

PHILIPPINE BENT-TOED GECKOS OF THE *CYRTODACTYLUS* *AGUSANENSIS* COMPLEX: MULTILOCUS PHYLOGENY, MORPHOLOGICAL DIVERSITY, AND DESCRIPTIONS OF THREE NEW SPECIES

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ABSTRACT: We review the taxonomic status of Philippine bent-toed geckos previously referred to *Cyrtodactylus agusanensis*. We delineate four evolutionary lineages within the *C. agusanensis* complex from the southeastern islands of the archipelago and describe three of these lineages as new species. The new species and true *C. agusanensis* are identified by numerous, nonoverlapping morphological characters and by allopatric ranges on separate islands. Our morphology-based taxonomic conclusions are bolstered by biogeographic evidence and marked interspecific divergence between monophyletic groups defined by mitochondrial and nuclear DNA sequences. To compliment these descriptions and enable future taxonomic work on Philippine *Cyrtodactylus*, we rediagnose and redescribe *C. agusanensis*. Because the holotype of *C. agusanensis* was destroyed in World War II, we designate a neotype for this species and restrict its geographic range to north central Mindanao Island. Our phylogenetic estimate suggests that the *C. agusanensis* complex originated in Mindanao and spread progressively north, diversifying incrementally with colonization of successive islands in a south-to-north pattern of biogeographic expansion and allopatric speciation.

Key words: Cyrtodactylus; Geckos; Gekkonidae; New species; Philippines; Species delimitation

PHILIPPINE gekkonids of the genus *Cyrtodactylus* include six currently recognized species: *C. agusanensis*, *C. annulatus*, *C. jambangan*, *C. philippinicus*, *C. redimiculus*, and *C. tautbatorum*. Two of these species, *C. jambangan* and *C. tautbatorum*, were recently described, having previously been assigned to the “widespread” species *C. annulatus* (Welton et al., 2009, 2010). Our recent survey of morphological variation in the Philippine members of the genus, supported by phylogenetic analysis of DNA sequences and new interpretation of biogeographic evidence, has identified multiple highly divergent lineages in the “widespread” species complexes of the archipelago’s bent-toed geckos (Siler et al., 2010; Welton et al., 2010).

Taylor (1915, 1922) described *C. agusanensis* on the basis of specimens from Bunawan, northeastern Mindanao Island. Brown and Alcala (1978) further documented the presence of *C. agusanensis* on the islands of Mindanao and Leyte, and Ross and Lazell (1991) reported *C. agusanensis* on Dinagat

Island on the basis of a single specimen collected by Everett (BMNH 77.10.9.25). At the time of their review, Brown and Alcala (1978) acknowledged the considerable degree of morphological variation in this group but considered these isolated insular populations to be representative of extremes at the ends of a continuous range of intraspecific variation.

A recent phylogenetic analysis of the combined data from the mitochondrial gene NADH dehydrogenase subunit 2 (ND2) and the second intron of the nuclear ribosomal protein gene L35 (RPL35) uncovered deeply divergent lineages of *C. agusanensis* from some islands in its range (Siler et al., 2010). We augmented that dataset with genetic samples of *C. agusanensis* from near the type locality on Mindanao (Fig. 1) and examined patterns of genetic and morphological variation across the range of *C. agusanensis*.

In this study, we examined morphological characters, meristic and mensural data, and color pattern characters from throughout the known range of *C. agusanensis*, including new localities from Samar, Leyte, Dinagat, and Mindanao islands. Our effort focused on

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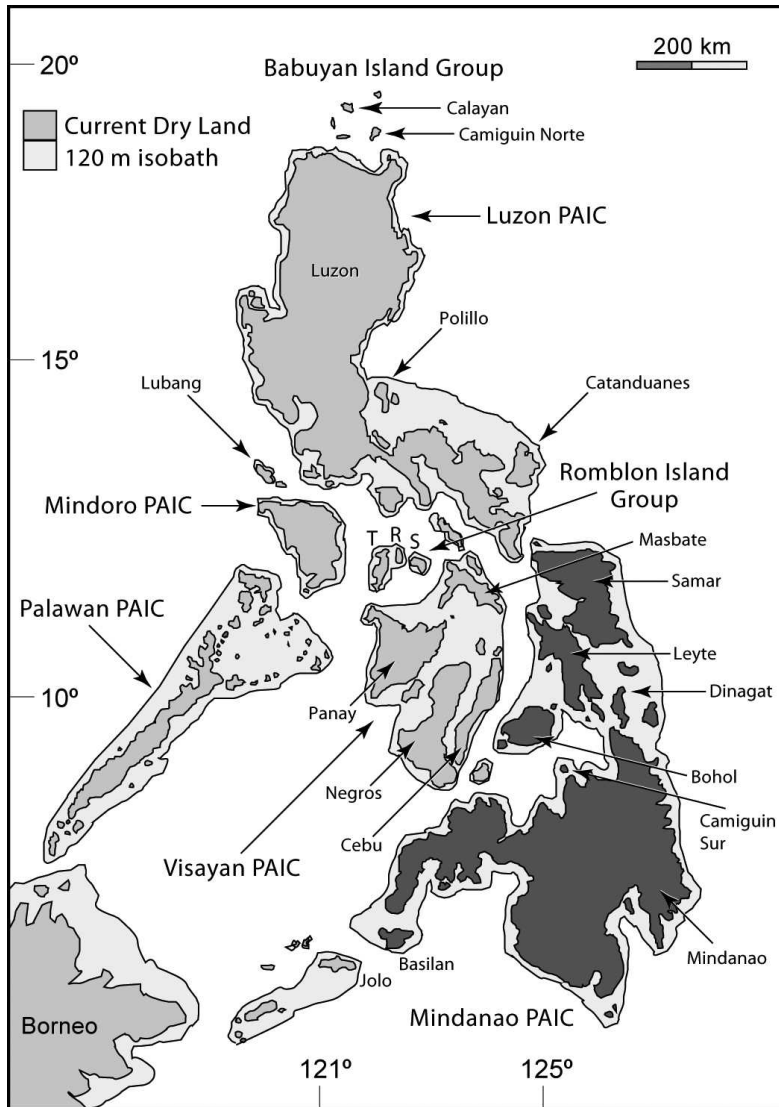


FIG. 1.—Map of the Philippine islands, with island labels provided for islands with representative samples used for this study. The five recognized major Pleistocene aggregate island complexes (PAICs), major island groups, and additional deep-water islands are labeled for reference. Islands of the Romblon Island group are designated by the first letter of the island name (T, Tablas Island; R, Romblon Island; S, Sibuyan Island). Current islands in the Philippines are shown in medium gray; light gray areas surrounded by 120-m bathymetric contours indicate the hypothesized maximum extent of land during the mid- to late Pleistocene. Darkly shaded islands indicate the potential geographical range of *Cyrtodactylus agusanensis* complex species.

characters that have proven in recent studies to be informative for delineating taxonomic boundaries in Philippine members of the genus (Welton et al., 2009, 2010).

Based on characteristics of body size and squamation, we identify three evolutionary lineages that are distinct from true *C.*

agusanensis from Mindanao Island. Our new phylogenetic estimate, plus an improved understanding of the allopatric nature of the included populations, further supports our taxonomic conclusions and provides insight into the evolutionary history of the group. Here, we clarify the status of true *C.*

agusanensis from the type locality and other nearby localities on Mindanao, provide a new diagnosis and redescription of this species, and identify three new allopatric lineage-based species. The three new species are endemic to the islands of Dinagat, Leyte, and Samar, respectively; and their descriptions bring the total diversity of Philippine bent-toed geckos to nine endemic taxa.

MATERIALS AND METHODS

Fieldwork, Sample Collection, and Specimen Preservation

Fieldwork on the islands of Mindanao, Samar, Leyte, and Dinagat (Fig. 1) between 2000 and 2009 provided the majority of the material necessary for this study. Collecting efforts were made between 1800 and 2400 h in variable habitats and at multiple elevations. Specimens were overanesthetized in an aqueous chloretone solution, genetically sampled (liver samples preserved in 95.0% ethanol or frozen in liquid nitrogen), and fixed in 10.0% formalin in the field. Upon deposition into U.S. and Philippine museum collections, specimens were transferred and stored in 70.0% ethanol. All older material, from the collections of E. H. Taylor, W. C. Brown, and A. C. Alcalá, deposited in U.S. institutions also was examined for diagnostic characters and morphometric data (see Specimens Examined and Table 1).

Taxon Sampling and Outgroup Selection for Phylogenetic Analyses

Our primary goal was to estimate phylogenetic relationships among the species in the *C. agusanensis* complex in relation to other Philippine species, and we therefore used only two to five exemplars per species (Table 1). We included representatives of all currently recognized Philippine *Cyrtodactylus* species (*C. annulatus*, *C. jambangan*, *C. philippinicus*, *C. tautatorium*, and *C. redimiculus*). In addition, we used two individuals of *C. intermedius* as outgroups based on relationships presented in a recent phylogenetic analysis of Philippine bent-toed geckos (Siler et al., 2010). In total, 32 ingroup samples were used in phylogenetic inferences. For all but two samples, sequences of the mitochondrial

gene NADH dehydrogenase subunit 2 (ND2) and the second intron of the nuclear ribosomal protein gene L35 (RPL35) were used in analyses (Table 1). Data for the nuclear marker were unavailable for one *C. intermedius* and one *C. redimiculus* sample. Most sequences were previously submitted to GenBank (Siler et al., 2010; Table 1); all newly collected data were deposited in GenBank under accessions GW67189–93 and GW69229–33.

DNA Extractions, Purifications, and Amplification

Genomic DNA was extracted from liver tissues stored in 95.0–100.0% ethanol following the guanidine thiocyanate method of Esselstyn et al. (2008). All primers and thermal cycler profiles used to amplify the target fragment using the polymerase chain reaction follow the methods of Siler et al. (2010). Amplified products were visualized on 1.0% agarose gels and then purified with 1 μ L of a 20.0% diluted solution of ExoSAP-IT (US78201; GE Healthcare Biosciences, Piscataway, NJ) for 31 min at 37°C and for 15 min at 80°C. We cycle sequenced in both directions with ABI Prism BigDye Terminator, version 3.1 (Applied Biosystems, Foster City, CA) chemistry and purified sequence reactions with Sephadex medium (NC9406038; GE Healthcare Biosciences) in Centri-Sep 96 spin plates (CS-961; Princeton Separations, Princeton, NJ). Targeted gene regions were analyzed with an ABI Prism 3130xl Genetic Analyzer (Applied Biosystems). Consensus gene sequences were assembled and edited in Sequencher 4.8 (Gene Codes Corp., Ann Arbor, MI).

Alignment and Phylogenetic Analyses

Initial alignments were produced with MUSCLE (Edgar, 2004), and manual adjustments were made in Se-Al Sequence Alignment Editor, version 2.0a11 (Rambaut, 2002). To assess phylogenetic congruence between the mitochondrial and nuclear data, we inferred the phylogeny for each subset independently using likelihood and Bayesian methods. In addition, we performed a partition homogeneity test with PAUP 4.0b10 (Swofford, 1999) with 100 replicates to assess

TABLE 1.—Summary of *Cyrtodactylus* specimens corresponding to genetic samples included in the study, general locality, and GenBank accession. KU = University of Kansas Natural History Museum and Biodiversity Research Institute. All specimens are from the Philippines unless otherwise noted.

Species	Voucher	Locality	GenBank accessions	
			ND2	RPL35
<i>C. intermedius</i>	KU 315781	Thailand, Sakaerat Environmental Research Station	GU550709	GU458034
<i>C. intermedius</i>	CUMZR 2005.07.30.139	Thailand, Sakaerat Environmental Research Station	GU550710	—
<i>C. redimiculus</i>	KU 309326	Palawan Island, Municipality of Brooke's Point	GU550744	—
<i>C. redimiculus</i>	KU 309327	Palawan Island, Municipality of Brooke's Point	GU550743	GU458065
<i>C. tautbatorum</i>	KU 309318	Palawan Island, Municipality of Brooke's Point	GU550751	GU458074
<i>C. tautbatorum</i>	KU 309322	Palawan Island, Municipality of Brooke's Point	GU550752	GU458075
<i>C. annulatus</i>	KU 309366	Camiguin Sur Island, Municipality of Mambajao	GU550763	GU458102
<i>C. annulatus</i>	KU 309364	Camiguin Sur Island, Municipality of Mambajao	GU550764	GU458103
<i>C. jambangan</i>	KU 314824	Mindanao Island, Municipality of Zamboanga City	GU550769	GU458108
<i>C. jambangan</i>	KU 314825	Mindanao Island, Municipality of Zamboanga City	GU550770	GU458109
<i>C. philippinicus</i>	KU 302640	Panay Island, Municipality of Pandan	GU550854	GU458182
<i>C. philippinicus</i>	KU 304786	Babuyan Claro Island, Municipality of Calayan	GU550899	GU458216
<i>C. philippinicus</i>	KU 308140	Catanduanes Island, Municipality of Gigmoto	GU550912	GU458227
<i>C. philippinicus</i>	KU 302649	Polillo Island, Municipality of Polillo, Site 1	GU550926	GU458232
<i>C. agusanensis</i>	KU 320014	Mindanao Island, Agusan Del Sur Province, Municipality of San Francisco, Barangay Bagusan II, Mt. Magdiwata	GW67189	GW69229
<i>C. agusanensis</i>	KU 320015	Mindanao Island, Agusan Del Sur Province, Municipality of San Francisco, Barangay Bagusan II, Mt. Magdiwata	GW67190	GW69230
<i>C. agusanensis</i>	KU 320016	Mindanao Island, Agusan Del Sur Province, Municipality of San Francisco, Barangay Bagusan II, Mt. Magdiwata	GW67191	GW69231
<i>C. agusanensis</i>	KU 320008	Mindanao Island, Agusan Del Sur Province, Municipality of San Francisco, Barangay Bagusan II, Mt. Magdiwata	GW67192	GW69232
<i>C. agusanensis</i>	KU 320009	Mindanao Island, Agusan Del Sur Province, Municipality of San Francisco, Barangay Bagusan II, Mt. Magdiwata	GW67193	GW69233
<i>C. gubaot</i>	KU 309336	Leyte Island, Municipality of Baybay	GU550779	GU458118
<i>C. gubaot</i>	KU 311131	Leyte Island, Municipality of Baybay	GU550781	GU458120
<i>C. gubaot</i>	KU 311132	Leyte Island, Municipality of Baybay	GU550782	GU458121
<i>C. gubaot</i>	KU 311139	Leyte Island, Municipality of Baybay	GU550783	GU458122
<i>C. gubaot</i>	KU 311140	Leyte Island, Municipality of Baybay	GU550780	GU458119
<i>C. mamananua</i>	KU 310102	Dinagat Island, Municipality of Loreto	GU550820	GU458154
<i>C. mamananua</i>	KU 310103	Dinagat Island, Municipality of Loreto	GU550821	GU458155
<i>C. mamananua</i>	KU 310104	Dinagat Island, Municipality of Loreto	GU550822	GU458156
<i>C. mamananua</i>	KU 305564	Dinagat Island, Municipality of Loreto	GU550823	GU458157
<i>C. mamananua</i>	KU 305565	Dinagat Island, Municipality of Loreto	GU550824	GU458158
<i>C. sumuroi</i>	KU 310798	Samar Island, Municipality of Taft	GU550772	GU458111
<i>C. sumuroi</i>	KU 310799	Samar Island, Municipality of Taft	GU550773	GU458112
<i>C. sumuroi</i>	KU 310800	Samar Island, Municipality of Taft	GU550774	GU458113
<i>C. sumuroi</i>	KU 310801	Samar Island, Municipality of Taft	GU550775	GU458114
<i>C. sumuroi</i>	KU 310802	Samar Island, Municipality of Taft	GU550776	GU458115

dataset congruence. After the observation of no statistically significant incongruence between datasets, we chose to conduct all subsequent analyses on a concatenated ND2 + RPL35 dataset. Exploratory analyses of this

combined dataset for all 34 individuals (including two lacking RPL35 sequences) and a reduced dataset of 32 individuals (no missing data) supported identical relationships; we therefore chose to include all

available data (34 individuals) for subsequent analyses.

