this region are small black (300) and smoky white (261) speckles. These speckles are not in a pattern on the head or limbs. On the trunk, the speckles appear in widely spaced rows of one color each; black (300) speckles in the center of the trunk and smoky white (261) speckles more laterally. On the tail, black (300) speckles again form a loose row down the center. The eyes are a lighter gray (296) with vertical black (300) pupils. The ventral base color of the head, trunk, and tail is smoky white (261), with suffuse sulphur yellow (92) in the center of the ventrum from base of head to approximately halfway down the tail, including the hindlimbs. Small black (300) speckles are present throughout the ventrum without a distinct pattern until the latter half of the tail, when the speckles converge to form a solid central line by the tip of the tail. The lateral portion of the head, trunk, and tail represents a gradual color mottle transition between the dorsal base color of gray (293) and the ventral base color of smoky white (261).

Coloration of holotype in preservative (Fig. 4).—Dorsal base color on head, trunk, and tail is clay (18), with dense stippling throughout the dorsum of burnt umber (48). The stippling is even more aggregated just above the orbits. Interspersed through the dorsum are small black (300) and smoky white (261) speckles. These speckles are not in a pattern on the head or limbs. On the trunk, the speckles appear in widely spaced rows of one color each; black (300) speckles in the center of the trunk and smoky white (261) speckles more laterally. On the tail, black (300) speckles

again form a loose row down the center. The eyes are verona brown (37) with vertical dark gray (299) pupils. The ventral base color of head, trunk, and tail is cream white (52). Small black (300) speckles are present throughout the ventrum without a distinct pattern until the latter half of the tail when the speckles converge to form a solid central line by the tip of the tail. The lateral portion of the head, trunk, and tail represents a gradual transition between the clay (18) with burnt umber (48) stippling of the dorsum and the cream white (52) of the ventrum.

Measurements (in mm) and scale counts of holotype and paratype.—SVL 41.8, 46.6; axilla–groin distance 23.6, 25.8; total length 87.8, 91.0; tail length 46.0, 49.2; head length 5.8; head width 5.7, 6.7; head height 4.0, 4.5; eye diameter 2.5, 3.0; snout length 4.0, 5.1; eye–nares distance 3.3, 3.5; internarial distance 1.3, 1.5; interorbital distance 1.1, 1.3; midbody width 5.4, 5.5; femur length 5.2, 5.5; tibia length 4.3, 4.7; Toe-I length 2.7, 2.7; Toe-IV length 3.3, 3.6; tail width 2.3, 2.7; tail height 2.0, 2.1; supralabials 14, 14; infralabials 13, 14; circumorbitals 46, 39; paravertebral scales 220, 224; ventral scales 106, 109; Finger-III scancers 11, 12; Toe-IV scancers 13, 14.

Molecular information.—*Pseudogekko sumiklab* is genetically distinct from its congeners, with uncorrected mtDNA pairwise distances ranging from 11.0–13.8% and uncorrected nuDNA pairwise distances ranging from 0.8–2.0% (Table 2), which is consistent with differences among other recognized species of *Pseudogekko* (e.g., Siler et al. 2014b; Davis et al. 2015).

Distribution, ecology, and natural history.—The holotype was discovered in a tree on the bank of a stream in a small patch of secondary-growth forest at low elevation on Mt. Mayon (Fig. 5). When first observed, it was perched



FIG. 5.—Photographs of Mt. Mayon, Luzon Island, Philippines, and habitat at the type locality of *Pseudogekko sumiklab* sp. nov. Photographs by CDS. A color version of this figure is available online.

on the upper surface of a leaf about 3 m from the forest floor. The paratype was collected from the upper surface of a small twig, near the distal portion of a branch of an understory sapling along a small stream on Mt. Cawayan. Over our 3-wk survey at on Mt. Cawayan, three additional individuals of *P. sumiklab* were observed in nearly identical microhabitats, and all escaped capture by dropping from 2–3-m high perches into leaf litter upon approach of biologists.

