

Phylogeny-based species delimitation of southern Philippines bent-toed geckos and a new species of *Cyrtodactylus* (Squamata: Gekkonidae) from western Mindanao and the Sulu Archipelago

LUKE J. WELTON¹, CAMERON D. SILER^{1,2}, ARVIN C. DIESMOS² & RAFE M. BROWN^{1,2}

¹Natural History Museum & Biodiversity Institute, Department of Ecology and Evolutionary Biology, The University of Kansas, Lawrence, Kansas 66045-7561, USA.

E-mail (LJW): furcifer@ku.edu; (RMB): rafe@ku.edu; (CDS) camsiler@ku.edu

²National Museum of the Philippines, Rizal Park, Padre Burgos Ave. Ermita 1000, Manila, Philippines.

E-mail: arvindiesmos@i-manila.com.ph

Abstract

Using a combination of fixed morphological character differences, mitochondrial DNA sequence data, and an estimate of phylogeny as our guide, we describe a new species of bent-toed gekkonid lizard (Genus: *Cyrtodactylus*) from southwestern Mindanao Island, and northeastern portions of the Sulu Archipelago, southern Philippines. The new species resembles *C. annulatus*, but differs from this and all other congeners by characteristics of external morphology, color pattern, and body size. In addition, the new species is distinguished from congeners by marked genetic divergence and reciprocal monophyly of mitochondrial DNA sequences. The new species is common in pristine, low elevation gallery forests throughout Pasonanca Natural Park, Zamboanga Peninsula, southwestern Mindanao Island, and the northeastern portions of the Sulu Archipelago.

Key words: New species; *Cyrtodactylus*; geckos; Mindanao; Pasonanca Natural Park; Philippines; Zamboanga

Introduction

Philippine lizards of the family Gekkonidae include 10 genera and 40 or 41 species: *Gehyra* (1), *Gekko* (11 when the doubtful record of *G. hokouensis* is excluded; Ota *et al.* 1989; Brown *et al.* 2008, 2009; Roesler *et al.* 2006), *Hemidactylus* (5), *Hemiphyllodactylus* (1), *Lepidodactylus* (6), *Luperosaurus* (6), *Ptychozoon* (1), *Pseudogekko* (4), and *Cyrtodactylus* (5), (Taylor 1922a, b; Brown & Alcala 1978; Brown *et al.* 2007; Gaulke *et al.* 2007; Welton *et al.* 2009). A single record from Mindanao for *Perochirus ateles* (Duméril 1856; Boulenger 1885; Taylor 1922a; Brown & Alcala 1978) has not been confirmed in the last 150 years, but so little work has been conducted in western Mindanao, that it is currently impossible to evaluate the status of this species in the Philippines.

New species of *Cyrtodactylus* are being described regularly (Bauer 2003; Batuwita & Bahir 2005; Grismer 2005; Grismer & Leong 2005; Grismer & Norhayarti 2008; Grismer *et al.* 2008; Hayden *et al.* 2008; Kraus 2008; Linkem *et al.* 2008; Tri *et al.* 2008; Welton *et al.* 2009). To date, approximately 115 species have been described (TIGR Reptile database 2009), five of which constitute the assemblage of endemic Philippine *Cyrtodactylus* (i.e., *Cyrtodactylus annulatus*, *C. agusanensis*, *C. philippinicus*, *C. redimiculus*, and a recently described species, *C. tautbatorum*, from southern Palawan; Welton *et al.* 2009).

Cyrtodactylus annulatus (Taylor) and *C. philippinicus* (Steindachner) are considered “widely distributed” on numerous islands throughout the archipelago (Brown & Alcala 1978), whereas *C. agusanensis* (Taylor) and *C. redimiculus* King are endemic to the southeastern (Samar, Leyte and eastern Mindanao islands) and southwestern (Palawan Island) portions of the archipelago, respectively. Currently, several additional morphologically distinct species of Philippine *Cyrtodactylus* await description (RMB and CDS, unpublished

data). The widespread (Brown & Alcala 1978) and biogeographically nonsensical (Brown & Diesmos 2002, 2009) distributions of *C. philippinicus* and *C. annulatus* suggest that these species may represent complexes of phenotypically similar but evolutionarily distinct species (Brown & Guttman 2002; Evans *et al.* 2003; Gaulke *et al.* 2007; Siler *et al.* in press).

Brown and Alcala (1978) delineated the distribution of *Cyrtodactylus annulatus* across several distinct Pleistocene Aggregate Island Complexes (PAICs; Brown & Guttman 2002; Brown & Diesmos 2002) including the Mindanao, Sulu, Visayan, and Palawan island complexes (Brown & Alcala 1978; Fig. 1). Because many Philippine endemics conform to these regional faunistic boundaries (Brown *et al.* 2000a, 2002; Gaulke *et al.* 2007) we have begun the process of scrutinizing such “widespread” species in an effort to diagnose any additional evolutionary lineages. This work has led to the discovery of a distinct species of *Cyrtodactylus* from southern Palawan (Welton *et al.* 2009), clarified the status and distribution of true *C. annulatus*, and uncovered a distinct western Mindanao and Sulu Archipelago lineage, which is the subject of this paper.