Partitioned Bayesian analyses were conducted with MrBayes, version 3.1.2 (Ronquist and Huelsenbeck, 2003) for the combined datasets. Because this dataset is a subset of the Siler et al. (2010) dataset, we followed the same partitioning strategy. The mitochondrial dataset was partitioned by codon position for the protein-coding region of ND2. The Akaike information criterion, as implemented with Modeltest, version 3.7 (Posada and Crandall, 1998), was used to select the best model of nucleotide substitution for each data partition. The best-fit model for each of the three subsets of mitochondrial data was the general time reversible (GTR) model with a proportion of invariable sites (I) and gamma distributed rate variation among sites (Γ). The best-fit model for the nuclear data was GTR + Γ . A rate multiplier model was used to allow substitution rates to vary among subsets, and default priors were used for all model parameters. We ran four independent Metropolis-coupled Markov chain Monte Carlo analyses, each with four chains and the default heating scheme (temperature, 0.2). All analyses were run for 20 million generations, sampling every 5000 generations. To assess stationarity, all sampled parameter values and log-likelihood scores from the cold Markov chain were plotted against generation time and compared among independent runs using Tracer, version 1.4 (Rambaut and Drummond, 2007). Furthermore, we plotted the cumulative and nonoverlapping split frequencies of the 20 most variable nodes and compared split frequencies among independent runs by using the graphical exploration system Are We There Yet? (Wilgenbusch et al., 2004). All samples showed patterns consistent with stationarity after 5 million generations; hence, the first 50.0% of samples were discarded as burn-in for all three analyses.

In preliminary Bayesian analyses of the combined dataset, the independent runs failed to converge. We tried (1) replacing all GTR + I + Γ models with GTR + Γ models, (2) increasing the number of rate categories to six, (3) lowering the incremental heating temperature to 0.02, and (4) using an

unconstrained branch length prior with an exponential distribution with a mean up to 100 (Brown et al., 2010; Marshall et al., 2006, 2010). After the combination of all of these changes, the chains converged.

Partitioned maximum likelihood (ML) analyses were conducted in RAxMLHPC, version 7.0 (Stamatakis, 2006) for the combined dataset under the same partitioning strategy as for Bayesian analysis. The model (GTR + Γ) was used for all subsets, and 100 replicate ML inferences were performed for each analysis. Each inference was initiated with a random starting tree and used the rapid hill-climbing algorithm (Stamatakis et al., 2007). Clade confidence was assessed with 1000 bootstrap pseudoreplicates. In all analyses, nodes receiving $\geq 95\%$ Bayesian posterior probability or $\geq 70\%$ ML bootstrap support were considered significantly supported (Hillis and Bull, 1993).

Morphological Data

Cyrtodactylus specimens were examined from throughout the Philippines, representing all of the known specific diversity of the Philippine species, as defined by Brown and Alcalá (1978) and Siler et al. (2010).

Morphological data were collected from fluid-preserved specimens (see Specimens Examined; institutional abbreviations follow Leviton et al., 1985). Sex was determined by scoring secondary sexual characteristics and inspection of gonads when possible. To eliminate any possible interobserver bias, all morphological data were scored only by LJW (with digital calipers; measured to 0.1 mm). Character definitions follow Brown and Alcalá (1978) as modified by Welton et al. (2009, 2010) and include snout-vent length (SVL), subdigital lamellae of fingers and toes, number of enlarged pore-bearing preloacals and femorals, number of scales separating the femoral and preloacal series, counts of midbody dorsal and ventral scales, paravertebral scale series, numbers of postloacal lateral tubercles, number of caudal annuli delineated by dorsal tubercles, aspects of dorsal coloration and patterning, ventral coloration, numbers and shapes of midbody transverse bands in axilla-groin region, and the presence or absence of a canthal stripe.

Species Concept

We adopt the general lineage species concept of de Queiroz (1998) as a natural extension to the evolutionary species concept of Simpson (1961), Frost and Hillis (1990), and Wiley (1978). We use an estimate of phylogenetic relationships to guide species delimitation and identification of relevant comparisons for species diagnoses, but molecular divergences were not used to diagnose taxa. We consider as distinct species those lineages that are morphologically and genetically diagnosable, and for which the hypothesis of conspecificity can be confidently rejected by analyses of morphological and genetic data. Analysis of Philippine biodiversity under this concept has proven straightforward and unambiguous for identifying unique lineages of island endemics (Brown and Diesmos, 2002; Brown and Guttman, 2002; Brown et al., 2000, 2008, 2009a,b; Gaulke et al., 2007).

RESULTS

Phylogeny and Genetic Divergences

Maximum likelihood and Bayesian inferences yield the same interspecific topology, with minor intraspecific topological changes (Fig. 2). Within each dataset, variable and parsimony-informative characters were observed as follows: 545 and 508 of 1038 for the mitochondrial data and 79 and 39 of 557 for the nuclear data. All analyses of the combined dataset recovered four major clades within the *C. agusanensis* complex. Although separate analyses of the mitochondrial data recover all four major clades, analyses of the nuclear gene sequences recover only the Dinagat and Mindanao Island lineages with significant support (data not shown). The combined analyses strongly support all species-level relationships except for the placement of *C. agusanensis* (Fig. 2). The placement of real *C. agusanensis* is tenuous even with individual analyses of mitochondrial and nuclear datasets (data not shown). The four lineages correspond to the three morphologically distinct new species from Samar, Leyte, and Dinagat islands and true *C. agusanensis* from Mindanao. Each species clade defined in our analysis is separated from the remaining

lineages by 10.0–16.8% uncorrected mitochondrial sequence divergence (Table 2), and divergences within species clades are much lower (0.0–1.3%; Table 2). Samar and Leyte populations are sister to one another and together form a clade with the Dinagat Island lineage. This clade of three new species is weakly supported as sister to true *C. agusanensis* from Mindanao; support for the monophyly of *C. agusanensis* complex is likewise weak. Although genetic material from the type locality was unavailable for inclusion in this study, we are confident in our assignment of the Mindanao Island population sampled to the name *C. agusanensis*. Our recently collected specimens come from a site <75 km from the type locality; are morphologically indistinguishable from the existing paratypes (CM P-1946–48, P-1950, and P-1952 and MCZ R-20105) and Taylor's (1915, 1922) descriptions; and along with the type series, share the diagnostic character states that distinguish them from the three new species (see Diagnoses).

Morphology

Body size (as measured by SVL) distinguishes the Samar population from the Leyte population but does not distinguish any other species pairs under consideration. Other mensural data varied in a similar pattern but included no discrete ranges for individual characters that could be used for diagnostic purposes. However, numerous persistent and nonoverlapping differences were detected in a variety of meristic and color pattern characters for each *C. agusanensis* complex member, readily defining four distinct island populations within the complex (Table 3). We observed no mensural or meristic differences between the sexes of any of the four species. Pore-bearing scales in the preloacal and femoral regions were observed only in males; similarly enlarged and dimpled scales lack pores but were clearly distinct in females.

Fixed differences in color and pattern are present between the four island lineages. Darkly pigmented transverse dorsal bands consist of transverse bars, each with longitudinally elongated projections that extend, anteriorly and posteriorly, from transverse bands. The extent of these projections varies

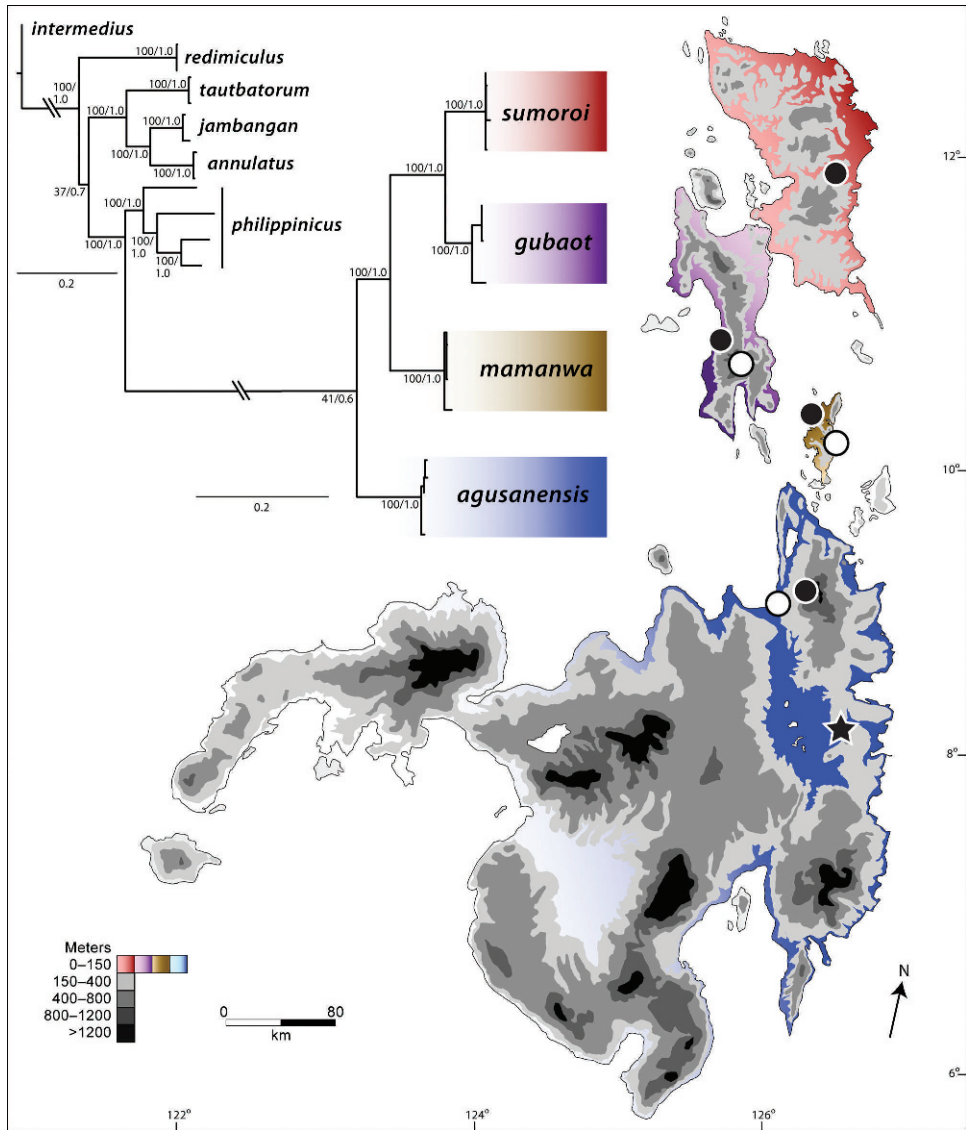


FIG. 2.—Maximum likelihood (ML) estimate of the phylogenetic relationships of *Cyrtodactylus agusanensis* complex species based on concatenated analysis of mitochondrial and nuclear DNA sequences (NADH dehydrogenase subunit 2 [ND2] + second intron of the nuclear ribosomal protein gene L35 [RPL35] genes; preferred ML tree, ln L = -8213.815320). Nodal support is indicated above branches (likelihood bootstraps/Bayesian posterior probabilities) and branch lengths are substitutions per site (branch leading to *C. agusanensis* complex not to scale). Nodes supported by $\geq 95\%$ Bayesian posterior probability and $\geq 70\%$ ML bootstrap proportion were considered significantly supported (Hillis and Bull, 1993). A reduced map of the Philippine islands showing the distribution of the four members of the *C. agusanensis* complex is shown with colors corresponding to clades in the phylogeny. Sampling localities are indicated by black circles, and historical records are indicated with open circles; the *C. agusanensis* type locality (Bunawan) is indicated with a star. Hypothesized geographic ranges of each species are indicated by colored gradients, with darker colors indicating greater confidence in a species' presence. (For interpretation of the references to color in this figure legend, see the online version of this article.)

TABLE 2.—Uncorrected pairwise sequence divergence (%) for mitochondrial data (below diagonal), nuclear data (above diagonal) for *Cyrtodactylus agusanensis*, *C. gubaot*, *C. mamanwa*, *C. sumuroi*, *C. annulatus*, *C. jambangan*, *C. philippinicus*, *C. tautbatorum*, and *C. redimiculus* (see Fig. 2). Bolded percentages on the diagonal represent intraspecific combined genetic diversity (NADH dehydrogenase subunit 2 [ND2] + second intron of the nuclear ribosomal protein gene L35 [RPL35]).

	<i>agusanensis</i>	<i>gubaot</i>	<i>mamanwa</i>	<i>sumuroi</i>	<i>annulatus</i>	<i>jambangan</i>	<i>philippinicus</i>	<i>tautbatorum</i>	<i>redimiculus</i>
<i>agusanensis</i>	0.4–0.9	1.1–1.8	1.3–2.0	0.7–2.4	3.1–3.6	3.3–4.4	0.9–2.6	3.7–4.4	3.5–4.0
<i>gubaot</i>	16.2–16.8	0.0–0.3	0.7–1.1	0.4–1.5	2.7–2.9	2.7–3.5	0.5–1.8	3.0–3.3	2.9–3.1
<i>mamanwa</i>	14.6–15.8	14.8–16.2	0.1–1.3	0.7–1.8	2.6–2.7	2.9–3.7	0.7–2.0	3.3–3.7	3.1–3.3
<i>sumuroi</i>	16.4–16.7	10.0–10.3	15.4–15.7	0.1–0.7	2.2–3.3	2.4–4.0	0.2–2.2	2.8–3.3	2.6–3.7
<i>annulatus</i>	17.4–18.1	19.6–20.4	20.7–21.2	19.6–19.8	0.5	0.5–1.1	2.4–3.5	1.5	2.9
<i>jambangan</i>	17.3–18.0	19.4–20.2	18.9–19.2	18.9–19.3	11.3–11.5	1.2	2.6–4.2	1.3–2.2	3.1–3.3
<i>philippinicus</i>	14.7–16.8	16.5–19.4	17.1–18.7	16.8–19.2	17.7–20.7	17.6–20.8	5.9–10.6	2.9–4.2	2.7–3.8
<i>tautbatorum</i>	16.4–16.7	19.7–20.6	20.5–20.9	19.3–19.5	14.7–14.9	13.8–14.3	18.1–19.7	0.4	3.3–3.5
<i>redimiculus</i>	17.2–17.7	19.6–20.1	21.2–21.5	18.3–18.6	17.4–17.7	18.4–18.6	18.9–20.6	19.6–19.7	0.1

in a consistent, fixed manner, consistent with putative species boundaries. Variation in this character forms a south–north gradient, with *C. agusanensis* (Mindanao) having the longest projections and populations from Samar having the shortest projections or with projections absent (see color descriptions for each species).