Despite several biodiversity surveys to various forested areas in the central and northern portions of the Bicol Peninsula (Brown and Gonzalez 2007; Siler et al. 2010a,b), no other observations of this species have been made over the last decade. As such, we have very little information on the species distribution, population size, or population viability. Although *Pseudogekko sumiklab* is known only from Mt. Mayon and Mt. Cawayan, it might possess a broader distribution on the Bicol Peninsula of Luzon Island (Fig. 1), and it almost certainly occurs in the areas intervening the two known collection localities. The type locality is a protected area, as is Mt. Bulusan volcano, located between the two known localities of Mt. Mayon and Mt. Cawayan (Fig. 1). The new species most likely also occurs around the foothills of Mt. Pocdol, a forested extinct volcano under private land tenure as an energy-producing geothermal plant (BacMan Geothermal). Thus, we suspect that a significant portion of the range of the new species is protected and forested, primarily with lower montane regenerating secondary forest.

The new species is the only known member of the *P. brevipes* complex distributed in the Luzon PAIC, with the two other species found in the West Visayan PAIC (*P. atiorum*; Brown and Alcala 1978; Ferner et al. 2000; Davis et al. 2015; Supsup et al. 2016) or the Mindanao PAIC (*P. brevipes*; Siler et al. 2014a,b, 2016a; Davis et al. 2015). Although widespread habitat destruction has occurred throughout the Bicol Peninsula of Luzon (Siler et al. 2014d), including the low-elevation forests surrounding Mt. Mayon and the privately owned, low-elevation agricultural and residential matrix of heavily disturbed land between the mountains of southern Bicol Peninsula (Fig. 1), the absence of available information about the species distribution and basic ecological traits prevents us from evaluating this species under the International Union for Conservation of Nature (IUCN) criteria for assessing conservation status (IUCN 2016). Therefore, we consider the species as Data Deficient and emphasize that immediate efforts should be made to locate and study wild populations on Mt. Mayon and other central to southern Bicol forested areas (e.g., Mts. Malinao, Isarog, and Bulusan; Fig. 1).

Etymology.—We derive the masculine specific epithet from the Tagalog (Filipino) verb *sumiklab*, meaning to burst out quickly, or hotly, or to ignite and flare up, in reference to the new species type locality, Mt. Mayon, and the other volcanos of the Bicol Peninsula. One of the world's most active and dangerous volcanoes, Mayon's near-perfect, symmetrical cone is an iconic feature of the Bicol Region volcanic landscape and a picturesque symbol of the national significance of Bicolandia in Philippine culture (Fig. 5). Suggested common name: Bicol False Geckos.

DISCUSSION

Recent biodiversity studies throughout the archipelago have resulted in discoveries of numerous endemic Philippine amphibians and reptiles previously unknown to science (e.g., Brown et al. 2000, 2013, 2016; Barley et al. 2013; Siler et al. 2014a; Davis et al. 2015). In the last decade, the number of *Pseudogekko* species has increased by 250%. At the end of the 1970s, the genus *Pseudogekko* consisted of four species distributed broadly across the archipelago (Brown and Alcala 1970, 1978). Of these, one species recently was removed from *Pseudogekko* and moved to the genus *Lepidodactylus* (*L. labialis*; Siler et al. 2014a) and two species (*P. brevipes* and *P. compresicorpus*) were found to consist of several morphologically, genetically, and biogeographically distinct lineages, with distributions reflective of PAIC geography (Voris 2000; Brown and Diesmos 2009; Siler et al. 2014a,b, 2016a; Davis et al. 2015). The description of *P. sumiklab* as part of the *P. brevipes* complex brings the total number of species within this clade to three and the total number of species in the genus *Pseudogekko* to nine. The combination of genetic data, nonoverlapping mensural and meristic character state data, and biogeographic information provides unequivocal support for the recognition of this unique lineage of *Pseudogekko* as a new species.

All species of *Pseudogekko* are endemic to the Philippines, each restricted to individual PAICs. *Pseudogekko sumiklab* is found uniquely on the Luzon PAIC whereas the other species within the *P. brevipes* complex inhabit the Mindanao PAIC (*P. brevipes*) and the West Visayan PAIC (*P. atiorum*). Although these PAICs are close in proximity to each other, they remain separated by a deep ocean channel (Brown et al. 2013), indicating that dispersal to Luzon from the south would be required to establish the lineage described here (Siler et al. 2012).