Taylor (1922a) recognized non-overlapping character differences between allopatric populations of *C. annulatus* but for reasons unknown, did not name them as distinct species. He wrote: “It was noted that specimens from various islands showed slight differences, especially in the arrangement and size of the preanal pores and scales surrounding them. Specimens from [the] Sulu have an average of only four preanal pores” (Taylor 1922a:46). Upon close examination of specimens of “*C. annulatus*” from the Zamboanga Peninsula, western Mindanao, Basilan Island, and Jolo Island, coupled with an analysis of molecular variation throughout the range of populations formerly referred to *C. annulatus*, it has become clear that the isolated populations at the tip of the Zamboanga Peninsula and the closely adjacent Sulu Archipelago represent a distinct evolutionary lineage. This lineage is identifiable because of the presence of morphological differences between it and *C. annulatus* which are consistent across large series of specimens. This fact, combined with the relatively high levels of genetic divergence and allopatric distributions on different geological components of Mindanao Island (Yumul *et al.* 2009), compel us to describe the Zamboanga and Sulu population as a new species. In this paper we identify the diagnostic characters that, coupled with reciprocally monophyletic, highly divergent mitochondrial sequence variation and biogeographical considerations, allow the diagnosis of these populations as a new species.

Materials and methods

Morphological data. We scored data from fluid-preserved specimens deposited in U.S. and Philippine collections (see Acknowledgments and Specimens Examined). Sex was determined by inspection of gonads or by scoring of prominent secondary sexual characteristics (Brown *et al.* 1997, 2000b; Brown 1999) when dissection was not possible. Measurements (to the nearest 0.1 mm) were taken with digital calipers following character definitions by Ota and Crombie (1989) and Brown *et al.* (1997), as modified by Brown (1999) and Brown *et al.* (2007). Characters include: snout–vent, snout, head, hand, forearm, upper arm, foot, tibia-fibula, femur, and tail lengths; head and tail widths, and heights; eye diameter; eye–naris, internarial, interorbital, eye–ear, and axilla–groin distances; Toes I and IV, and Fingers I and III lengths; scale counts of supralabials and infralabials to the center of the eye and posteriorly to the terminus of differentiation; enlarged circumorbitals dorsoanterior to orbit; transverse midbody dorsals and ventrals; paravertebrals through axilla–groin region; pore-bearing precloacals and pore-bearing preanofemorals (or enlarged pore-less scales in females); postmentals; transverse midbody tubercle rows, paravertebral tubercles; postcloacal tubercles; subdigital lamellae of fingers and toes; transverse midbody tubercle rows; paravertebral tubercles through axilla–groin region; tail annuli; subcaudals; and number of transverse bands in the axilla-groin region. Additional qualitative characters included predominant color pattern; number, size, and shape of transverse bands across the body; dorsolateral tubercle coloration; and supraciliary scale series coloration.

Molecular data. The ingroup sampling strategy included 24 individuals collected from 10 localities, with sampling spanning the known distribution of the currently recognized species *Cyrtodactylus annulatus*

as well as the recently discovered species *Cyrtodactylus tautbatorum* from Palawan (Welton *et al.* 2009; Table 1). Two samples of *Cyrtodactylus baluensis* were included as outgroups in the analyses. For all 26 samples, the mitochondrial gene NADH Dehydrogenase Subunit 2 (ND2) and components of six flanking transfer RNA genes (tRNA^{met}, tRNA^{trp}, tRNA^{ala}, tRNA^{asn}, tRNA^{cys}, and tRNA^{tyr}) were sequenced. All sequences were deposited in GenBank under accession numbers provided in Table 1.

DNA extractions, PCR, and purification protocols. Genomic DNA was extracted from liver tissues stored in 95–100% ethanol following the guanidine thiocyanate method of Esselstyn *et al.* (2008). The external primers Metf6 (5'-AAGCTTCGGGCCATACC-3') and CO1H (5'-AGRGTGCCAATGTCTTGTGRTT-3') were used to amplify the target fragment using the polymerase chain reaction (PCR), and were taken from Macey *et al.* (1999). We used the following thermal cycler profile for ND2: 4 min at 94°, followed by 35 cycles of 94° for 30 sec, 52–53° for 30 sec, and 72° for 1 min 30 sec, and a final extension phase at 72° for 7 min. Amplified products were visualized on 1.0% agarose gels. The PCR product was purified with 1 µL of a 20% diluted solution of ExoSAP-IT (US78201, Amersham Biosciences, Piscataway, NJ) on the following thermal cycler profile: 31 min at 37°, followed by 15 min at 80°. Cycle sequencing reactions were run using ABI Prism BigDye Terminator chemistry (Ver. 3.1; Applied Biosystems, Foster City, CA), and purified with Sephadex (NC9406038, Amersham Biosciences, Piscataway, NJ) in Centri-Sep 96 spin plates (CS-961, Princeton Separations, Princeton, NJ). Additionally, we designed internal primers [CyrtInt.F1 (5'- TAGCCYTCTCYTCYATYGCCC -3') and CyrtInt.R1 (5'- ATTGTKAGDGTRGYAGGSTKGG -3')] for cycle sequencing. All samples were sequenced in both forward and reverse directions. Purified products were analyzed with an ABI Prism 3130xl Genetic Analyzer (Applied Biosystems). Consensus gene sequences were assembled and initially edited using Sequencher 4.8 (Gene Codes Corp., Ann Arbor, MI).