In summary, each island population possesses unique and nonoverlapping suites of diagnostic character states of morphology, perfectly corresponding to the clades defined in phylogenetic analyses of DNA sequence data. Combined with biogeographic evidence, and clearly separate geographical ranges, our data suggest the presence of four evolutionary lineages, worthy of taxonomic recognition.

Definition of the *C. agusanensis* Complex

Taylor (1915, 1922) defined *C. agusanensis* with the following combination of characters: 18–20 dorsal tubercle rows, males and females with differentiated prelocofemoral scales with pores (pores reportedly smaller in females), preloicals 10–12, and caudal tubercles arranged in whorls. At the time of description, Taylor recognized *C. agusanensis* as the largest Philippine species. In later identifying *C. agusanensis* (from Mindanao and Leyte), Brown and Alcalá (1978) emphasized body size (85–103 mm for adult males), prelocaal (7–11) and femoral (3–11) pores in males (pores in female not discussed), dorsal tubercle rows (18–20), and subdigital lamellae beneath Toe IV (23–31).

We provide the following revised definition for the *C. agusanensis* complex: (1) SVL of

70–103 mm; (2) differentiated prelocofemoral pore-bearing scales 10–25, noncontinuous (i.e., interrupted, and separated into differentiated preloicals and femorals with pores in males); (3) Toe IV subdigital lamellae 23–31; (4) supralabials 7–10; (5) midbody ventrals 53–70; (6) midbody dorsals 87–124; (7) paravertebrals 150–196; (8) postlocaal tubercles 4–11; and (9) dorsal tubercles moderate in size, in 14–19 rows at midbody, 19–31 paravertebrally. See Welton et al. (2009, 2010) for exhaustive comparisons of the *C. agusanensis* complex to other Philippine species and all Sunda Region taxa.

Recognition of New Species

Our phylogeny suggests close relationships with other Philippine *Cyrtodactylus*, including *C. annulatus* (Bohol, Cebu, Leyte, Mindanao, and Siquijor islands); *C. jambangan* (Zamboanga Peninsula, Mindanao Island, and the Sulu Archipelago); and *C. philippinicus* (the Babuyan and Sibuyan island groups, as well as Catanduanes, Lubang, Luzon, Mindoro, Negros, Panay, and Polillo islands), *C. redimiculus* (Palawan), and *C. tautbatorum* (Palawan). Morphological comparisons of each new species with all Philippine congeners are presented below. Because each of the new species differs from non-Philippine congeners by the same characters that have distinguished *C. agusanensis* (and have never been challenged; Brown and Alcalá, 1978; Taylor, 1915, 1922), we choose not to include exhaustive comparisons to all those species (but see Welton et al., 2009, 2010). Rather, we focus on the most relevant comparisons for

TABLE 3.—Distribution of diagnostic characters in the three new species, *Cyrtodactylus agusanensis*, and other Philippine species of the genus *Cyrtodactylus*. Measurements are presented in millimeters, and all specimens were considered adults. Data from juveniles were excluded. See Materials and Methods for character definitions.

	<i>sumuroi</i>	<i>namanuca</i>	<i>agusanensis</i>	<i>annulatus</i>	<i>tantibatorum</i>	<i>jambangan</i>	<i>redimitulus</i>	<i>philippinus</i>
Sample size (male/female)	2/2	11/7	14/9	4/6	8/8	10/10	7/3	21/17
Snout-vent length	73.9–84.9	67.5–92.01	67.1–105.4	59.3–80.5	47.2–68.7	60.4–72.3	76.9–94.2	63.2–97.6
Finger III lamellae	18–22	18–23	21–24	15–21	15–17	16–22	17–22	17–25
Toe IV lamellae	21–24	22–25	20–28	17–22	17–21	20–24	19–24	19–26
Supralabials	8–10	7–10	9–10	7–10	6–9	8–10	7–11	6–10
Infralabials	6–8	6–8	7–8	7–8	6–7	6–8	6–8	5–8
Precloacofemoral scales	23–32	18–30	23–29	6	4–6	2–5	17–23	7–10
Midbody dorsals	87–98	95–112	111–124	81–95	76–93	86–96	104–121	87–125
Midbody tubercles	18–19	18–21	16–21	14–18	13–17	17–19	13–16	17–20
Midbody ventrals	53–58	57–70	56–68	49–60	46–58	48–63	46–54	40–75
Parvertebrals	163–180	173–192	184–196	124–166	140–170	150–170	190–212	152–212
Parvertebral tubercles	23–29	25–31	20–28	17–28	23–28	23–31	18–22	21–31
Postcloacal lateral tubercles	4–6	4–7	8–11	2–4	1–4	2–5	4–6	2–5
Dark ventral color with white flecks	–	–	–	–	–	–	–	–
Canthal stripe	+	–	–	–	–	+	–	–
Anterior–posterior band	Minimal	Moderate	Extensive	Moderate	Minimal to moderate	Minimal to moderate	Minimal	Minimal to moderate
Dark dorsal band enclosing light band	+	+	–	+	–	–	+	+
Cephalic tubercles	Moderate	Large	Moderate	Small to moderate	Small to moderate	Small to moderate	Small	Small to moderate
Undifferentiated scales separating precloacals from femorals	19–21	14–22	13–17	Femorals absent	Femorals absent	Femorals absent	8–16	Femorals absent
No. of caudal annuli with dorsal tubercles	3–7	7–12	7–12	7–13	9–12	4–7	4–12	8–12
Range	East Samar	West Leyte	Dinagat	Mindanao, Visayas	Palawan	Western Mindanao and Sulus	Palawan	Northern and central Philippines

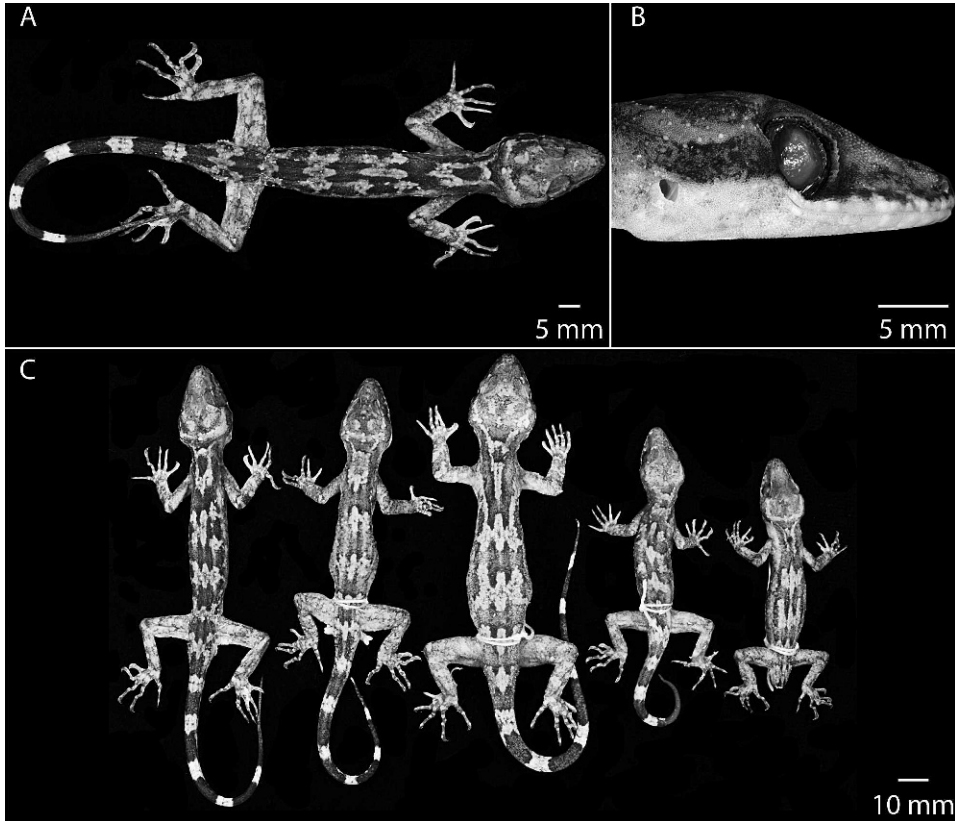


FIG. 3.—Photographic plate of *Cyrtodactylus agusanensis*. (A) Dorsal view of neotype. (B) Lateral view of neotype head. (C) Panel of types showing variation in color pattern.

recognition and diagnosis of the new species: those taxa within the *C. agusanensis* complex and all other closely related members of the endemic and monophyletic (Siler et al., 2010) Philippine clade.

TAXONOMIC ACCOUNTS

Cyrtodactylus agusanensis (Taylor 1915)

Figs. 3, 4A

Gymnodactylus philippinicus: Günther, 1879: 76 (part); Boulenger, 1885: 46 (part).

Gymnodactylus agusanensis: Taylor, 1915: 90. Holotype: Philippine Bureau of Science R 1686 (destroyed); type locality: Bunawan, Agusan del Sur Province, Mindanao Island, Philippines; Taylor, 1922: 49; Wermuth, 1965: 47.

Cyrtodactylus agusanensis: Underwood, 1954: 475; Brown and Alcalá, 1978: 16.

Designation of a neotype for C. agusanensis.—Due to the absence of an existing holotype (Taylor's holotype for *C. agusanensis* was destroyed in World War II; Philippine Bureau of Science R 1686, collected June 1913), and in accordance with Article 75 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999), we designate a neotype for *C. agusanensis* (Fig. 3A). The action is necessary because the existing *C. agusanensis* descriptions (Brown and Alcalá, 1978; Taylor, 1915, 1922) are inadequate to distinguish true *C. agusanensis* from the new taxa recognized below. All existing specimens from the original type series (from Bunawan, Agusan del Sur Province, Mindanao) deposited at the Carnegie Museum and Harvard's Museum of Comparative Zoology, were examined as potential candidates for a neotype.

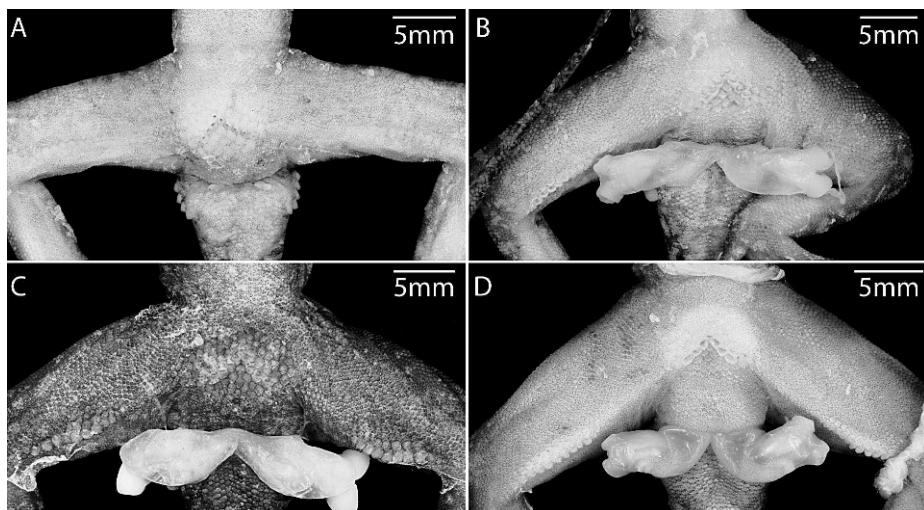


FIG. 4.—Pre-cloacal view of all four *Cyrtodactylus* species: *C. agusanensis* (A), *C. sumuroi* (B), *C. gubaot* (C), and *C. mamananca* (D).

Unfortunately, original specimens are either poorly preserved or incomplete and thus lack important diagnostic characters; no other specimens from Bunawan exist in museum collections. As the next best alternative, we choose an adult male specimen (KU 320014) from the closest available locality, Mt. Magdiwata, Misamis Oriental Province (approximately 75 km N of the type locality). The neotype is an adult male, collected as part of a series of both sexes, all of which clearly demonstrate the salient diagnostic characters. This more recent sample agrees with Taylor's (1915) holotype description (but see Comment) and extant paratype specimens from the same locality (CM P-1946–48, P-1950, P-1952, and MCZ R-20105) and is a well-preserved adult male in excellent condition. Lastly, this action has the added benefit of restricting the (neo) type locality to a definite, easily accessible location with intact forest where a known population of *C. agusanensis* can still be found and studied further.

Neotype.—KU 320014 (ACD 3918), an adult male, collected by ACD in Agusan del Sur Province, Municipality of San Francisco, Barangay Bagus II, Mt. Magdiwata (350 m), Mindanao Island, Philippines, on 26 October 2008.

Referred specimens.—See Appendix.

Description of neotype.—Adult male (Fig. 3A, B; characters scored for right side of body unless otherwise noted), SVL 93.1 mm; head triangular, moderately long, distinct from neck, 29.0% SVL; head width 67.0% and depth 37.0% head length; tip of snout rounded in dorsal aspect; snout elongate, 43.0% head length; lores slightly concave posterior to narial openings; eye diameter 24.0% head length, 87.0% eye–ear distance; auricular opening oval, longer (vertical) axis 8.0% head length.

Rostral wider than tall, height 62.0% width, bordered by single medial anterior internasal, paired secondary posterior internasals, supranasals, and first supralabials; internarial distance 3.1 mm; nostril bordered by supranasal, rostral, first supralabial, and four postnasals; supralabials and infralabials generally rectangular and decreasing in size posteriorly, 9/9 to midpoint of eye (12/12 total) and 8/7 to beneath midpoint of eye (12/11 total), respectively; supralabials bordered dorsally by one to two rows of secondary, slightly differentiated scales, extending to supralabial 8; infralabials bordered ventrally by enlarged secondary row, extending posteriorly to infralabial 6.

Dorsal head scalation heterogeneous, with the smallest scales dorsomedially and the largest along the canthal ridge; superciliaries decrease in size posteriorly, dorsal most

superciliaries laterally elongated and approximately triangular. Mental subtriangular, bordered laterally by first infralabials, posteriorly by paired longitudinally elongated postmentals; nine differentiated scales posterior to postmentals; gular scales generally homogeneous, small and granular, but increasing slightly in size laterally at jaw line and toward pectoral region.