Even though members of the *Pseudogekko brevipes* complex occupy nonoverlapping geographical distributions, they are believed to occupy similar microhabitats and, as a result, might face similar conservation threats. Our specimens of *P. sumiklab* were collected in secondary forest at the base of Mt. Mayon and Mt. Cawayan, near Mt. Bulusan. We suspect that, like most other species of *Pseudogekko*, the new species might be restricted to relatively undisturbed forest habitats. Currently, the protected area network in the Philippines protects a small fraction of the archipelago's remaining forested habitat in coastal and low elevations (Baconguis et al. 1990; Primavera 2000; Primavera et al. 2004; Millenium Ecosystem Assessment 2005; Posa and Sodhi 2006; Polidoro et al. 2010; Rickart et al. 2011; Siler et al. 2014d). Recent estimates suggest that for other low-elevation Bicol Region species (e.g., sailfin lizards of the genus *Hydrosaurus*), <1% of remaining suitable habitat is protected (Siler et al. 2014d). Therefore, the continued loss of primary and secondary growth forest habitats might be a direct threat to the survival of many rare, patchily distributed, or range-restricted Bicol endemics (Brown and Gonzalez 2007; Siler et al. 2010a,b, 2011). Expansion of Bicol's protected areas, and establishment of new protected areas, might be critical for the continued existence of endemic Philippine forest species, including the newest member of the genus *Pseudogekko*.

Acknowledgments.—We thank the Biodiversity Management Bureau (BMB) of the Philippine Department of Environment and Natural Resources (DENR) for facilitating collecting and export permits necessary for this and related studies; we are particularly grateful to M. Lim, C. Custodio, J. de Leon, and A. Tagtag. Fieldwork was conducted under the Memorandum of Agreement with the BMB of the Philippines (2015–2020), Gratuitous Permits to Collect Nos. 247 (University of Oklahoma; OU) and 258 (University of Kansas Natural History Museum; KU), and Institutional Animal Care and Use Committee (IACUC) Approval R13-011 (OU) and 158-04 (KU). Financial support for fieldwork was provided by National Science Foundation, Division of Integrative Organismal Systems (NSF, IOS) 1353683 to CDS and DEB 1655553 to RMB. For the loans of specimens, we thank J. Vindum (CAS) and T. LaDuc (Biodiversity Collections, University of Texas at Austin; TNHC). For access to the Sam Noble Museum Invertebrate Paleontology Stacking Photography Lab we thank S. Westrop and R. Burkharter. Special thanks to N. Huron for assistance in field expeditions. Members of the Siler and Brown labs, and anonymous reviewers, provided critical feedback on the manuscript.