Alignment and phylogenetic analysis. An initial alignment was produced in Muscle v3.7 (Edgar 2004), and manual adjustments were made in MacClade 4.08 (Maddison & Maddison 2005). Phylogenetic analyses were conducted using parsimony, likelihood and Bayesian optimality criteria. Parsimony analyses were conducted in PAUP* 4.0b10a (Swofford 2002) with gaps treated as missing data and all characters weighted equally. Most parsimonious trees were estimated using heuristic searches with 1000 random addition-sequence replicates and tree bisection and reconnection (TBR) branch swapping. We assessed clade support with 1000 nonparametric bootstrap replicates, each with 100 random addition-sequence replicates and TBR branch swapping.

Partitioned maximum likelihood (ML) analyses were conducted in RAxMLHPC v7.0 (Stamatakis 2006). The dataset was partitioned by codon position for the protein-coding region of ND2, and the six flanking tRNAs (tRNA^{met}, tRNA^{trp}, tRNA^{ala}, tRNA^{asn}, tRNA^{cys}, and tRNA^{tyr}) were analyzed as a single partition. The Akaike Information Criterion (AIC) as implemented in Modeltest v3.7 (Posada & Crandall 1998) was used to find appropriate models of evolution for our data. The best-fit model for each of the four partitions of the mitochondrial data was the general time reversible (GTR) model, with a proportion of invariable sites (I) and a parameter for variation in rates among sites (Γ). Partitioned ML analyses were then run under the closest model approximation available in RAxMLHPC v7.0 (GTR MIX) with 100 replicate best tree inferences. Clade support was assessed with 1000 bootstrap pseudoreplicates.

Partitioned Bayesian analyses were performed in MrBayes 3.1 (Ronquist & Huelsenbeck 2003) under the GTR + I + model for the mitochondrial dataset. The same partitioning strategy used for maximum likelihood analyses was also used for the Bayesian analyses. Searches over tree space were conducted with four runs, each with four chains, and were run for 10×10^6 generations. Trees were sampled every 1000 generations, with 2000 samples discarded as burn-in, this left 8001 post-burnin trees from each run included in the summary. Visual inspection for chain stationarity was conducted with the program Tracer v1.4 (Rambaut & Drummond 2007).

Species concept. We embrace the General Lineage Concept of species (de Queiroz 1998 1999) as a logical extension of the Evolutionary Species Concept (Simpson 1961; Wiley 1978). We use an estimate of phylogenetic relationships to guide species delimitation and identification of relevant comparisons for species diagnoses. We consider as distinct species lineages that are morphologically and genetically distinct, and for

which the hypothesis of conspecificity can be confidently rejected by analyses of morphological and genetic data.

TABLE 1. Specimens corresponding to genetic samples included in the phylogenetic analysis, general locality, and GenBank accession number. * = deposited in the National Museum of the Philippines; **; = deposited in the Cincinnati Museum of Natural History; ***= holotype.