Body elongate, axilla–groin distance 43.0% SVL, lacking distinct ventrolateral folds; dorsal scalation granular, heterogeneous, with semiregular rows of round, slightly convex and weakly spinose, moderately distributed tubercles; transverse midbody tubercle rows 19; longitudinal paravertebral tubercle rows 25; paravertebral scales 189; transverse midbody dorsal and ventral scales 122 and 60, respectively; ventral scales imbricate, 2–3 times larger than dorsals; precloacal scales in four chevron-shaped differentiated transverse rows, anterior to 10 (5/5) pore-bearing scales, followed posteriorly by 21 triangularly arranged differentiated scales; precloacal groove absent (Fig. 4A).

Forelimbs slender, elongate; forearm and upper arm 14.0% and 13.0% SVL, respectively; dorsal forelimb scalation heterogeneous, scales larger than ventrals, largest in aggregation just medial to wrist; tubercle distribution sparse on upper arm, more dense and slightly more spinose on forearm; ventral limb scales homogeneous, small and granular, and lacking tubercles; fingers elongate and well developed, Fingers I and III 36.0% and 64.0% forearm length, respectively; subdigital scales differentiated, lamellae distal to third interphalangeal joint enlarged and raised; finger number followed by subdigital lamellae (in parentheses): I (13), II (17), III (22), IV (21), V (16); all fingers clawed; claws well developed, sheathed by single dorsal and ventral scales.

Hind limbs slender, elongate; femur and tibia, 19.0% and 16.0% SVL, respectively; dorsal hind limb scalation heterogeneous, generally small and granular, with tubercles regularly distributed and tuberculation similar to that of dorsal trunk; ventral limb scales heterogeneous, most scales slightly smaller than dorsals, lacking tubercles; enlarged femoral scales in two rows extending from

knee to midfemur, consisting of 11/10 differentiated (but poreless) prefemorals and 10/12 differentiated (eight and nine pore-bearing) femorals; toes well developed; Toes I and IV 35.0% and 86.0% tibia length, respectively; subdigital scales differentiated, lamellae distal to third interphalangeal joint enlarged and raised; toe number followed by subdigital lamellae (in parentheses): I (14), II (19), III (23), IV (26), V (24); all toes clawed; claws well developed, sheathed by single dorsal and ventral scales.

Tail original except for terminal 22.5 mm (regenerated), total length 104.2 mm, tapering abruptly posterior to hemipenial bulge and then gradually to terminus; 12 basal caudal annuli discernible; distal annuli cannot be distinguished, owing to the absence of dorsal tubercles associated with annuli; caudal tubercles more spinose than those of body; lateral postcloacal tubercles 5/4, highly spinose; anterior margin of hemipenial bulge with paired, postcloacal glandular openings. Complete meristic and mensural data for the neotype are presented in Table 4.

Measurements from Taylor, 1915 (holotype, PBS 1686, destroyed), 1922 (EHT 639), respectively.—Total length 170, 220 mm; SVL 88, 106; head width 18, 23; head length 24, 29; foreleg 36, 40; hindleg 48, 55.

Coloration of neotype in preservative.—Dorsal ground coloration (of head, body, and limbs; Fig. 3A) light brown to gray, with indistinct dark brown speckling; head patterning indistinct in canthal and temporal regions, but dark brown at tip of snout and continuing intermittently along supralabials to ventral margin of eye (Fig. 3B); occiput with conspicuous, paired, dark brown ocelli with light gray centers; laterally, head with dark brown longitudinal band extending from posterior margin of eye to nuchal region (running dorsal to auricular opening) and then bifurcating and continuing both dorsally along posterior margin of parietal region, as well as continuing on lateral surface through nuchal and into axilla–groin region; nuchal region lacking complete band, but with large dark brown medial blotch (and dark brown longitudinal lateral stripes); trunk with dark brown transverse bands (three within axilla–groin region, four total) characterized in axilla–groin and sacral region by

TABLE 4.—Complete meristic and mensural data for the holotypes of *Cyrtodactylus sumuroi*, *C. gubaot*, and *C. amanwa*, and the neotype of *C. agusanensis*. All meristic data are from the right side of the body unless otherwise indicated, with counts separated by a slash (L/R, left/right); all mensural data are presented in millimeters. See text and Welton et al. (2009, 2010) for character definitions.

Catalog no.	<i>C. sumuroi</i>	<i>C. gubaot</i>	<i>C. amanwa</i>	<i>C. agusanensis</i>
	PNM 9723	PNM 9724	PNM 9725	KU 320014
Snout-vent length	82.3	87.5	86.5	93.1
Head length	23.6	28.6	24.0	26.9
Head width	16.1	18.8	16.6	18.1
Head depth	9.4	11.3	9.6	9.9
Snout length	9.1	11.1	10.5	11.5
Eye diameter	5.5	6.3	5.9	6.4
Eye-ear distance	6.8	7.6	7.0	7.4
Ear diameter	2.0	2.6	2.6	2.0
Rostrum height	2.0	2.8	2.4	2.4
Rostrum width	3.5	4.0	3.5	3.9
Internarial distance	2.8	3.3	2.7	3.1
Supralabials to eye	8	10/9	8/7	9
Supralabials total	12/13	13/14	11/10	12
Infralabials to eye	8/6	7	7/6	7/8
Infralabials total	11/10	13/11	9/9	12/11
Axilla-groin distance	34.6	41.7	39.8	40.2
Midbody tubercles	18	19	20	19
Paravertebral tubercles	23	21	30	25
Paravertebrals	177	159	192	189
Midbody dorsals	97	98	103	122
Midbody ventrals	58	61	57	60
Precloacal scales	4/4	5/4	4/3	5/5
Forearm length	12.5	14.7	12.5	13.2
Upper arm length	10.1	11.4	11.4	12.2
Finger I length	4.9	4.9	4.6	5.2
Finger III length	8.0	8.7	8.1	8.5
Finger I lamellae	13	16	13	13
Finger II lamellae	19	21	18	17
Finger III lamellae	22	26	21	22
Finger IV lamellae	23	26	23	21
Finger V lamellae	20	22	19	16
Femur length	17.1	18.8	17.5	17.4
Tibia length	12.9	16.0	14.0	14.7
Femoral scales	9L/10R	8L/8R	10L/10R	8L/9R
Toe I length	4.3	5.9	4.3	5.2
Toe IV length	9.7	11.5	9.9	12.6
Toe I lamellae	15	16	14	14
Toe II lamellae	20	23	20	19
Toe III lamellae	22	25	24	23
Toe IV lamellae	24	30	23	26
Toe V lamellae	25	24	26	24
Tail length	95.7	111.5	106.7	104.2
Caudal annuli with tubercles	5	8	9	12
Postcloacal tubercles	2L/2R	2L/2R	2L/2R	5L/4R

longitudinal elongations on either side of vertebral column, conferring a vaguely “bow-tie” shape; laterally, dorsal bands connected by irregularly broken dark brown longitudinal stripe (continuing from head and nuchal region); limbs with medium brown, faded bands and irregular speckling; Fingers I and

III light brown but all other fingers and toes with irregular dark bands; ground color of tail light gray just posterior to sacral region, gradually becoming light cream to white distally; tail with five light, and six dark brown bands; regenerated terminus of tail medium gray, with indistinct dark brown speckling.

Ventral coloration (except that of hands, feet, and tail) light cream; lighter coloration extending from infralabials, auricular opening, and dark brown lateral stripe on head and through nuchal region, from lateral tubercle row through axilla-groin region, and from midway of lateral surfaces on limbs; hands and feet coloration slightly darker than body, originating at wrists and ankles; subcaudal region light gray to cream, with irregular dark brown speckling anteriorly, becoming more consistent and eventually forming ventral continuance of dark dorsal bands at midtail; regenerated tail terminus ventral coloration similar to that of dorsum.

Color in life.—From Taylor (1915: 91): “Grayish white above with 4 or 5 enlarged, irregular dark black-brown crossbands, strongly contrasted; tail annulated with broad black rings and narrow white interspaces; a broad dark line from behind eye joins the dark band which crosses the shoulder; a broad light line from the angle of the mouth to the shoulder; a somewhat darker band below the white line; a narrow white line from behind the upper part of the eye to a point above ear opening, and across the occiput; head darker than the back, with a few distinct markings; labials with several small white spots; abdomen and throat yellowish white, powdered with brown; arms and legs marbled with brown; toes with dark and white spots alternating.” Live coloration of more recent specimens was not recorded, and no photographs are available. Based on experience with Philippine congeners (personal observation), we do not expect dramatic color changes to have occurred as a result of preservation.

Variation.—The available series of *C. agusanensis* consists of 23 specimens, including Taylor’s (1915) type series: paratypes CM P-1946 (male), 1947 (juvenile), and 1948 (female), P-1950 and P-1952, and MCZ R-20105 (males), 10 additional adult males (neotype KU 320014, 320015, CAS 133424, 133426, 133510, 139317–18, 133634–35, 133697), six adult females (KU 320019, CAS 133425, 133505–07, 133511), and five juveniles (KU 320016–18, 320020–21) all from eastern Mindanao Island. Postnasals three or four; internasals variable, either (1) a single longitudinally elongated medial scale followed

posteriorly by two enlarged scales, in medial contact (neotype KU 320014 and KU 320015) or separated by undifferentiated rostrals (KU 320016); (2) a single subtriangular scale followed by three posterior enlarged scales (KU 320019); or (3) a single pair of enlarged internarial scales (KU 320017).

Due to the preservation status of the original type series, we cannot comment on color or pattern variation in those specimens, although Taylor (1922) mentioned that the type series and other specimens were gray with dark brown dorsal transverse bands and that younger specimens were dorsally darker and more boldly contrasting in color than adults. One juvenile (KU 320018) has a medium brown ground color, making for a less contrasting dorsal pattern; one adult female (KU 320019) and three juveniles (KU 320017, 320020–01) lack a dark medial spot in the nuchal region; cephalic patterning in all three adults (KU 320014–15, 320019) consists of paired anterior and single posterior medial ground colored spots, whereas the juveniles lack discernible cephalic patterning; three juveniles (KU 320018, 320020–21) lack a dorsolateral longitudinal ground colored stripe extending posteriorly from the eye; one female (KU 320019) has discontinuous dark brown lateral banding through anterior portion of axilla-groin region; all juveniles are slightly darker than adults, with two juveniles (KU 320018, 320020) having a medium brown ground color; regenerated portions of tails on all specimens lack discernible bands; juveniles with four highly contrasting light and dark bands through caudal region. Although our sample (Fig. 3C) suggests the potential presence of ontogenetic differences in dorsal banding, examination of a larger series of the species is needed to adequately diagnose this possibility. Taylor stated that when first captured, specimens of the type series were more boldly contrasting in color extremes, which faded later when exposed to daylight (Taylor, 1922: 51).

Comment.—Taylor remarked on the presence of scale perforations and precloacal and femoral pores in both males and a specimen he identified as a female (the holotype, destroyed). In the original description, Taylor (1915) used the presence of pores in both

males and females as a diagnostic character for the species and remarked on the rarity of prelocofemoral pores in females of the genus *Cyrtodactylus*. Brown and Alcalá (1978) mentioned pore counts for males only. We have examined all available specimens of this species, and we also find pores in males only. As in other gekkonids, females exhibit enlarged and differentiated preloacal and femoral scales in the same positions as males, and these scales are often dimpled but, in our experience, always poreless. Taylor did remark that pores in the females he examined were smaller than pores of males (Taylor, 1915: 92). The discrepancy between our observations and those of Taylor indicates that this character may be polymorphic in *C. agusanensis*. Confirmation of this possibility must await the collection of additional female specimens from Mindanao Island.

Ecology and natural history.—Mindanao Island specimens have been collected in a variety of forest types, from disturbed to intact forest, usually along riparian vegetation corridors. Our specimens were collected on boulders on the banks of a 4–5-m-wide river, at 700 m above sea level. Brown and Alcalá (1978) reported that their specimens were taken from rocks on the bank of a river on northeastern Mindanao. Taylor's (1922) specimens were collected at the type locality (Bunawan, Mindanao) from inside a pile of rotting logs, and one specimen was collected from inside a tree hole, 2 m from the ground. Taylor stated the species was rare at the type locality (Taylor, 1922), but it seems to be fairly common on Mt. Magdiwata. Sympatric gekkonids include *C. annulatus*, *Gehyra mutilata*, *Gekko gekko*, *Hemidactylus frenatus*, *Hemidactylus platyurus*, *Lepidodactylus aureolineatus*, *Pseudogekko compressicorpus*, *Pseudogekko labialis*, and *Ptychozoon intermedium*. It is conceivable that *C. jambangan* and *Luperosaurus joloensis* may co-occur with *C. agusanensis* if populations of the latter species extend into western Mindanao.

Cyrtodactylus sumuroi sp. nov.

Figs. 4B, 5

Holotype.—PNM 9723 (formerly KU 305566; field no. CDS 1834), adult male, Samar Island, Eastern Samar Province, Municipality of Taft, Barangay San Rafael, Taft

Forest (11.829° N, 125.273° E; WGS84), collected on 16 June 2006 by CDS.

Paratypes.—Samar Island, Eastern Samar Province, Municipality of Taft, Barangay San Rafael (11.831° N, 125.279° E, 187 m; WGS84), all specimens collected by CDS: one male, one juvenile: KU 310796 and 310797 (17 October 2007; 11.803° N, 125.293° E, 140 m); one female: KU 310798 (17 October 2007; same locality); three juveniles: KU 310799–801 (22 October 2007; same locality); and one female: KU 310802 (23 October 2007). All specimens collected between 1800 and 2200 h, in secondary growth forest, on shrubs or young saplings, 1–2 m above the ground.

Diagnosis.—The critical comparisons for this species are congeners from the *C. agusanensis* complex. *Cyrtodactylus sumuroi* is distinguished from *C. agusanensis* by midbody dorsals 87–98 (vs. 111–124); paravertebrals 163–180 (vs. 184–196); postloacal tubercles 4–6 (vs. 8–11); scales separating preloacals and femorals 19–21 (vs. 13–17); caudal annuli with tubercles 3–7 (vs. 7–12); canthal stripe present (vs. absent); anterior–posterior dorsal band projections minimal or absent (vs. extensive); and dark dorsal bands enclosing light bands (vs. light bands not enclosed). *Cyrtodactylus sumuroi* also exhibits tendencies toward fewer subdigital lamellae beneath Finger III (18–22 vs. 21–24), and midbody ventral scales (53–58 vs. 56–68).