LITERATURE CITED

- Baconguis, S., D. Cabahug, and S. Alonzo-Pasicolan. 1990. Identification and inventory of Philippine forested-wetland resource. *Forest Ecology and Management* 33:21–44.
- Barley, A., J. White, A.C. Diesmos, and R.M. Brown. 2013. The challenge of species delimitation at the extremes: Diversification without morphological change in Philippine sun skinks. *Evolution* 67:3556–3572.
- 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: The Technical Journal of Philippine Ecosystems and Natural Resources* 10:107–124.
- Brown, R.M., and A.C. Diesmos. 2009. Philippines, biology. Pp. 723–732 in *Encyclopedia of Islands* (R. Gillespie and D. Clague, eds.). University of California Press, USA.
- Brown, R.M., and J.C. Gonzalez. 2007. A new forest frog of the genus *Platymantis* (Amphibia: Anura: Ranidae) from the Bicol Peninsula of Luzon Island, Philippines. *Copeia* 2007:251–266.
- 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*, London 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: Squamata: Gekkonidae): Redescription, designation of a neotype, and comparisons with related species. *Herpetologica* 53:357–373.
- Brown, R.M., J.A. McGuire, and A.C. Diesmos. 2000. Status of some Philippine frogs referred to *Rana everetti* (Anura: Ranidae), description of a new species, and resurrection of *Rana igorota* Taylor 1922. *Herpetologica* 56:81–104.
- Brown, R.M., A.C. Diesmos, and M.V. Duya. 2007. A new species of *Luperosaurus* (Squamata: Gekkonidae) from the Sierra Madre mountain range of northern Luzon Island, Philippines. *Raffles Bulletin of Zoology* 55:153–160.
- Brown, R.M., C.H. 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, R.M., C.D. Siler, I. Das, and Y. Min. 2012a. Testing the phylogenetic affinities of Southeast Asia's rarest geckos: Flap-legged geckos (*Luperosaurus*), flying geckos (*Ptychozoon*) and their relationship to the pan-Asian genus *Gekko*. *Molecular Phylogenetics and Evolution* 63:915–921.
- Brown, R.M., C.D. Siler, L.L. Grismer, I. Das, and J.A. McGuire. 2012b. Phylogeny and cryptic diversification in Southeast Asian flying geckos. *Molecular Phylogenetics and Evolution* 65:351–361.
- Brown, R.M., C.H. Oliveros, C.D. Siler, J.B. Fernandez, L.J. Welton, P.A.C. Buenavente, M.L.D. Diesmos, and A.C. Diesmos. 2012c. Amphibians and reptiles of Luzon Island (Philippines), VII: Herpetofauna of Ilocos Norte Province, Northern Cordillera Mountain Range. *Check List* 8:469–490.
- Brown, R.M., C.D. Siler, C.H. Oliveros, . . . , A.C. Alcalá. 2013. Evolutionary processes of diversification in a model island archipelago. *Annual Review of Ecology, Evolution, and Systematics* 44:411–435.
- Brown, R.M., Y.-C. Su., B. Barger, C.D. Siler, M.B. Sangula, A.C. Diesmos, and D.C. Blackburn. 2016. Phylogeny of the island archipelago frog genus *Sanguirana*: Another endemic Philippine radiation that diversified 'Out-of-Palawan.' *Molecular Phylogeny and Evolution* 94:531–536.
- Brown, W.C., and A.C. Alcalá. 1970. The zoogeography of the Philippine Islands, a fringing archipelago. *Proceedings of the California Academy of Sciences* 38:105–130.
- Brown, W.C., and A.C. Alcalá. 1978. *Philippine Lizards of the Family Gekkonidae*. Silliman University Press, Philippines.