Species	Museum Catalog No.	Locality	GenBank Accession No.
<i>C. baluensis</i>	SP 06891	Malaysia, Borneo, Sabah, Mt. Kinabalu National Park, Headquarters	GU 366079
<i>C. baluensis</i>	SP 06906	Malaysia, Borneo, Sabah, Mt. Kinabalu National Park, Headquarters	GU 366080
<i>C. tautbatorum</i>	KU 309319	Philippines, Palawan Island, Palawan Province, Municipality of Brooke's Point	GU 366083
<i>C. tautbatorum</i>	KU 309320	Philippines, Palawan Island, Palawan Province, Municipality of Brooke's Point	GU 366082
<i>C. tautbatorum</i>	KU 309321	Philippines, Palawan Island, Palawan Province, Municipality of Brooke's Point	GU 366081
<i>C. annulatus</i>	ACD 2661*	Philippines, Mindanao Island, Eastern Mindanao, Diwata Mountain Range.	GU 366084
<i>C. annulatus</i>	ACD 2637*	Philippines, Mindanao Island, Eastern Mindanao, Diwata Mountain Range.	GU 366085
<i>C. annulatus</i>	PNM/CMNH H-1646**	Philippines, Mindanao Isl., South Cotobato Prov., Municipality of Kiamba, Barangay Banate, Mt. Busa	GU 366086
<i>C. annulatus</i>	PNM/CMNH H-1503**	Philippines, Mindanao Isl., South Cotobato Prov., Municipality of Kiamba, Barangay Banate, Mt. Busa	GU 366087
<i>C. annulatus</i>	KU 314944	Philippines, Mindanao Isl., Agusan del Sur Prov., Municipality of San Francisco, Barangay Kaimpugan, Agusan Marsh	GU 366088
<i>C. annulatus</i>	KU 314945	Philippines, Mindanao Isl., Agusan del Sur Prov., Municipality of San Francisco, Barangay Kaimpugan, Agusan Marsh	GU 366089
<i>C. annulatus</i>	KU 311157	Philippines, Leyte Island, Leyte Province, Municipality of Baybay	GU 366090
<i>C. annulatus</i>	PNM 1417	Philippines, Leyte Island, Leyte Province, Municipality of Baybay	GU 366091
<i>C. annulatus</i>	KU 305567	Philippines, Cebu Island, Cebu Province, Municipality of Alcoy	GU 366092
<i>C. annulatus</i>	KU 305568	Philippines, Cebu Island, Cebu Province, Municipality of Alcoy	GU 366093
<i>C. annulatus</i>	TNHC 56457	Philippines, Siquijor Island, Siquijor Province, Municipality of San Juan, Barangay Kang-adiang	GU 366094
<i>C. annulatus</i>	TNHC 56467	Philippines, Bohol Island, Bohol Province, Municipality of Camern, Barangay Riverside	GU 366095
<i>C. annulatus</i>	RMB 2881*	Philippines, Bohol Island, Bohol Province, Municipality of Bilar, Barangay Logarita	GU 366096
<i>C. annulatus</i>	PNM 1474	Mindanao Isl., Agusan del Norte Prov., Diuata Mountain Range	GU 366097
<i>C. annulatus</i>	KU 309363	Philippines, Camiguin Sur Island, Camiguin Province, Municipality of Mambajao	GU 366099
<i>C. annulatus</i>	KU 309365	Philippines, Camiguin Sur Island, Camiguin Province, Municipality of Mambajao	GU 366098
<i>C. jambangan</i>	KU 314793	Philippines, Mindanao Island, Zamboanga del Sur Prov., Municipality of Pasonanca, Pasonanca Natural Park, Tumaga River	GU 366100
<i>C. jambangan</i>	KU 314806	Philippines, Mindanao Island, Zamboanga del Sur Prov., Municipality of Pasonanca, Pasonanca Natural Park, Tumaga River	GU 366101
<i>C. jambangan</i>	KU 314835	Philippines, Mindanao Island, Zamboanga del Sur Prov., Municipality of Pasonanca, Pasonanca Natural Park, Tumaga River	GU 366102
<i>C. jambangan</i>	PNM 9593; KU 314810***	Philippines, Mindanao Island, Zamboanga del Sur Prov., Municipality of Pasonanca, Pasonanca Natural Park, Baragnay Baluno, Sitio Kilometer 24	GU 366103
<i>C. jambangan</i>	KU 314823	Philippines, Mindanao Island, Zamboanga del Sur Prov., Municipality of Pasonanca, Pasonanca Natural Park, Baragnay Baluno, Sitio Kilometer 24	GU 366104