Cyrtodactylus sumuroi is readily diagnosed from *C. gubaot* (Leyte) by SVL 73.9–84.9 (vs. 85.6–100.1), paravertebrals 163–180 (vs. 150–162), ventral color cream (vs. dark gray with white flecks), anterior–posterior dorsal band projections minimal or absent (vs. moderate); dark dorsal bands enclosing light bands (vs. light bands not enclosed); cephalic tubercles moderate (vs. large); and number of caudal annuli with dorsal tubercles 3–7 (vs. 9–12). *Cyrtodactylus sumuroi* also exhibits tendencies toward fewer midbody ventrals (53–58 vs. 54–67), midbody dorsals (87–98 vs. 92–105), and subdigital lamellae beneath Finger III (18–22 vs. 20–26) and Toe IV (21–24 vs. 24–30).

From *C. mamananwa* (Dinagat), *C. sumuroi* is distinguished by the presence (vs. absence) of a canthal stripe, anterior–posterior dorsal

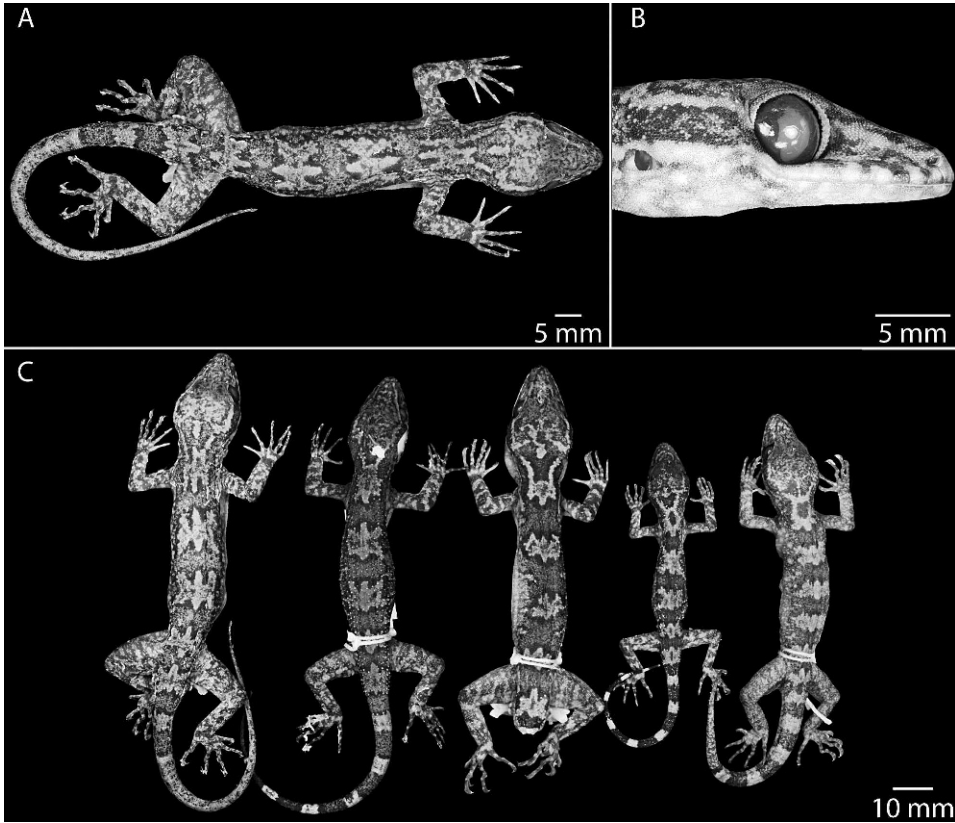


FIG. 5.—Photographic plate of *Cyrtodactylus sumuroi*. (A) Dorsal view of holotype. (B) Lateral view of holotype head. (C) Panel of types showing variation in color pattern.

band projections minimal or absent (vs. moderate), cephalic tubercles moderate (vs. small), and caudal annuli with dorsal tubercles 3–7 (vs. 7–12). *Cyrtodactylus sumuroi* also exhibits tendencies toward fewer midbody dorsals (87–98 vs. 95–112), midbody ventrals (53–58 vs. 57–70), and paravertebrals (163–180 vs. 173–192).

Cyrtodactylus sumuroi is diagnosable from all other Philippine congeners (*C. annulatus*, *C. jambangan*, *C. tautbatorum*, *C. redimiculus*, and *C. philippinicus*) by characters of body size and scalation (Table 3). The new species can be distinguished from *C. jambangan* and *C. tautbatorum* by larger SVL and the presence of dark dorsal bands enclosing light bands (vs. light bands not enclosed); from *C. tautbatorum* by a greater number of subdigital lamellae beneath Toe IV; from *C. annulatus*, *C. jambangan*, *C. tautbatorum*, and *C. philippinicus* by the presence (vs. absence) of

femoral pore-bearing scales; from *C. tautbatorum* and *C. redimiculus* by a greater number of midbody tubercle rows; from *C. redimiculus* by fewer paravertebral scales, fewer midbody dorsals, a greater number of dorsal tubercle rows, and larger cephalic tubercles; from *C. annulatus*, *C. tautbatorum*, *C. redimiculus*, and *C. philippinicus* by the presence of a canthal stripe (vs. absence); from *C. annulatus* by the presence of anterior–posterior dorsal band projections (vs. absence); and from *C. annulatus*, *C. tautbatorum*, and *C. philippinicus* by having fewer caudal annuli with dorsal tubercles (Table 3).

Description of holotype.—Adult male (Fig. 5A; characters scored for right side of body unless otherwise noted), SVL 82.3 mm; head triangular, moderately long, distinct from neck, 28.0% SVL; head width 68.0% and depth 40.0% head length; tip of snout

rounded in dorsal aspect; snout moderately elongate, 39.0% head length; lores flat; eyes relatively large, eye diameter 23.0% head length 81.0% eye-ear distance; auricular opening tear-shaped, oriented longitudinally, longer (horizontal) axis 8.0% head length.

Rostral wider than tall, height 57.0% width, bordered by two undifferentiated granular internasals, supranasals, and first supralabials; internarial distance 2.8 mm; nostril bordered by supranasal, rostral, first supralabial, and three postnasals; supralabials and infralabials generally rectangular and decreasing in size posteriorly, 8/8 (left/right) to midpoint of eye (12/13 total) and 8/6 to beneath midpoint of eye (11/10 total), respectively; supralabials bordered dorsally by one to two rows of secondary, slightly differentiated scales, extending to supralabial 7; infralabials bordered ventrally by enlarged secondary row, extending posteriorly to infralabial 6/5.

Dorsal head scalation heterogeneous, scales relatively small and granular; superciliaries decrease in size posteriorly; anterodorsal most superciliaries laterally elongated and approximately triangular. Mental subtriangular, bordered laterally by first infralabials, posteriorly by paired longitudinally elongated postmentals; differentiated scales posterior to postmentals 12; gular scales homogenous, small and granular but increasing slightly through pectoral region.

Body elongate, axilla-groin distance 42.0% SVL, lacking distinct ventrolateral folds; dorsal scalation granular, heterogeneous, with semiregular rows of round, slightly convex and moderately spinose tubercles; transverse midbody tubercle rows 18; longitudinal paravertebral tubercle rows 23; paravertebral scales 177; transverse midbody dorsal and ventral scales 97 and 58, respectively; ventral scales imbricate, up to twice the size of dorsals; precloacal scales in four chevron-shaped differentiated transverse rows, anterior to eight (4/4) pore-bearing scales, followed posteriorly by 22 triangularly arranged differentiated scales; precloacal groove absent (Fig. 4B).

Forelimbs slender, elongate; forearm and upper arm 15.0% and 12.0% SVL, respectively; dorsal forelimb scalation nearly homogenous, scales larger than ventrals, only slightly

larger in aggregation just medial to wrist; tubercles absent on upper arm, distributed sparsely on forearm; ventral limb scales homogeneous, granular, lacking tubercles, and slightly smaller than trunk ventrals; fingers elongate and well developed, Fingers I and III 39.0% and 65.0% forearm length, respectively; subdigital scales differentiated, lamellae distal to third interphalangeal joint enlarged and raised; finger number followed by subdigital lamellae (in parentheses): I (13), II (19), III (22), IV (23), V (20); all fingers clawed; claws well developed, sheathed by single dorsal and ventral scales.

Hind limbs slender, elongate; femur and tibia, 21.0% and 16.0% SVL, respectively; dorsal hind limb scalation heterogeneous, generally small and granular, with tubercles regularly distributed and tuberculation larger than that of dorsal trunk; ventral limb scales heterogeneous, most scales slightly smaller than dorsals, lacking tubercles; enlarged femoral scales in two rows extending from knee to midfemur, consisting of 8/12 differentiated (but poreless) prefemorals and 12/12 differentiated (9/10 pore-bearing) femorals; toes well developed; Toes I and IV 33.0% and 75.0% tibia length, respectively; subdigital scales differentiated, lamellae distal to third interphalangeal joint enlarged and raised; toe number followed by subdigital lamellae (in parentheses): I (15), II (20), III (22), IV (24), V (25); all toes clawed; claws well developed, sheathed by single dorsal and ventral scales.

Tail regenerated except for initial 17.4 mm, total length 95.7 mm, tapering abruptly posterior to hemipenial bulge and then gradually to terminus; five basal caudal annuli discernible; distal annuli cannot be distinguished, owing to the absence of dorsal tubercles associated with annuli; caudal tubercles more spinose than those of body; lateral postcloacal tubercles 2/2, rounded; anterior margin of hemipenial bulge with paired, postcloacal glandular openings. Complete meristic and mensural data for the neotype are presented in Table 4.

Color of holotype in preservative.—Dorsal base coloration (of head, body, and limbs; Fig. 5A) light brown to tan, with medium to dark brown patterning; head patterning moderately distinct, with irregular dark brown

speckling in loreal and temporal regions; canthal stripe light tan, bordered ventrally by medium brown stripe and extending from nostril to eye, stripes continuing from posterior margin of eye to nuchal region (Fig 5B); supralabials with alternating light and dark blotches, not corresponding to scales; occipital region with irregular medium brown speckling over light brown; nuchal region with medium brown "V"; dark brown lateral stripe (extending from posterior margin of eye) continuing in nuchal region, and joined ventrally by more narrow medium brown stripe extending from posterior margin of auricular opening; trunk with medium brown transverse bands (three through axilla-groin region, four total) characterized by longitudinal elongations on either side of vertebral column, the tips of which are dark brown and confer a vague "bow-tie" shape; transverse bands connected dorsolaterally, by dark brown longitudinal stripe (continuing from head and nuchal region); lateral pattern blotched medium brown from dorsolateral stripe to lateral tubercle row; limbs with medium brown irregular bands and blotches; wrists with conspicuous solid dark brown bands; Fingers I and II absent of dorsal coloration but all other fingers and toes with irregular medium brown bands; ground color of tail tan to gray, including that of regenerated portion; dorsal bands medium to dark brown, lacking conspicuous longitudinal projections of trunk; regenerated portion lacking bands, but with sparsely distributed dark brown speckling.

Ventral coloration (except that of hands and feet) tan to light cream; lighter coloration extending from infralabials, auricular opening, from medium brown lateral stripe in nuchal region, from lateral tubercle row in axilla-groin region, and from ventrolateral margin on limbs; hands and feet medium gray, originating at wrists and ankles; subcaudal region with tan ground color, becoming medium gray in regenerated region; irregular dark brown blotches overlay ground color, and reduce to speckling in regenerated portion of tail; no bands discernible.

Color in life.—Coloration in life was not recorded, and no photographs are available. Based on experience with Philippine congeners (personal observation), we do not expect

dramatic changes in coloration to have occurred as a result of preservation.

Variation.—The type series of *C. sumuroi*, consisting of four adults (all from type series; two male, two female) and four juveniles, shows minimal levels of meristic scalation variation (Table 3) and color pattern variation (Fig. 5C). Differentiated post nasals 4–6/3–5; internarial region scalation variable, consisting of either (1) space between supranasals with five minimally enlarged scales (holotype, PNM 9723); (2) three minimally differentiated internasals, two anterior, one posterior (KU 310798); or (3) a single enlarged scale between supranasals (KU 310796, 310801, 310802).

All paratypes are darker than the holotype, with the darkest individuals being two juveniles (KU 310797, 310799); one adult female (KU 310798) resembles the holotype in ground color but has slightly darker and more bold dorsal bands; one adult female (KU 310798) has four dorsal bands through axilla-groin region (compared with three in all other samples); the cephalic patterning of all specimens is variable, with the least amount of dark pigment present on the holotype, and two juveniles (KU 310797, 310799) with nearly all of their cephalic coloration dark; regenerated portions of tails lack discernible bands; minimal ontogenetic variation is evident in the type series.

Ecology and natural history.—Like all Philippine *Cyrtodactylus*, the new species is associated with riparian habitat corridors, gallery forests, and vegetation a few meters from the banks of rivers and streams. The new species has been collected on exposed roots overhanging stream banks, from trunks of trees bordering flowing water, and from large boulders in river and stream beds. Other gekkonids collected sympatrically include *C. annulatus*, *C. philippinicus*, *Gehyra mutilata*, *Hemidactylus frenatus*, *Lepidodactylus herrei*, *Pseudogekko brevipes*, *Pseudogekko compressicorpus*, and *Pseudogekko labialis* (Gaulke, 1994).

Distribution.—*Cyrtodactylus sumuroi* is known from forested habitat on Samar Island, Philippines. Specimens referable to this species all originate on the east side of the central mountain range that latitudinally divides Samar. However, the new species also may

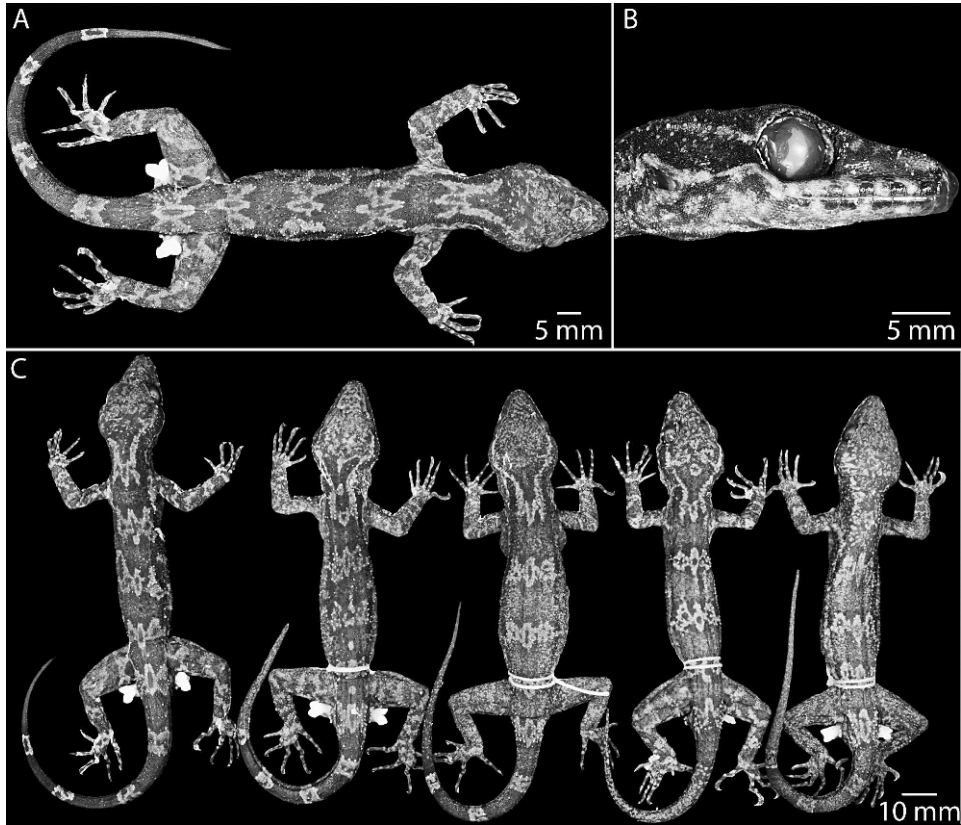


FIG. 6.—Photographic plate of *Cyrtodactylus gubaot*. (A) Dorsal view of holotype. (B) Lateral view of holotype head. (C) Panel of types showing variation in color pattern.

occur on some of the many small islands bordering Samar.