- Davis, D.R., K.D. Feller, R.M. Brown, and C.D. Siler. 2014. Evaluating the diversity of Philippine slender skinks of the *Brachymeles bonitae* complex (Reptilia: Squamata: Scincidae): Redescription of *B. tridactylus* and descriptions of two new species. *Journal of Herpetology* 48:480–494.
- Davis, D.R., J.L. Watters, G. Köhler, C. Whitsett, N.A. Huron, R.M. Brown, A.C. Diesmos, and C.D. Siler. 2015. Redescription of the rare Philippine false gecko *Pseudogekko brevipes* (Reptilia: Squamata: Gekkonidae) and description of a new species. *Zootaxa* 4020:357–374.
- Davis, D.R., A.D. Geheber, J.L. Watters, . . . , C.D. Siler. 2016. Additions to Philippine Slender Skinks of the *Brachymeles bonitae* Complex (Reptilia: Squamata: Scincidae) III: A new species from Tablas Island. *Zootaxa* 4132:30–43.
- de Queiroz, K. 1998. The general lineage concept of species, species criteria, and the process of speciation: A conceptual unification and terminological recommendations. Pp. 57–75 in *Endless Forms: Species and Speciation* (D.J. Howard and S.H. Berlocher, eds.). Oxford University Press, USA.
- de Queiroz, K. 1999. The general lineage concept of species and the defining properties of the species category. Pp. 49–89 in *Species: New Interdisciplinary Essays* (R.A. Wilson, ed.). Massachusetts Institute of Technology Press, USA.
- de Queiroz, K. 2005. A unified concept of species and its consequences for the future of taxonomy. *Proceedings of the California Academy of Sciences* 56:196–215.
- Edgar, R.C. 2004. MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32:1792–1797.
- 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.
- Ferner, J.W., R.M. Brown, R.V. Sison, and R.S. Kennedy. 2000. The amphibians and reptiles of Panay Island, Philippines. *Asiatic Herpetological Research* 9:34–70.
- Frost, D.R., and D.M. Hillis. 1990. Species in concept and practice: Herpetological applications. *Herpetologica* 46:87–104.
- 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 cumingi* (Gray, 1845). *Copeia* 2007:413–425.
- Geheber, A.D., D.R. Davis, J.L. Watters, . . . , C.D. Siler. 2016. Additions to Philippine Slender Skinks of the *Brachymeles bonitae* Complex (Reptilia: Squamata: Scincidae) I: A new species from Lubang Island. *Zootaxa* 4132:1–14.
- Grismer, L.L., P.L. Wood Jr., S. Anuar, M.A. Muin, E.S.H. Quah, J.A. McGuire, R.M. Brown, N.V. Tri, and P.H. Thai. 2013. Integrative taxonomy uncovers high levels of cryptic species diversity in *Hemiphyllodactylus* Bleeker, 1860 (Squamata: Gekkonidae) and the description of a new species from Peninsular Malaysia. *Zoological Journal of the Linnean Society* 169:849–880.
- IUCN (International Union for Conservation of Nature). 2015. The IUCN Red List of Threatened Species, Version 2016-2. Available at <http://www.iucnredlist.org>. Archived by WebCite at <http://www.webcitation.org/6h7AfveTK> on 26 September 2016.
- Köhler, G. 2012. *Color Catalog for Field Biologists*. Herpeton, Germany.
- Linkem, C.W., C.D. Siler, A.C. Diesmos, E. Sy, and R.M. Brown. 2010. A new species of *Gekko* (Squamata: Gekkonidae) from central Luzon Island, Philippines. *Zootaxa* 2396:37–49.