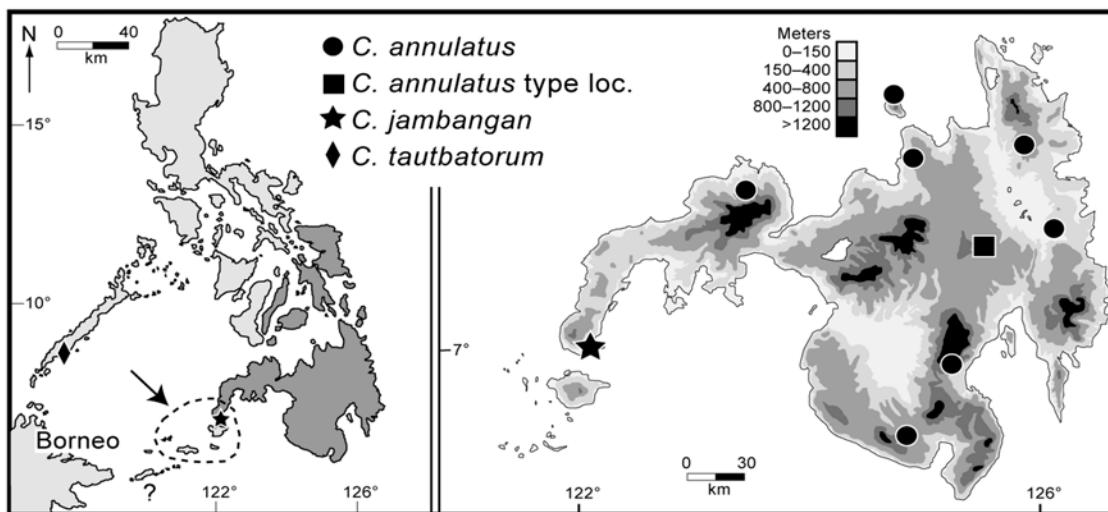


FIGURE 1. The potential distribution of *Cyrtodactylus annulatus* in the southern and central Philippines (left, darkly shaded islands), known *C. annulatus* localities on Mindanao Isl. (right, black circles; square = Bunawan, type locality), the distribution of *C. tautbatorum* from Palawan (Welton *et al.* 2009; left, diamond, southern Palawan) and know localities for *C. jambangan*, n. sp. (the type locality indicated with a star; additional localities substantiated with specimens encircled with dashed line). The question mark adjacent to Tawi-tawi Island indicates uncertainty with respect to the taxonomic status of the *Cyrtodactylus* of the southwestern Sulu Archipelago. The occurrence of *Cyrtodactylus* from these islands was reported by Taylor (1922; as *C. annulatus*), but specimens from southern Sulu Archipelago islands currently are not available in collections. The single dark spot north of Mt. Malingdang at the base of the Zamboanga peninsula is the westernmost locality for true *C. annulatus*.

Results

Morphological data. Body size and other continuously varying morphometric characters showed overlapping ranges of variation among sampled localities (Tables 2, 3). Slight differences were detected in meristic characters (precloacal pore number, number of enlarged scale rows anterior to the cloacal region; Table 2). We noted no mensural or meristic differences between sexes of *C. annulatus* and *C. tautbatorum* (Table 3) except that *C. annulatus* specimens, on average, are larger than the new species (Fig. 3). However, we noted fixed differences in color patterns, with the Zamboanga and Sulu populations of the new species described here differing from all populations of *C. annulatus*. These included a faded, dark, marbled color pattern, reduction in contrast between light and dark transverse body bands, bright yellow dorsolateral trunk tubercles, a yellow canthal stripe, and bright yellow superciliaries (See color description of new species, below; Figs. 3, 5).

Molecular data. Of the 1423 characters, 321 were parsimony-informative. Uncorrected pairwise sequence divergences between *C. annulatus* populations and *C. tautbatorum* ranged from 11.4–12.3% (mean= 11.8%), and between *C. annulatus* and *C. n. sp.* from Zamboanga and Sulu sequence divergences varied from 7.9–9.5% (mean = 8.6%; Table 1). We provide these genetic distances as general, demonstrative measures of evolutionary divergence and isolation, but we do not use them as criteria for recognizing species (see Taxonomic Conclusions, below).

Phylogeny. Parsimony, ML, and Bayesian inferences all yielded the same interspecific topology, with only minor differences in the placement of individuals within species (Fig. 2). Three major monophyletic mitochondrial lineages were recovered, each strongly supported in all analyses (Fig. 2). Of these, one lineage from Palawan (formerly considered an allopatric population of *C. annulatus*; Brown & Alcala 1978) is sister to all remaining *C. annulatus* populations. This lineage is the morphologically distinct, newly described species *C. tautbatorum* (Welton *et al.* 2009). Another, more widespread, lineage corresponds to true *C. annulatus* and consists of populations from throughout Mindanao, Cebu, Siquijor, Camiguin Sur, Bohol, and Leyte islands (Fig. 1)—a distribution enumerated by Taylor (1922a) and Brown and Alcala (1978). We are confident of the correct assignment of the name *C. annulatus* to this clade because it includes gene sequences derived from the type locality for *C. annulatus* (Bunawan, Agusan Province, Mindanao Isl.; Taylor 1922a). The clade most closely related to *C. annulatus* is a divergent, reciprocally monophyletic lineage from the tip

of the Zamboanga Peninsula (and presumably Basilan Island and parts of the Sulu Archipelago). As discussed above, the Sulu Archipelago + Zamboanga form was first identified as morphologically distinct by Taylor (1922a, b) but not described at that time.