Etymology.—The specific epithet is chosen in recognition of Juan Ponce (Agustin) Sumuroy, a Waray hero and popular Visayan leader of the “Sumuroy Rebellion” attempt of 1649. Although the Spanish suppressed the uprising and executed many of its leaders, by all accounts, Sumuroy and his coconspirators did much to spread the quest for independence among the peoples of the central Philippines during Spanish rule.

Cyrtodactylus gubaot *sp. nov.*
Figs. 4C, 6, 7A

Cyrtodactylus agusanensis: Brown and Alcalá, 1978: 16 (part).

Holotype.—PNM 9724 (formerly KU 311184; field no. CDS 3273), adult male, Leyte Island, Leyte Province, Municipality of

Baybay, Barangay Pilim, Sitio San Vicente (10.731° N, 124.826° E, 82 m; WGS84), collected on 3 November 2007 by CDS and J. Fernandez.

Paratopotypes.—Same general locality and collectors as holotype (10.741° N, 124.842° E, 310 m), one male and one female, KU 309336, 309337 (1 November 2007); three males, KU 309338–40 (2 November 2007); three males, KU 309341, 309343, 309344 (3 November 1997); one male and one female, KU 309345, 309346 (5 November 1997); one male, KU 311134 (1 November 2007; 10.731° N, 124.826° E, 82 m); 25 males, 42 females, and 7 juveniles, KU 311131–33, 311135–210 (1–5 November 2007; 10.729° N, 124.822° E, 50 m); one male and two females, KU 311211–13 (8 and 9 November 2007; 10.726° N, 124.818° E, 53 m); and one female, KU 311303 (2 November 2007).



FIG. 7.—Photographs in life of *Cyrtodactylus gubaot* (A) and *C. mamanwa* (B). (To view the figure in color, see the online version of this article.)

Other paratype.—One adult male, CAS-SU 24624, collected on Leyte Island by D. S. Rabor and party (May–June 1964).

Referred specimens.—Leyte Island, Leyte del Sur Province, Municipality of Mahaplag, CAS-SU 24598–99, CAS-SU 24624, 24630.

Diagnosis.—*Cyrtodactylus gubaot* most closely resembles congeners from the *C. agusanensis* complex and is distinguished from *C. agusanensis* by midbody dorsals 92–

105 (vs. 111–124), paravertebrals 150–162 (vs. 184–196), postcloacal lateral tubercles 4–6 (vs. 8–11), venter dark gray with white flecks (vs. cream throughout), the presence (vs. absence) of a canthal stripe, anterior–posterior dorsal band projections moderate (vs. extensive), and cephalic tubercles large (vs. moderate).

Cyrtodactylus gubaot is diagnosed from *sumuroi* (Samar) by SVL 85.6–100.1 mm (vs. 73.9–84.9), paravertebrals 150–162 (vs. 163–

180), venter dark gray with white flecks (vs. cream throughout), anterior–posterior dorsal band projections moderate (vs. minimal), dark dorsal bands not enclosing light bands (vs. light bands enclosed), cephalic tubercles large (vs. moderate), and caudal annuli with dorsal tubercles 9–12 (vs. 3–7). *Cyrtodactylus gubaot* also exhibits tendencies toward a greater number of midbody ventrals (54–67 vs. 53–58), midbody dorsals (92–105 vs. 87–98), and subdigital lamellae beneath Finger III (20–26 vs. 18–22) and Toe IV (24–30 vs. 21–24).

Cyrtodactylus gubaot is readily diagnosed from *C. mahanwa* (Dinagat) by paravertebrals 150–162 (vs. 173–192), venter dark gray with white flecks (vs. cream throughout), the presence of a canthal stripe (vs. absence), dark dorsal bands not enclosing light bands (vs. light bands enclosed), and cephalic tubercles large (vs. small). *Cyrtodactylus gubaot* also shows a tendency toward fewer paravertebral tubercles (19–27 vs. 25–31).

Cyrtodactylus gubaot is distinguished from all other Philippine congeners by characters of body size and scalation (Table 3). *Cyrtodactylus gubaot* can be distinguished from *C. annulatus*, *C. tautbatorum*, *C. jambangan*, *C. redimiculus*, and *C. philippinicus* by dark gray venter with white flecks, larger cephalic tubercle size, and the presence (vs. absence) of a canthal stripe; from *C. annulatus*, *C. tautbatorum*, *C. jambangan*, and *C. redimiculus* by a greater number of subdigital lamellae beneath Toe IV; from *C. annulatus*, *C. tautbatorum*, *C. jambangan*, and *C. philippinicus* by the presence of femoral pore-bearing scales; from *C. annulatus*, *C. tautbatorum*, and *C. redimiculus* by a greater number of midbody tubercle rows; from *C. redimiculus* and *C. philippinicus* by dark dorsal bands enclosing light bands (vs. light bands not enclosed); from *C. tautbatorum* and *C. jambangan* by larger SVL; from *C. annulatus* and *C. tautbatorum* by more postloocal lateral tubercles; from *C. tautbatorum* by a greater number of subdigital lamellae beneath Finger III; from *C. jambangan* by a greater number of caudal annuli with dorsal tubercles; and from *C. redimiculus* by a greater number of midbody ventrals, fewer paravertebrals, and moderate anterior–posterior dorsal band projections (vs. minimal).

Description of holotype.—Adult male (Fig. 6A; characters scored for right side of body unless otherwise noted), SVL 87.5 mm (head triangular, elongate, distinct from neck, 33.0% SVL; head width 66.0% and depth 40.0% head length; tip of snout rounded in dorsal aspect; snout elongate, 42.0% head length; lores slightly concave midway through canthal ridge; eye diameter 22.0% head length, 83.0% eye–ear distance; auricular opening triangular, longest (diagonal) axis 9.0% head length.

Rostral wider than tall, height 57.0% width, bordered by single small and medial anterior internasal, paired secondary posterior internasals, supranasals, and first supralabials; internarial distance 3.3 mm; nostril bordered by supranasal, rostral, first supralabial, and three postnasals; supralabials and infralabials generally rectangular and decreasing in size posteriorly, 10/9 (left/right) to midpoint of eye (13/14 total) and 7/7 to beneath midpoint of eye (13/11 total), respectively; supralabials bordered dorsally by one to two rows of secondary, slightly differentiated scales, extending to supralabial 9; infralabials bordered ventrally by enlarged secondary row, extending to infralabial 6.

Dorsal head scalation heterogeneous, with smallest scales aggregated medially in parietal region; superciliaries decrease in size posteriorly, anterodorsally most superciliaries are laterally elongated and approximately triangular. Mental nearly triangular, bordered laterally by first infralabials, posteriorly by paired longitudinally elongated postmentals; 10 differentiated scales posterior to postmentals; gular scales heterogeneous, small and granular but increasing slightly in size laterally at jaw line and through pectoral region.

Body elongate, axilla–groin distance 48.0% SVL, lacking distinct ventrolateral folds; dorsal scalation granular, heterogeneous, with semiregular rows of round, slightly convex and moderately spinose tubercles; transverse midbody tubercle rows 19; longitudinal paravertebral tubercle rows 21; paravertebral scales 159; transverse mid-body dorsal and ventral scales 98 and 61, respectively; ventral scales imbricate, up to twice the size of dorsals; differentiated preloocal scales in three or four chevron-shaped differentiated transverse

rows, anterior to nine (5/4) pore-bearing scales, followed posteriorly by 30 triangularly arranged differentiated scales; preloacal groove absent.

Forelimbs slender, elongate; forearm and upper arm 17.0% and 13.0% SVL, respectively; dorsal forelimb scalation heterogeneous, scales larger than ventrals, increasing in size distally; tubercle distribution sparse, slightly more dense on forearm; tubercles less spinose than those of trunk; ventral limb scales homogeneous, small and granular, slightly smaller than trunk ventrals, and lacking tubercles; fingers elongate and well developed, Fingers I and III 33.0% and 59.0% forearm length, respectively; subdigital scales differentiated, lamellae distal to third interphalangeal joint enlarged and raised; finger number followed by subdigital lamellae (in parentheses): I (16), II (21), III (26), IV (26), V (22); all fingers clawed; claws well developed, sheathed by single dorsal and ventral scales.

Hind limbs slender, elongate; femur and tibia 22.0% and 18.0% SVL, respectively; dorsal hind limb scalation heterogeneous, generally small and granular, with tubercles regularly distributed and tuberculation similar to that of dorsal trunk; ventral limb scales heterogeneous, most scales similar in size to dorsals, lacking tubercles; enlarged femoral scales in two rows extending from knee to midfemur, consisting of 11/6 differentiated (but poreless) prefemorals and 11/9 differentiated (8/8 pore-bearing) femorals; toes well developed; Toes I and IV 37.0% and 72.0% tibia length, respectively; subdigital scales differentiated, lamellae distal to third interphalangeal joint enlarged and raised; toe number followed by subdigital lamellae (in parentheses): I (16), II (23), III (25), IV (30), V (24); all toes clawed; claws well developed, sheathed by single dorsal and ventral scales.

Tail original except for terminal 24.5 mm (regenerated), total length 111.5 mm, tapering abruptly posterior to hemipenial bulge and then gradually to terminus; eight basal caudal annuli discernible; distal annuli cannot be distinguished, owing to the absence of dorsal tubercles associated with annuli; caudal tubercles oriented posteriorly, larger and more spinose than those of body; lateral postloacal tubercles 2/2, rounded; anterior margin of

hemipenial bulge with paired, postloacal glandular openings. Complete meristic and mensural data for the holotype are presented in Table 4.

Color of holotype in preservative.—Dorsal ground coloration medium brown (Fig. 6A), overlain by dark brown bands and blotches; head patterning indistinct; canthal stripe medium brown, extending from nostril to anterior margin of eye, and continuing from eye to nuchal region; canthal stripe bordered ventrally by dark brown longitudinal stripe, medium brown stripe (extending through and past auricular opening), and dark brown stripe between posterior margin of eye and auricular opening (Fig 6B); supralabials and infralabials with conspicuous light cream to white irregular spots, not corresponding to individual scales; snout, interocular region, and parietal region with irregular dark brown mottling over medium brown ground color; parietal region with large dark brown blotch medially; occipital region with subtriangular, posteriorly oriented dark brown blotch extending to midnuchal region; nuchal region with dark brown longitudinal stripe laterally, bordered ventrally by ground colored partial longitudinal stripe and then by ventrolateral region of mottled dark and medium brown region; trunk with dark brown transverse bands (three through scapular and axilla-groin, four total) characterized by moderately severe anterior and posterior longitudinal elongations on either side of vertebral column, conferring a vague “bow-tie” shape; laterally, dorsal bands occasionally connected by irregularly broken dark brown longitudinal lateral stripe (continuing from head and nuchal region); ground-colored dorsal bands with conspicuous dark brown spots totaling two or three and occurring in alternation with longitudinal elongation of dark brown dorsal bands; limbs with dark brown, wavy, and slightly faded bands and irregular speckling; all fingers and toes banded, although contrast in bands is less severe on Fingers I and II; ground color of tail medium to light brown, becoming lighter distally, and overlain by wide, dark brown bands; caudal bands lacking characteristic longitudinal projections; tail with four ground colored, and five dark brown bands; regenerated terminus of tail dark brown throughout.

Ventral coloration generally medium brown throughout, although becoming slightly darker through ventrolateral margins, and accented with cream to tan irregular speckles; speckles concentrated in ventrolateral regions, especially that of head; subdigital surfaces, as well as surfaces of hands and feet, lacking distinguishable patterning; tail with same constituent of bands as on dorsal surface but dark bands slightly faded ventrally.

Color in life.—Dorsal ground coloration blue-gray overlain with medium to dark brown transverse bands (based on photograph of RMB 4363, deposited at National Museum of the Philippines [PNM]; Fig. 7A); on anterior portions of body, ground color medium brown, yellow-brown in labial region; irregular dark brown blotches present on head; ground color overlain with light to medium brown irregular speckling laterally; dark brown transverse bands with moderate longitudinal projections overlaying ground color on trunk and limbs; limb bands more variable in shape; caudal banding similar to that of trunk but with greater contrast between ground color and dark bands and longitudinal projections absent; regenerated tail with light brown ground color, overlain with irregular dark brown speckling.

Ventral surfaces of body dark gray with black speckling; preloacal and femoral scales light gray with orange pores; ventral surfaces of manus and pes nearly black.

Variation.—The type series exhibits moderate meristic scalation variation (Table 3) minimal color variation, and some pattern variation (Fig. 6C). Differentiated post nasals 4–6; internarial region scalation variable, consisting of either (1) single undifferentiated anterior scale followed by two enlarged scales in medial contact and then three undifferentiated internasals (holotype, PNM 9724); (2) a single anterior medial scale, followed by two enlarged scales separated medially by a single longitudinally elongated subtriangular scale and then three posterior internasals (KU 309344); (3) a single anterior medial scale, followed by two enlarged scales in medial contact and then two slightly smaller internasals (KU 309346); or (4) four enlarged internasals, in two pairs (KU 309338).

All individuals are conspicuously darker than any other population in the *C. agusanensis* complex. Two adult males (KU 309340, 309345) have a slightly lighter ground color; cephalic coloration of one juvenile (KU 311165) is nearly solid dark brown, whereas all others are variable in the pattern but consistent with roughly 50.0% coverage of dark brown and medium gray ground color; patterning in the nuchal region is variable but generally as a V- or Y-shaped dark brown pattern, a smaller V-shaped dark brown blotch anterior to a single medial dark brown spot, or paired anterior spots followed by a single medial dark brown spot; three adult males (KU 309338–39, 309341) lack a discernible canthal stripe; one adult male (KU 309345) is medium tan ventrally; five adult males (KU 309340, 309344, 309336, 309338–39) and two adult females (KU 309337, 309406) are medium brown ventrally, with irregular cream speckling; three adult males (KU 309341, 309343, 311189) and two juveniles (KU 311165, 311179) are medium gray ventrally, with irregular cream speckling; regenerated portions of tails on all relevant specimens lack discernible bands; no ontogenetic variation is present in this series.