- Millennium Ecosystem Assessment. 2005. Ecosystems and Human Well-being: Synthesis. Island Press, USA.
- Palumbi, S., A. Martin, S. Romano, W.O. McMillan, L. Stice, and G. Grabowski. 1991. The Simple Fool's Guide to PCR, Version 2.0. Privately published, USA.
- Polidoro, B.A., K.E. Carpenter, L. Collins, . . . , J.W.H. Yong. 2010. The loss of species: Mangrove extinction risk and geographic areas of global concern. *PLoS ONE* 5:e10095. DOI: <http://dx.doi.org/10.1371/journal.pone.0010095>
- Posa, M., and N. Sodhi. 2006. Effects of anthropogenic land use on forest birds and butterflies in Subic Bay, Philippines. *Biological Conservation* 129:256–270.
- Posada, D. 2008. jModelTest: Phylogenetic model averaging. *Molecular Biology and Evolution* 25:1253–1256.
- Primavera, J.H. 2000. Development and conservation of Philippine mangroves: Institutional issues. *Ecological Economics* 35:91–106.
- Primavera, J.H., R.B. Sadaba, M.J.H.L. Leбата, and J.P. Altamirano. 2004. Handbook of Mangroves in the Philippines—Panay. SEAFDEC Aquaculture Department, Philippines.
- Rickart, E., D. Balete, R. Rowe, and L. Heaney. 2011. Mammals of the northern Philippines: Tolerance for habitat disturbance and resistance to invasive species in an endemic insular fauna. *Diversity and Distributions* 17:530–541.
- Rosler, 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* 42:193–206.
- Sabaj, M.H. (ed.). 2016. Standard Symbolic Codes for Institutional Resource Collections in Herpetology and Ichthyology: An Online Reference (v6.5). American Society of Ichthyologists and Herpetologists, USA. Available at <http://www.asih.org/resources>. Archived by WebCite at <http://www.webcitation.org/6lkBdh0EO> on 3 November 2016.
- Siler, C.D., D.S. Balete, A.C. Diesmos, and R.M. Brown. 2010a. A new legless loam-swimming lizard (Reptilia: Squamata: Scincidae: genus *Brachymeles*) from the Bicol Peninsula, Luzon Island, Philippines. *Copeia* 2010:114–122.
- Siler, C.D., A.C. Diesmos, and R.M. Brown. 2010b. A new loam-swimming skink, genus *Brachymeles* (Reptilia: Squamata: Scincidae) from the Bicol faunal region, Luzon and Catanduanes islands, Philippines. *Journal of Herpetology* 44:49–60.
- Siler, C.D., A.M. Fuiten, R.M. Jones, A.C. Alcala, and R.M. Brown. 2011. Phylogeny-based species delimitation in Philippine slender skinks (Reptilia: Squamata: Scincidae) II: Taxonomic revision of *Brachymeles samarensis* and description of five new species. *Herpetological Monographs* 25:76–112.
- Siler, C.D., J.R. Oaks, L.J. Welton, C.W. Linkem, J. Swab, A.C. Diesmos, and R.M. Brown. 2012. Did geckos ride the Palawan raft to the Philippines? *Journal of Biogeography* 39:1217–1234.
- Siler, C.D., L.J. Welton, D.R. Davis, J.L. Watters, C.S. Davey, A.C. Diesmos, M.L. Diesmos, and R.M. Brown. 2014a. Taxonomic revision of the *Pseudogekko compresicorpus* Complex (Reptilia: Squamata: Gekkonidae), with descriptions of three new species. *Herpetological Monographs* 28:110–139.
- Siler, C.D., T.A. Dececchi, C.L. Merkord, D.R. Davis, T.J. Christiani, and R.M. Brown. 2014b. Cryptic diversity and population genetic structure in the rare, endemic, forest-obligate, slender geckos of the Philippines. *Molecular Phylogenetics and Evolution* 70:204–209.
- Siler, C.D., C.W. Linkem, K. Cobb, J.L. Watters, S.T. Cummings, A.C. Diesmos, and R.M. Brown. 2014c. Taxonomic revision of the semi-aquatic skink *Parvoscinus leucospilos* (Reptilia: Squamata: Scincidae), with description of three new species. *Zootaxa* 3847:388–412.
- Siler, C.D., A. Lira-Noriega, and R.M. Brown. 2014d. Conservation genetics of Australasian sailfin lizards: Flagship species threatened by coastal development and insufficient protected area coverage. *Biological Conservation* 169:100–108.
- Siler, C.D., D.R. Davis, A.C. Diesmos, F. Guinto, C. Whitsett, and R.M. Brown. 2016a. A new species of *Pseudogekko* (Squamata: Gekkonidae) from the Romblon Island Group, Central Philippines. *Zootaxa* 4139:248–260.
- Siler, C.D., D.R. Davis, E.S. Freitas, . . . , R.M. Brown. 2016b. Additions to Philippine Slender Skinks of the *Brachymeles bonitae* Complex (Reptilia: Squamata: Scincidae) II: A new species from the northern Philippines. *Zootaxa* 4132:15–29.
- Simpson, G.G. 1961. Principles of Animal Taxonomy. Columbia University Press, USA.
- Stamatakis, A. 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22:2688–2690.
- Stamatakis, A., P. Hoover, and J. Rougemont. 2008. A rapid bootstrap algorithm for the RAxML web servers. *Systematic Biology* 57:758–771.
- Supsup, C.E., N.M. Puna, A.A. Asis, B.R. Redoblado, M.F.G. Panaguinit, F.M. Guinto, E.B. Rico, A.C. Diesmos, R.M. Brown, and N.A.D. Mallari. 2016. Amphibians and reptiles of Cebu, Philippines: The poorly understood herpetofauna of an island with very little remaining natural habitat. *Asian Herpetological Research* 7:151–179.
- Swofford, D.L. 2002. PAUP*: Phylogenetic Analysis Using Parsimony (*and Other Methods), Version 4. Sinauer Associates, USA.
- Taylor, E.H. 1922. The lizards of the Philippine Islands. Philippine Bureau of Science 17:1–269.
- Voris, H.K. 2000. Maps of Pleistocene sea-levels in Southeast Asia: Shorelines, river systems, time durations. *Journal of Biogeography* 27:1153–1167.
- Welton, L.J., C.D. Siler, A. 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* 65:328–343.
- Welton, L.J., C.D. Siler, A.C. Diesmos, and R.M. Brown. 2010a. Phylogeny-based species delimitation of southern Philippines 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.D. Siler, C.W. Linkem, A.C. Diesmos, and R.M. Brown. 2010b. Philippine bent-toed geckos of the *Cyrtodactylus agusanensis* complex: Multilocus phylogeny, morphological diversity, and descriptions of three new species. *Herpetological Monographs* 24:55–85.
- Wiley, E.O. 1978. The evolutionary species concept reconsidered. *Systematic Zoology* 21:17–26.