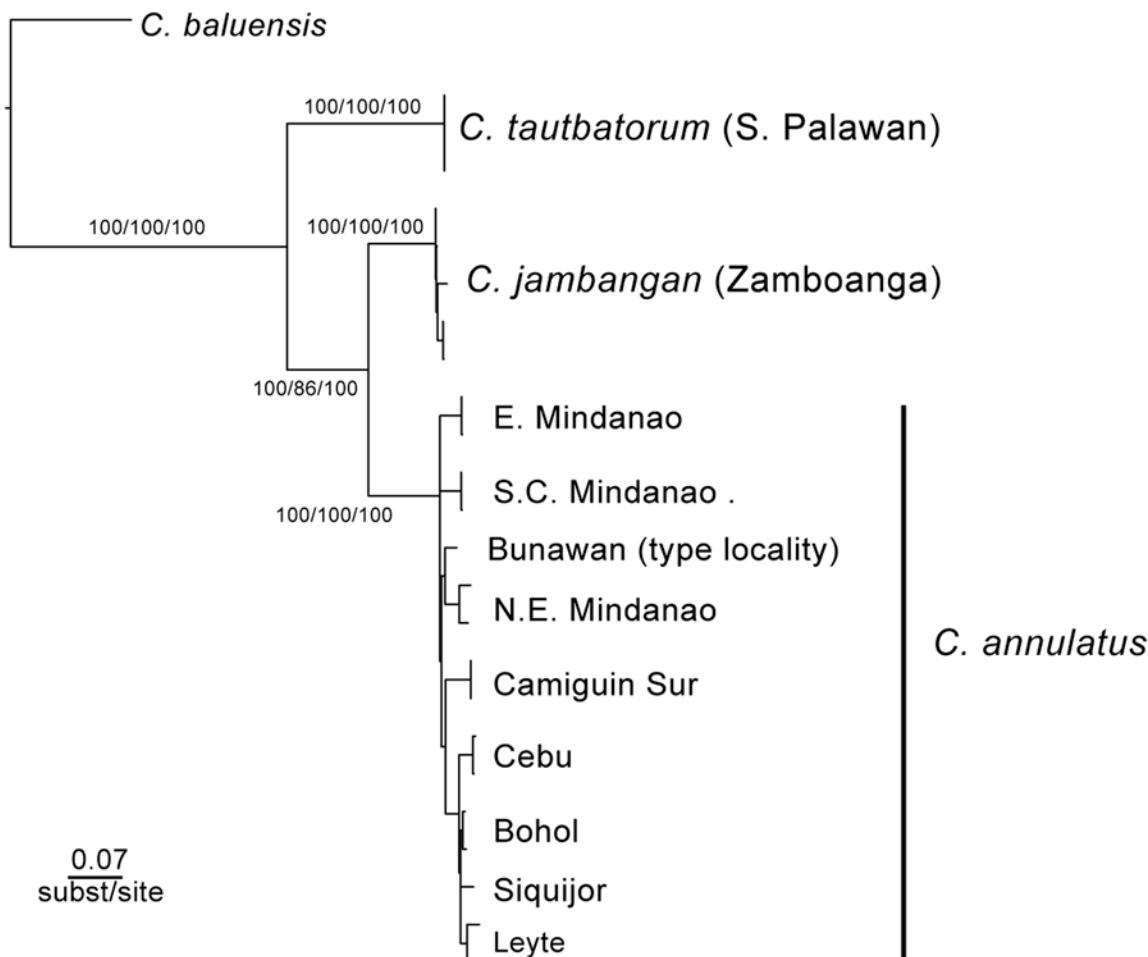


FIGURE 2. The preferred phylogenetic estimate for *C. annulatus* group species, inferred in partitioned Bayesian and likelihood analyses, and equally weighted parsimony analyses of ND2 sequence data. Numbers adjacent to nodes are likelihood and parsimony bootstraps, and Bayesian posterior probability support values, respectively.

Taxonomic conclusions. Despite the absence of statistically significant, non-overlapping variation in body size and mensural characters, we note consistent, non-overlapping, and thus diagnostic, character state differences in meristic characters of scalation and color pattern of the Zamboanga and Sulu Archipelago populations. These characters unambiguously diagnose the new species from the widely distributed *C. annulatus*, the newly discovered *C. tautbatorum* from southern Palawan (Welton *et al.* 2009), and all other Philippine (Table 2) and morphologically relevant (Table 3) congeners. This suite of diagnostic character states corresponds to a genetically divergent, monophyletic mitochondrial gene lineage, which further supports the need to recognize this population as a distinct taxonomic entity. Based on our examination of specimens from throughout the southern Philippines, we assign northeast Sulu Archipelago populations to the new species as well.

Species description

Cyrtodactylus jambangan sp. nov.

Figs. 3–5

Holotype. PNM 9593 (formerly KU 314810, RMB Field No. 10,005), adult male, collected on the trunk of a sapling (20:00–23:00) in Pasonanca Natural Park, Barangay Baluno, Zamboanga City Province, Mindanao Island, Philippines (N: 07° 1.0554, E: 122° 1.731, WGS-84; 758 m above sea level), on 12 July, 2008 by L.

Welton, R. Brown, C. Siler, J. Fernandez, M. and V. Yngente, and J. Phenix.