Ecology and natural history.—We collected *C. gubaot* in riparian, stream side habitats in well-regenerated secondary growth forest and gallery forests through heavily disturbed habitats. The new species is extremely common on Leyte and was collected on tree trunks, bankside rocks and debris, and midstream boulders. Sympatric gekkonids include *C. annulatus*, *Gehyra mutilata*, *Gekko gekko*, *Gekko monarchus*, *Hemidactylus frenatus*, *Hemidactylus platyurus*, *L. herrei*, *Pseudogekko compressicarpus*, and *Ptychozoon intermedium*.

Distribution.—*Cyrtodactylus gubaot* is known from forested habitats on the west side of Leyte Island, Philippines. The new species may also occur on some of the many small islands bordering Leyte.

Etymology.—The specific epithet is a combination of the Leyte dialect (Waray-waray) terms *guba* (forest) and *buot* (spirit, essence) in reference to our observation that the new species is one of the most abundant and commonly observed reptiles from the forests of central Leyte Island.

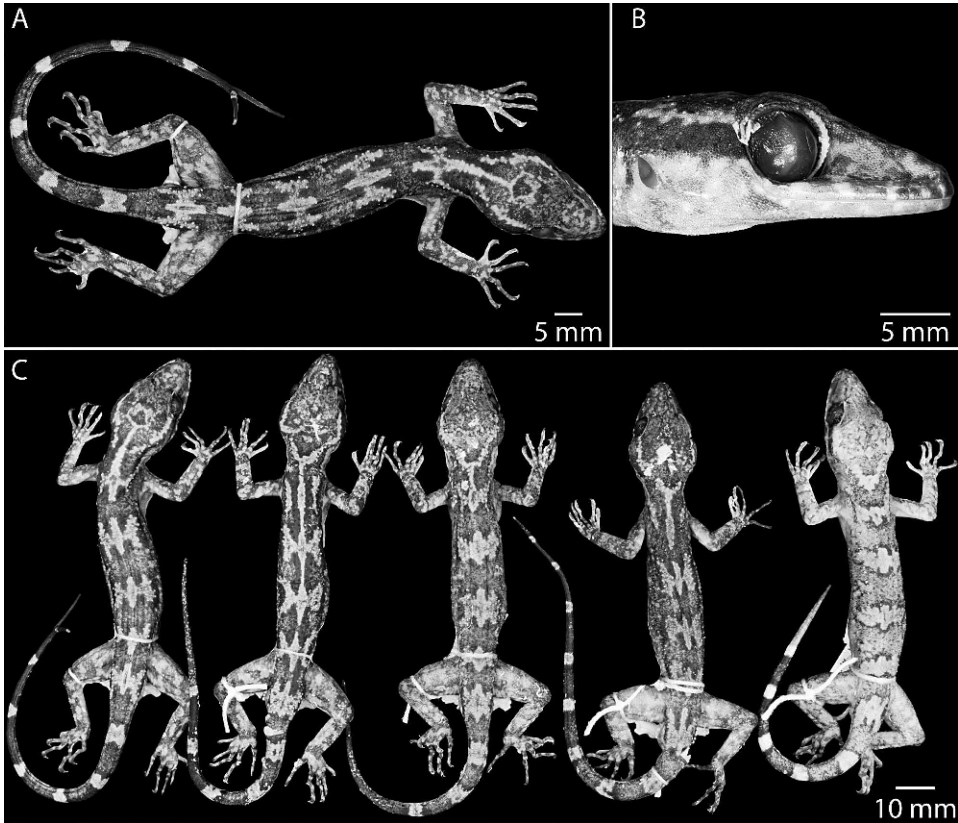


FIG. 8.—Photographic plate of *Cyrtodactylus mamanwa*. (A) Dorsal view of holotype. (B) Lateral view of holotype head. (C) Panel of types showing variation in color pattern.

Cyrtodactylus mamanwa sp. nov.
Figs. 4D, 7B, 8

Gymnodactylus philippinicus Günther, 1879: 76; Boulenger 1885: 46 (part).

Gymnodactylus agusanensis Taylor, 1915: 90; 1922: 49.

Cyrtodactylus agusanensis Brown and Alcalá, 1978: 16 (part).

Holotype.—PNM 9725 (formerly KU 310109; field no. RMB 8380), adult male, Dinagat Island, Dinagat Province, Municipality of Loreto, Barangay Santiago, Sitio Cambinlia (Sudlon), Mt. Cambinlia (10.344° N, 125.618° E, 195 m; WGS84), collected on 30 July 2007 by Jason B. Fernandez.

Paratopotypes.—Same locality and collection data as holotype but 28 July–14 August 2007, 10 males, 5 females, and 3 juveniles: KU 310095, 310098, 310100, 310103, 310105–08,

310110–11, 310094, 310097, 310101, 310102, 310112, 310096, 310099, and 310104.

Paratypes.—Dinagat Island, Dinagat Islands Province, Municipality of Loreto, Barangay Esperanza (10.385° N, 125.614° E, 48 m; WGS84), one male, and one juvenile collected by CDS and CWL: KU 305564 and 305565, respectively (24 June 2006).

Diagnosis.—*Cyrtodactylus mamanwa* is distinguished from *C. agusanensis* by post-cloacal tubercles 4–7 (vs. 8–11); anterior-posterior dorsal band projections moderate (vs. extensive); dark dorsal band enclosing light bands (vs. light bands not enclosed); and cephalic tubercles small (vs. moderate). *Cyrtodactylus mamanwa* also shows tendencies toward fewer subdigital lamellae beneath Finger III (18–23 vs. 21–24) and midbody dorsals (95–112 vs. 111–124); and a greater number of scales separating pore-bearing

preloacal and femoral scales (15–21 vs. 13–17).

From *C. gubaot* (Leyte), *C. mamananwa* is distinguished by paravertebrals 173–192 (vs. 150–162); venter cream (vs. dark gray with white flecks); the absence (vs. presence) of a canthal stripe; dark dorsal bands enclosing light bands (vs. light bands not enclosed); and cephalic tubercles small (vs. large). *Cyrtodactylus mamananwa* also shows tendencies toward a greater number of paravertebral tubercles (25–31 vs. 19–27).

From *C. sumuroi* (Samar), *C. mamananwa* is distinguished by the absence (vs. presence) of a canthal stripe; anterior–posterior dorsal band projections moderate (vs. minimal or absent); cephalic tubercles small (vs. moderate); and caudal annuli with dorsal tubercles 7–12 (vs. 3–7). *Cyrtodactylus mamananwa* also exhibits tendencies toward a greater number of midbody dorsals (95–112 vs. 87–98), midbody ventrals (57–70 vs. 53–58), and paravertebrals (173–192 vs. 163–180).

The new species can be readily diagnosed from all other Philippine congeners by characters of body size and scalation (Table 3). *Cyrtodactylus mamananwa* can be distinguished from *C. annulatus*, *C. tautbatorum*, *C. jambangan*, and *C. philippinicus* by the presence (vs. absence) of femoral pore-bearing scales; it is further distinguished from all these species and *C. redimiculus* by having a greater number of pore-bearing preloacofemorals; from *C. annulatus*, *C. tautbatorum*, and *C. jambangan* by having a greater number of midbody dorsals and paravertebrals; from *C. annulatus*, *C. tautbatorum*, and *C. redimiculus* by having a greater number of midbody tubercle rows; from *C. annulatus* and *C. tautbatorum* by having a greater number of subdigital lamellae beneath Toe IV; from *C. tautbatorum* and *C. jambangan* by dark dorsal bands enclosing light bands (vs. light bands not enclosed); from *C. tautbatorum* by having a greater number of subdigital lamellae beneath Finger III and the absence of a canthal stripe; from *C. redimiculus* by having a greater number of paravertebral tubercles and pronounced anterior–posterior dorsal band projections; and from *C. jambangan* by having a greater number of caudal annuli with dorsal tubercles.

Description of holotype.—Adult male (Fig. 8A; characters scored for right side of body unless otherwise noted), SVL 86.5 mm; head triangular, moderately long, distinct from neck, 30.0% SVL; head width 69.0% and depth 40.0% head length; tip of snout rounded in dorsal aspect; snout elongate, 44.0% head length; lores flat; eye diameter 25.0% head length, 84.0% eye–ear distance; auricular opening tear shaped, longer (vertical) axis 11.0% head length.

Rostral wider than tall, height 69.0% width, bordered by single medial internasal, supranasals, and first supralabials; internarial distance 2.7 mm; nostril bordered by supranasal, rostral, first supralabial, and 4/3 postnasals; supralabials and infralabials generally rectangular and decreasing in size posteriorly, 8 left/7 right to midpoint of eye (11/10 total) and 7/6 to beneath midpoint of eye (9/9 total), respectively; supralabials bordered dorsally by one to two rows of secondary, slightly differentiated scales, extending to supralabial 7; infralabials bordered ventrally by enlarged secondary row, extending to infralabial 6.

Dorsal head scalation heterogeneous, with smallest scales aggregated medially in parietal region; superciliaries decrease in size posteriorly; anterodorsal most superciliaries laterally elongate and approximately triangular. Mental triangular, bordered laterally by first infralabials, posteriorly by paired longitudinally elongate postmentals; differentiated scales posterior to postmentals 9; gular scales generally homogenous, small and granular but increasing slightly in size laterally at jaw line and through pectoral region.

Body elongate, axilla–groin distance 46.0% SVL, lacking distinct ventrolateral folds; dorsal scalation granular, heterogeneous, with semiregular rows of round, slightly convex and moderately spinose tubercles; transverse midbody tubercle rows 20; longitudinal paravertebral tubercle rows 30; paravertebral scales 192; transverse midbody dorsal and ventral scales 103 and 57 respectively; ventral scales imbricate, up to twice the size of dorsals; preloacal scales in three or four chevron-shaped differentiated transverse rows, anterior to seven (4/3) pore-bearing scales, followed posteriorly by 29 triangularly arranged differentiated scales; preloacal groove absent.

Forelimbs slender, elongate; forearm and upper arm 15.0% and 13.0% SVL, respectively; dorsal forelimb scalation heterogeneous, scales larger than ventrals; tubercles sparsely distributed on upper arm, more densely on forearm; ventral limb scales homogeneous, granular, slightly smaller than trunk ventrals, and lacking tubercles; fingers elongate and well developed, Fingers I and III 37.0% and 65.0% forearm length, respectively; subdigital scales differentiated, lamellae distal to third interphalangeal joint enlarged and raised; finger number followed by subdigital lamellae (in parentheses): I (13), II (18), III (21), IV (23), V (19); all fingers clawed; claws well developed, sheathed by single dorsal and ventral scales.

Hind limbs slender, elongate; femur and tibia 20.0% and 16.0% SVL, respectively; dorsal hind limb scalation heterogeneous, generally small and granular, with tubercles distributed evenly, but slightly more dense on lower legs; tuberculation more spinose than that of trunk; ventral limb scales heterogeneous, most scales slightly smaller than dorsals, lacking tubercles; enlarged femoral scales in two rows extending from knee to mid-femur, consisting of 11/10 differentiated (but poreless) prefemorals and 12/13 differentiated (10/10 pore-bearing) femorals; toes well developed; Toes I and IV 31.0% and 71.0% tibia length, respectively; subdigital scales differentiated, lamellae distal to third interphalangeal joint enlarged and raised; toe number followed by subdigital lamellae (in parentheses): I (14), II (20), III (24), IV (23), V (26); all toes clawed; claws well developed, sheathed by single dorsal and ventral scales.

Tail original, but with bifurcation due to regenerating at 10.5 mm from terminus, total length (with original tip) 106.7 mm, tapering abruptly posterior to hemipenial bulge and then gradually to terminus; nine basal caudal annuli discernible; distal annuli cannot be distinguished, owing to the absence of dorsal tubercles associated with annuli; caudal tubercles slightly more spinose than those of body; lateral postcloacal tubercles 2/2, rounded; anterior margin of hemipenial bulge with paired, post-cloacal glandular openings. Complete meristic and mensural data for the holotype are presented in Table 4.

Color of holotype in preservative.—Dorsal ground coloration (of head, body, and limbs; Fig. 8A) light brown to light gray, with minimal medium to dark brown speckling; head patterning indistinct anteriorly, with irregular medium to dark brown speckles and blotches; labials with conspicuous light cream to white spots, not corresponding to scales; frontal and parietal region with anterior and posterior dark brown blotches medially, and paired longitudinally elongate dark brown blotches dorsolaterally (Fig 8B); lateral surface of head with dark brown longitudinal stripe extending from posterior margin of eye (running dorsal to auricular opening) and continuing through nuchal and trunk regions on dorsolateral surface; dorsally, nuchal region with paired subtriangular posteriorly oriented blotches extending from posterior margin of parietal region to mid-nuchal region and then joining dark brown dorsolateral stripe; trunk with three dark brown dorsal bands (four total), characterized by extensive longitudinal elongations on either side of vertebral column, conferring a vaguely “bow-tie” shape; laterally, dorsal bands connected by unbroken dark brown longitudinal stripe (continuing from head and nuchal region); forelimbs without distinguishable bands but adorned with irregular medium to dark brown spots and blotches; hind limbs with medium to dark brown slightly faded wavy bands and irregular speckling; Fingers I and II and Toe I absent of dorsal coloration but all other fingers and toes with irregular dark bands; ground color of tail light gray, gradually becoming light cream to white distally; tail with eight light, and eight dark brown bands; bands becoming more bold distally; tail terminus bifurcated at second to last dark band, with original portion having a single light band and terminating in a light band, whereas regenerated portion is solid dark brown.

Ventral coloration (except that of hands, feet, and tail) light tan; lighter coloration extending from infralabials, auricular opening, and dark brown lateral stripe on head and through nuchal region, from ventrolateral margin in axilla-groin region, and from midway of lateral surfaces on limbs; hand and feet coloration slightly darker than body, originating at wrists

and ankles; subcaudal region light tan to cream, with irregular medium brown blotches anteriorly, becoming more consistent and eventually forming ventral continuance of dark dorsal bands at one-third distance from tail base; original and regenerated tail termini similar to that of dorsum.

Color in life.—(Fig. 7B) Coloration in life was not recorded, so our description is based on the photograph of a specimen deposited at PNM. Dorsal ground coloration yellow-brown, overlain with medium to dark brown patterning; anteriorly, ground color slightly darker; irregular dark brown blotches present on head; ground color overlain with light to medium brown irregular lateral speckling; dark brown bands with moderate longitudinal projections overlay ground color on trunk and limbs, limb bands more variable in shape; caudal banding similar to that of trunk, but with greater contrast between ground color and dark bands and less-severe longitudinal projections; regenerated tail with light brown ground color, overlain with irregular dark brown speckling. Ventral coloration in life not documented.