APPENDIX I Summary of specimens corresponding to genetic samples included in the study. ACD = Arvin Diesmos field series, deposited at the National Museum of the Philippines; KU = University of Kansas Natural History Museum; PNM = National Museum of the Philippines; TNHC = Biodiversity Collections, University of Texas at Austin (Sabaj 2016); (—) = sequence data not available.

Species	Voucher	Locality	GenBank accession numbers			
			ND2	I6S	PTGER4	
<i>Cyrtodactylus annulatus</i>	KU 314944	Barangay Kainpugan, Municipality of San Francisco, Agusan del Sur Province, Mindanao Island, Philippines	GU366088	—	—	—
<i>Cyrtodactylus philippinicus</i>	KU 304784	Barangay Babuyan Claro, Municipality of Calayan, Cagayan Province, Babuyan Claro Island, Philippines	GU550900	—	—	—
<i>Luperosaurus anglit</i>	KU 322189	Barangay Zabali, Municipality of Baler, Aurora Province, Luzon Island, Philippines	JQ437903	—	—	—
<i>Luperosaurus cumingi</i>	TNHC 61910	Philippines, Luzon Island, Albay Province, Municipality of Tawi, Mt. Malinao	JQ437902	—	—	—
<i>Pseudogekko atiorum</i>	KU 302818	Mt. Talinis, Barangay Bongbong, Municipality of Valencia, Negros Oriental Province, Negros Island, Philippines	KF875323	KY786057	—	KF875349
<i>P. atiorum</i>	KU 327770	Mt. Talinis, Barangay Bongbong, Municipality of Valencia, Negros Oriental Province, Negros Island, Philippines	KF875324	KY786058	—	KF875350
<i>Pseudogekko brevipes</i>	ACD 7255	Municipality of Sogud, Leyte Province, Leyte Island, Philippines	KF875330	KY786059	—	KF875357
<i>Pseudogekko ditoy</i>	KU 326438	Sitio Cienda, Barangay Gubas, Municipality of Baybay, Leyte Province, Leyte Island, Philippines	KF875329	KY786060	—	KF875356
<i>P. ditoy</i>	KU 326437	Sitio Cienda, Barangay Gubas, Municipality of Baybay, Leyte Province, Leyte Island, Philippines	KF875333	KY786061	—	KF875360
<i>Pseudogekko chatacano</i>	KU 314963	Sitio Canucutan, Barangay Pasanonca, Municipality of Pasonanca, Zamboanga City Province, Mindanao Island, Philippines	KF875339	KY786062	—	KF875366
<i>P. chatacano</i>	KU 314964	Sitio Canucutan, Barangay Pasanonca, Municipality of Pasonanca, Zamboanga City Province, Mindanao Island, Philippines	KF875341	KY786063	—	KF875368
<i>Pseudogekko pungkaipinit</i>	KU 324426	Barangay Danicop, Municipality of Sierra Bullones, Bohol Province, Bohol Island, Philippines	JQ437898	KY786064	—	KF875352
<i>P. pungkaipinit</i>	ACD 7577	Municipality of Sogud, Leyte Province, Leyte Island, Philippines	KF875331	KY786065	—	KF875358
<i>P. pungkaipinit</i>	ACD 7637	Municipality of Sogud, Leyte Province, Leyte Island, Philippines	KF875332	KY786066	—	KF875359
<i>Pseudogekko compresicorpus</i>	KU 330735	Mt. Makling Forest Reserve, Barangay Bagong Silang, Municipality of Los Baños, Laguna Province, Luzon Island, Philippines	KF875337	KY786067	—	KF875364
<i>P. compresicorpus</i>	KU 331657	Mt. Makling Forest Reserve, Barangay Bagong Silang, Municipality of Los Baños, Laguna Province, Luzon Island, Philippines	KF875338	KY786068	—	KF875365
<i>Pseudogekko smaragdinus</i>	KU 302821	Barangay Pinaaglubayan, Municipality of Polillo, Quezon Province, Polillo Island, Philippines	KF875344	KY786069	—	KF875372
<i>P. smaragdinus</i>	KU 302819	Barangay Pinaaglubayan, Municipality of Polillo, Quezon Province, Polillo Island, Philippines	JQ437897	KY786070	—	KF875370
<i>Pseudogekko sumiklab</i> sp. nov.	PNM 9843	Mt. Mayon, Sitio Nagspiit, Barangay Marirac, Municipality of Tabaco, Albay Province, Luzon Island, Philippines	—	KY786071	—	KY785182

APPENDIX II

Specimens Examined

Numbers in parentheses following species names indicate the number of specimens examined. All specimens examined are from the Philippines. Several sample sizes are greater than those observed in the description because of the examination of subadult specimens, which were excluded from morphometric analyses.