Paratotypes. Four males (KU 314813, 314815, 314825, and 314828), fourteen females (KU 314808, 314811, 314816–18, 314820, 3134822–24, 314826–27, and 314829–31), and five juveniles (KU 314809, 314812, 314814, 314819, and 314821) collected on the trunks of trees (18:00–23:00), 12–18 July 2008, other data identical to holotype.

Paratypes. Four males (KU 314793–94 and 314796–97), two females (KU 314795 and 314798), and three juveniles (KU 314792, and 314833–34), collected 7 July 2008, in Pasonanca Natural Park, Tumaga River (N: 6° 35.174, E: 122° 2.426, 94m, WGS-84), by L. Welton, R. Brown, C. Siler, J. Fernandez, M. and V. Yngente, and J. Phenix; one male (KU 314835), one female (KU 314806), and one juvenile (KU 314799), collected 8 July 2008, in Pasonanca Natural Park, Tumaga River (N: 6° 58.624, E: 122° 3.043, 104m, WGS-84), by the same collectors; two males (KU 314807 and 314836) collected 9–11 July 2008, in Pasonanca Natural Park, Tumaga River (N: 6° 59.534, E: 122° 3.626, 94m, WGS-84), by the same collectors; two males (KU 314803 and 314805), one female (KU 314804), and three juveniles (KU 314800–02), collected 9 July 2008, Pasonanca Natural Park, Tumaga River (N: 6° 58.624, E: 122° 4.043, 104m, WGS-84), by the same collectors; two males (KU 314781 and 314784), one female (KU 314780), and four juveniles (KU 314778–79 and 314782–83), collected 20–22 April 2008, in Pasonanca Natural Park, Barangay Pasonanca, Sitio Canucutan (N: 6° 59.534, E: 122° 3.626, 104m, WGS-84), by R. Brown and A. Diesmos; one male (KU 319654), one female (KU 319655), and one juvenile (KU 319652), collected 3–5 April 2009, in Pasonanca Natural Park, Barangay La Paz, Sitio Nancy (N: 7° 5.099, E: 122° 1.620, 1130m, WGS-84), by R. Brown, C. Infante, and A. Diesmos; two males (KU 319656 and 319657), collected 6–9 April 2009, in Pasonanca Natural Park, Barangay Tulosa, Sitio Santa Clara, Cabo Negros outpost (N: 7° 6.479, E: 122° 7.139, 620m, WGS-84), by the same collectors; three males (KU 319660–62), and one female (KU 319658), collected 11 April 2009, in Pasonanca Natural Park, Tumaga River (N: 6° 35.174, E: 122° 2.426, 94m, WGS-84), by the same collectors; twelve males (CAS 60195, 60197, 60199, 60203–205, 60208, 60212, 60217–18, 60221, and 60453), 15 females (CAS 60196, 60200–201, 60207, 60209–10, 60213–16, 60220, 60454–55, 60458, and 60460), and six juveniles (CAS 60222–24, 60456–57, and 60459) collected at Abung-Abung and Port Holland on Basilan Island, 5–25 October, 1921, by E. H. Taylor; two males (CAS 60622–23), three females (CAS 60619–21), and one juvenile (CAS 60624) collected on New Govenen Island, 5–25 October, 1920, by E. H. Taylor; one male (CAS 60669), four females (CAS 60670–72 and 60887), and two juveniles (CAS 60886 and 60888) collected on Bud Daho Mt. on Jolo Island, 25 October–17 November, 1920, by E. H. Taylor; two males (CAS 62020 and 62022), three females (CAS 62017, 62019, and 62021), and one juvenile (CAS 62018) collected in Zamboanga del Sur Province, 23 September–6 October, 1920, by E. H. Taylor.

Diagnosis. The new species differs from most of Asia's 115 *Cyrtodactylus* species by the same suite of character states that has facilitated the recognition and distinction of *C. annulatus*: (1) small body size; (2) light gray body, with dark transverse bands; (3) presence of a weak precloacal groove; (4) absence of enlarged femoral scales and pores; (5) moderately spinose tuberculation; (6) presence of forelimb tuberculation; (7) and absence of enlarged, median subcaudal scales (Taylor 1922; Brown & Alcala 1978; Manthey & Grossman 1997; Grismer 2005; Welton *et al.* 2009). Because the new species differs from non-Philippine congeners by characters that have distinguished *C. annulatus* (and have never been challenged; Taylor 1922a; Brown & Alcala 1978), we do not provide exhaustive comparisons to all those species (see Welton *et al.* 2009). Instead we focus on the comparisons relevant for the recognition of the new species: the closely related taxa within the *C. annulatus* complex and other *Cyrtodactylus* endemic to the Philippines.