Variation.—The type series is moderately variable for meristic scalation (Table 3), color and color pattern (Fig. 8C). Differentiated post nasals 5–6/4–7; internarial region scalation variable, consisting of either (1) single enlarged diamond-shaped internasal, followed by two slightly enlarged scales (holotype PNM 9725); (2) two anterior enlarged scales in medial contact, followed by a single enlarged scale and then two enlarged internasals (KU 310108); or (3) a single anterior subtriangular enlarged medial scale, followed by a cluster of four or five smaller internasals (KU 310012, 310095, 310098).

Five adult males (KU 310095, 310103, 310107–08, 310110), one adult female (KU 310102), and one juvenile (KU 310099) have a light gray ground color, making for a higher contrast of dark brown dorsal bands; one adult male (KU 310101) has a dark gray ground color overlain by dark brown bands, making for a minimal amount of contrast; two adult females (KU 310105, 310112) have a medium gray ground color with irregular dark brown speckling, overlain by faded medium brown dorsal bands; one adult male (KU 310095) has a near continuous paravertebral stripe bisecting dark brown dorsal bands; cephalic pat-

terning variable, with heads of two adult males (KU 310103, 310108) and three adult females (KU 310094, 310101, 310112) nearly solid dark brown with irregular light gray speckling; one adult female (KU 310102) nearly absent of dark brown pigment; and all others irregularly patterned but with even proportions of light and dark pigment; patterning in the nuchal region highly variable, with four adult males (KU 310095, 310098, 310100, 310108), four adult females (KU 310097, 310101, 310105, 310112), and three juveniles (KU 305565, 310096, 310099) having a darkly pigmented V anteriorly and paired longitudinally elongated blotches laterally extending to or past scapular region; three adult males (KU 310103, 310106, 310110), two adult females (KU 310094, 310102), and one juvenile (KU 310104) with consecutive darkly pigmented V-shaped blotches medially; and three adult males (KU 305564, 310107, 310111) with paired subtriangular posteriorly oriented darkly pigmented blotches extending from parietal to mid-nuchal or scapular region; four males (KU 305564, 310095, 310098, 310107), one female (KU 310101), and two juveniles (KU 310096, 310104) with light to medium brown color ventrally, versus cream or light tan; regenerated portions of tails on all relevant specimens lack discernible bands; no ontogenetic variation is present in this series.

Ecology and natural history.—The type series was collected at night on large boulders and fallen logs on the banks of a 3–4-m-wide stream. *Cyrtodactylus annulatus* was the only gekkonid collected sympatrically during our visits to Dinagat, but Ross and Lazell (1991) reported *Gehyra mutilata*, *Gekko monarchus*, *Hemidactylus frenatus*, *Hemidactylus platyurus*, *Pseudogekko compressicarpus*, and *Ptychozoon intermedium* as co-occurring on the island.

Distribution.—*Cyrtodactylus mamamwa* is known from forested habitat on Dinagat Island. However, it may be expected to occur on the islands of Siargao and Bucas Grande, but future surveys are required to fully document the distribution of this species.

Etymology.—The specific epithet is chosen in recognition of the rapidly disappearing southern Leyte, Dinagat, and Agusan Del Norte Province indigenous people's group, the Mamanwa ("people of the mountains" or

“first forest dwellers”). Believed by some archeologists and anthropologists to be the oldest tribal group in the Philippines, the history of the Mamanwa is characterized by peace; seasonal movements of clan groups to follow food sources; and recently, mass tribal migration to escape logging and mining company intrusion into their ancestral homelands.

DISCUSSION

In hindsight, the recognition of additional species diversity from within the widespread *C. agusanensis* complex is not surprising. Philippine gekkonid diversity, in particular within *Cyrtodactylus*, has been shown in recent years to be substantially underestimated, and new species descriptions are now steadily being published as workers review widespread species groups with new data (Rösler et al., 2006; Brown et al., 2009a,b, 2010; Welton et al., 2009, 2010; Linkem et al., 2010). In the past few years, the diversity of bent-toed geckos endemic to the Philippines has grown from four to nine with the descriptions of *C. jambangan*, *C. tautbatorum*, and the three new species described here (Siler et al., 2010; Welton et al., 2009, 2010).

Despite the rapid rate of species accumulation, the currently recognized diversity of Philippine *Cyrtodactylus* is probably still underestimated. For example, isolated deep-water islands and upland geological formations harboring isolated populations of the widespread *C. philippinicus* may be expected to contain multiple distinct evolutionary lineages. Future analysis of both genetic and morphological diversity is required to fully resolve the taxonomic status of the many populations currently referred to *C. philippinicus*. Our results underscore the need for continued fine-scale morphological analysis of “widespread” species, especially those distributed across multiple island platforms. In addition, our results underscore the need for continued biotic surveys of isolated habitats throughout the archipelago.

The number of *C. sumuroi* specimens consists of eight individuals from the type locality and two additional adjacent sites on Samar Island. However, we anticipate *C. sumuroi* also may occur on the nearby smaller islands surrounding Samar. The total number

of *C. gubaot* specimens in museum collections is 86 individuals from the type locality and three additional adjacent sites on Leyte Island. As with *C. sumuroi*, *C. gubaot* also may occur on the nearby smaller islands surrounding Leyte. Although the total number of *C. mamananwa* specimens consists of 19 individuals from the type locality and one adjacent site, this species also may occur on Siargao (although it was not reported there by Ross and Lazell, 1991). Our impression is that all three new species are relatively common and that *C. gubaot* may actually be the most common forest reptile on Leyte Island. Taylor (1915, 1922) considered *C. agusanensis* to be rare at the type locality. Our impression during our short visit to Mt. Magdiwata, Agusan Del Sur Province, was that the species was fairly common. Although continued surveys are needed to accurately assess the viability of bent-toed gecko populations, our experience suggests that none of the new species, or *C. agusanensis*, is under particular threat. However, given the niche specificity exemplified by gekkonids, continued habitat loss will probably pose a threat to the group’s diversity in the future. Therefore, we recommend that steps be taken to conserve large tracts of intact forest, especially those areas that are associated with geographically and biologically diverse ecosystems. This strategy, although comprehensively attempting to conserve diversity among many lineages of gekkonids, will undoubtedly have a positive impact on the conservation of numerous other lineages as well.

Future gekkonid surveys should focus on diverse habitats, because species of *Cyrtodactylus* often exhibit highly specific microhabitat preferences. Limestone formations, riparian corridors, and both forested and nonforested, isolated habitats should be targeted during surveys. These habitat types are often patchily distributed and have been shown to facilitate evolutionary change and promote divergence (Brown and Alcalá, 2000; Linkem et al., 2010; Rösler et al., 2006; Siler et al., 2007, 2009; Tri et al., 2008).

The genetic and morphological differentiation between *C. sumuroi* (Samar) and *C. gubaot* (Leyte) warrants comment. These islands are now separated by a very narrow, very shallow ocean channel and have clearly

been united during much of their very recent history (Hall, 1998, 2002; Voris, 2000; Yumul et al., 2009). Despite the absence of a compelling history of isolation by ocean barriers, the two species are highly distinct, easily diagnosed, and cannot be considered conspecific. How then have these two lineages become isolated? It is interesting to note that available sampling of *C. sumuroi* comes from the eastern coast of Samar, whereas genetic samples for *C. gubaot* originated from the western coast of Leyte. It is tempting to speculate that the most probable geographic barrier leading to the isolation of these lineages may have been the central spine of high elevation mountains that run down both the middle of Samar and Leyte, north to south. As such, it may not be ocean barriers but in fact montane topography that drove the divergence of the two new species. Thus, it is conceivable that *C. sumuroi* may eventually be discovered on eastern Leyte and likewise that *C. gubaot* may occur on western Samar. This compelling problem is grounds for future research, should dense geographic genetic sampling become available from both the east and west coasts of both islands.

The topology of our phylogenetic estimate derived from mitochondrial and nuclear genes provides phylogenetic evidence for hypothesized dispersion or dispersal from a center of origin (Mindanao), which may have initiated a series of biogeographic expansions coupled with allopatric speciation, northward to Dinagat, then Leyte, then Samar. Thus, our data suggest an incremental south-to-north “stepping-stone” model of diversification. The pattern of incremental, south-to-north allopatric speciation detected here is similar to patterns revealed by spotted stream frogs (Brown and Guttman, 2002) on both east and west island arcs and to litter frogs of the genus *Leptobrachium* (Brown et al., 2009b) on the west Philippine arc. Interestingly, the range of discrete variation in anterior-posterior projections of the dorsal bands shows morphological congruence with the pattern inferred from our phylogeny, and the same general trend is apparent in numbers of midbody dorsal scales and vaguely in numbers of postcloacal lateral tubercles (Table 1).

Finally, the enumeration of four distinct evolutionary lineages with coincident taxonomic

distinctiveness underscores the need for continued biotic surveys throughout the Philippines and bolsters the use of molecular phylogenetics to identify candidate lineages for detailed morphological study and possible taxonomic revision. Increased taxonomic diversity of *Cyrtodactylus* throughout Southeast Asia, and especially that of the Philippines where documented species diversity has more than doubled in just the past 2 yr (from four to nine described species), indicates the need for continued revision of the genus throughout its distribution. As has been indicated previously (Siler et al., 2010; Welton et al., 2009, 2010), the widespread *C. philippinicus* of the northern Philippines is comprised of multiple divergent genetic lineages and is undoubtedly in need of comprehensive phylogeographic analysis, coupled with a study of morphological variation from throughout the range of this species. This approach, together with continued surveys on numerous small islands surrounding the reasonably well-studied larger islands of the archipelago, provides compelling opportunities for future work.

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- Cyrtodactylus annulatus***.—(65) BOHOL ISLAND: BOHOL PROVINCE: *Municipality of Camern*: Barangay Riverside: TNHC 56467; CEBU ISLAND: CEBU PROVINCE: Minglanilla area Dipterocarp forest: CAS-SUR 139048; Taptap Barrio, Cebu City: CAS-SUR 142063; *Municipality of Alcoy*: Nug-as, CBCF field station: KU 305567; INAMPULUGAN ISLAND: ILOILO PROVINCE: ca. 8 km West Pulupandan Town: CAS-SUR 28009–10; 8 km West Pulupan Town: CAS-SUR 28036–38; MINDANAO ISLAND: AGUSAN DEL NORTE PROVINCE: W. side Mt. Hilonghilong: CAS-SUR 133556–57, 133574, 133694; *Municipality of Bunawan*: Agusan (1912): MCZ R-20102, and R-20104; COTOBATO OR SULTURAN KUDARAT PROVINCE: Tatayan to Saub, Cotobato coast (March–April, 1923): MCZ R-26009–16, and R-162947–52; ZAMBOANGA DEL NORTE PROVINCE: Gumay: CAS-SUR 23500–31, 23535–36; PACIJAN ISLAND: CEBU PROVINCE: San Isidro area: CAS-SUR 131982; PONSON ISLAND: CEBU PROVINCE: 2 km SW Pilar Town: CAS 125082; SIQUIJOR ISLAND: SIQUIJOR PROVINCE: *Municipality of San Juan*: Barangay Kang-adiang: TNHC 56457.
- Cyrtodactylus jambangan***.—(108) BASILAN ISLAND, Port Holland, Abung-Abung (1921): CAS 60195–97, 60199–201, 60203–205, 60207–10, 60212–18, 60220–24, and 60453–60; JOLO ISLAND, Bud Dato Mt. (1920): CAS 60669–72, and 60886–88; NEW GOVENEN ISLAND (1920): CAS 60619–24; MINDANAO ISLAND: ZAMBOANGA CITY PROVINCE: Barangay Baluno, Sitio km 24, Pasonanca Natural Park: PNM 9593 (holotype), KU 314808–09, and 314811–31; Barangay Pasonanca, Sitio Canucutan, Pasonanca Natural Park: KU 314778–84; Barangay La Paz, Sitio Nancy, Pasonanca Natural Park: KU 319652, 319654–55; Barangay Tulosa, Sitio Santa Clara, Cabo Negros Outpost, Pasonanca Natural Park: KU 319656 and 319657; Tumaga River, Pasonanca Natural Park: KU 314792–807, 314833–36, and 319658; ZAMBOANGA DEL SUR PROVINCE (1920): CAS 62017–22.
- Cyrtodactylus philippinicus***.—(29) BOHOL ISLAND: BOHOL PROVINCE: *Municipality of Baler*: just outside Raja Sikatuna National Park: PNM 9544; LUZON ISLAND: ALBAY PROVINCE: Mt. Malinao: PNM 9548–51; CAMARINES DEL SUR PROVINCE: *Municipality of Naga*: KU 305571; QUEZON PROVINCE: Quezon National Park: PNM 9553–54, and KU 307452; SORSOGON PROVINCE: *Municipality of Irosin*: Barangay San Roque, ridge above Bulusan Lake, Mt. Bulusan: PNM 9552; ZAMBALES PROVINCE: Ilamin Forest, “Nav-Mag” area, SBMA Naval Base: PNM 9555; MINDORO ISLAND: OCCIDENTAL MINDORO PROVINCE: *Municipality of Sablayan*: Barangay Batong Buhay Batulai, Mt. Siburan: KU 303866, 303870, 303873–5, 303879, 303881–3, 303886, 303888–9, 303892–4, 303898; NEGROS ISLAND: ORIENTAL NEGROS PROVINCE: Mt. Talinis: PNM 9547; SIBUYAN ISLAND: ROMBLON PROVINCE: edge of Guiting-Guiting National Park: PNM 9545.
- Cyrtodactylus taubatorum***.—(16) PALAWAN ISLAND: PALAWAN PROVINCE: *Municipality of Brooke's Point*: Barangay Maimit, Maimit Falls: PNM 9507–14, KU 309318–25.
- Cyrtodactylus redimiculus***.—(21) PALAWAN ISLAND: PALAWAN PROVINCE: *Municipality of Brooke's Point*: Barangay Samariñana, Mt. Mantalingajan, 900m: KU 309526–30; 1200 m: KU 309342, 309347–61.

APPENDIX

Additional Specimens Examined

All specimens are from the Philippines. Numbers in parentheses indicate the number of specimens examined. Several sample sizes are greater than those observed in the description due to the examination of subadult specimens that were excluded from morphometric analyses.

Cyrtodactylus agusanensis.—(34) MINDANAO ISLAND: AGUSAN DEL NORTE PROVINCE: *Municipality of Cabadbaran*: Mt. Hilong-hilong (west of Hilong-hilong Peak): CAS 133424–26, 133507–13, 133634–35, 133662–63, 133697, 133708, 139316–18, 186129; AGUSAN DEL SUR PROVINCE: *Municipality of Bunawan*: CM P-1946–48, P-1950 and P-1952, and MCZ R-20105 (paratypes); *Municipality of San Francisco*: Barangay Bagusan II, Mt. Magdiwata: KU 320014 (neotype), and 320015–21.