Lepidodactylus labialis (10).—MINDANAO ISLAND: AGUSAN DEL NORTE PROVINCE: *Municipality of Cabadbaran* (CAS 133317, 133318 [neotype], 133329, 133396, 133687, 133790); DAVAO DEL SUR PROVINCE: *Municipality of Malalag* (CAS 124813, 139714–139716).

Pseudogekko atiorum (16).—NEGROS ISLAND: NEGROS OCCIDENTAL PROVINCE: *Municipality of Cauayan* (CAS-SUR 19372, 21122); NEGROS ORIENTAL PROVINCE: *Municipality of Valencia (presumed)*: Cuernos de Negros, Mt. Talinis (CAS 134292); *Municipality of Sibulan* (CAS 128956, 128959, 128963, 128971); *Municipality of Valencia*: Barangay Bongbong (PNM 9518 [holotype, formerly KU 302818], 327770, TNHC 62478); *Municipality of Pamplona* (CAS 138097, 145793, 147491); *Municipality of Siatan* (CAS 134269, CAS-SUR 26778); SIKUIJOR PROVINCE: *Municipality of San Juan* (CAS 145710).

Pseudogekko brevipes (7).—SAMAR ISLAND (SMF 8988 [holotype]); BOHOL ISLAND: BOHOL PROVINCE: *Municipality of Sierra Bullones* (CAS 131855, 147527, 147528, CAS-SU 24596, 25108, 25111).

Pseudogekko chavacano (4).—MINDANAO ISLAND: ZAMBOANGA CITY PROVINCE: *Municipality of Zamboanga City* (PNM 9812 [holotype, formerly KU 314963], KU 314964 [paratype]); ZAMBOANGA DEL NORTE PROVINCE: Cuot Creek (CAS-SU 23548, 23549).

Pseudogekko compresicorpus (8).—POLILLO ISLAND: QUEZON PROVINCE: *Municipality of Polillo* (KU 326242); LUZON ISLAND: CAGAYAN PROVINCE: *Municipality of Gonzaga* (KU 330058); LAGUNA PROVINCE: *Municipality of Los Baños*: Barangay Batong Maiake (KU 326434, 326436); Barangay Bagong Silang (KU 330735, 331657); QUEZON PROVINCE: *Municipality of Infanta*: Barangay Magsaysay (KU 334017); MASBATE ISLAND: MASBATE PROVINCE: *Municipality of Mobo* (CAS 141560).

Pseudogekko ditoy (2).—LEYTE ISLAND: LEYTE PROVINCE: *Municipality of Baybay*: Barangay Gabas, Sitio Cienda (PNM 9811 [holotype, formerly KU 326437], KU 326438 [paratype]).

Pseudogekko isapa (2).—SIBUYAN ISLAND: ROMBLON PROVINCE: *Municipality of Magdiwang*: Mt. Guiting-Guiting Natural Park (PNM 9816 [holotype]); TABLAS ISLAND: ROMBLON PROVINCE: *Municipality of San Agustin* (CAS 139713 [paratype]).

Pseudogekko pungkaypinit (6).—BOHOL ISLAND: BOHOL PROVINCE: *Municipality of Sierra Bullones*: Barrio Dusita (CAS 131854 [paratype], CAS-SU 23655 [paratype]); Raja Sikatuna Natural Park (KU 324426 [paratype]); LEYTE ISLAND: LEYTE PROVINCE: *Municipality of Baybay* (KU 326243 [paratype]); Barangay Guadalupe (PNM 9810 [holotype, formerly KU 326435]); MINDANAO ISLAND: MISAMIS ORIENTAL PROVINCE: *Municipality of Gingoog City*: Barangay Lawaan, Sitio Kibuko, Mt. Lumot (KU 334019 [paratype]).

Pseudogekko smaragdinus (35).—POLILLO ISLAND: QUEZON PROVINCE: *Municipality of Polillo* (KU 302819–302831, 303995–304002, 307638–307647, 326240, 326241, 331721); LUZON ISLAND: CAMARINES DEL NORTE PROVINCE: *Municipality of Labo*: Barangay Tulay Na Lupa (KU 313828).

Pseudogekko sumiklab (2).—See holotype and paratypes section.