Cyrtodactylus jambangan differs from all other species of Philippine *Cyrtodactylus* (i.e., *C. agusanensis*, *C. philippinus*, *C. redimiculus*, and *C. tautbatorum*; Table 2) by the following combination of characters: (1) small body size (2) dorsum darkly marbled lavender and brown or brown with indistinct wavy lavender blotches; (3) presence of bright yellow superciliaries, canthal stripe, and dorsal tubercles; (4) low dorsal scale counts (as measured by midbody dorsal and paravertebral scales; Table 2); (5) moderate numbers of midbody dorsal tubercle rows (Table 2); (6) absence of femoral pores in both sexes; (7) presence of precloacal pores in males and similarly enlarged, dimpled, scales in females, arranged in an inverted "V"-shaped configuration; (8) moderately depressed precloacal groove; (9) scales anterior to precloacal region undifferentiated; (10) lamellae under Finger III 17–22; (11) lamellae under Toe IV 20–24 (12) supralabials to beneath eye 8–11; (13) infralabials to beneath the eye 6–8; (14) absence of stripes connecting the lateral margins of transverse bands on trunk; and (15) midbody ventral scales 48–63. Comparisons with additional Southeast Asian species are provided in Table 3.

TABLE 2. Summary of the distribution of diagnostic character states that distinguish *Cyrtodactylus jambangan*, n. sp., from Philippine congeners. See Table 3 for comparisons to non-Philippine species. Body size for males and general geographic distribution are included for reference. See Materials and Methods for character definitions.

	<i>jambangan</i>	<i>annulatus</i>	<i>agusensis</i>	<i>philippinicus</i>	<i>redimiculus</i>	<i>taubatorium</i>
Geographic range	Southern Zamboanga and Sulu Archipelago	Visayan and Mindanao regions	Samar, Leyte and eastern Mindanao	Throughout the Philippines	Palawan Island	Southern Palawan Island
Male snout-vent length	60.4–72.3	68.8–79.4	82.3–100.1	70.0–93.6	76.9–90.0	47.2–68.7
Midbody tubercle rows (males)	17–19	14–16	18–21	17–20	13–16	13–17
Precioacal pores	2–5 (4 in 96% of specimens)	6	6–9	7–10	4–6	4–6
Scale rows anterior to cloacal groove	undifferentiated	3 or 4 enlarged	5 or 6 enlarged rows	4–6 enlarged rows	4–6 enlarged rows	2–4 enlarged rows
Nuchal band shape	V	M	M	M	M	V
Pre-cloacal groove	shallow	moderate	-	deep	-	moderate
Lateral flank stripe	-	+	+	+	+	-
Supraciliaries	bright yellow	light gray	white to yellow	light gray	dark brown	light gray
Yellow canthal stripe (adults)	+	-	-	-	-	-
Predominant dorsal color pattern	dark, marbled or with indistinct transverse bands	light gray with 4 or 5 dark distinct transverse bands	light gray with 5 dark distinct transverse bands	light gray with 4 dark distinct transverse bands	dark brown or black with 3–5 transverse bands or tan reticulum	light gray with 4 or 5 dark distinct transverse bands

TABLE 3. Diagnostic table of character states (1: present; 0: absent; ?: data unavailable) used to distinguish *Cyrtodactylus jambangan* from other Bornean (B), Peninsular Malaysian (M), Sumatran (S) and Javan (J) *Cyrtodactylus* species (see Grismer 2005, and Linkem et al. 2008, for recent summaries of diversity outside of Southeast Asia). Philippine species (P) are included, for reference and detailed comparisons of characters distinguishing *C. jambangan* from all remaining Philippine species are included in Table 2. Characters include 1: tubercles moderate to strong; 2: tubercles on forelimbs; 3: tubercles on hind limbs; 4: tubercles on head and/or occiput; 5: tubercles on at least 1/3 of tail; 6: number of ventral scales; 7: median subcaudals enlarged; 8: proximal subdigital lamellae broad; 9: number of subdigital lamellae on toe IV; 10: contact of posterior thigh scales abrupt; 11: femoral scales enlarged; 12: number of femoral pores; 13: pre-cloacal groove; 14: enlarged pre-cloacal pores; 15: number of pre-cloacal pores; 16: pre-cloacal and femoral pores/scales continuous; 17: reticulate pattern on head; 18: body banded; 19: body striped. When derived from the literature, data sources include: A—Günther and Rösl (2002), B—Brown and Alcala (1978), C—Younmans and Grismer (2006), D—Grismer (2005), E—Taylor (1963), F—Bauer et al. (2003), G—de Rooij (1915), H—Brown and Parker (1973), I—Dring (1979), J—Brongersma (1934), K—Darevsky (1964), L—Werner (1896), M—Bauer et al. (2002), N—Smith (1925), O—Das and Lim (2000).

Taxon	n	SVL	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>jambangan</i> (P)	20	60–81.5	1	1	1	0	48–63	0	1	20–24	0	0	0	1	1	2–5	0	0	1	1	0	
<i>baliensis</i> (B)	1 ^D	72–86	1	1	1	0	40–45	1	1	21–23	1	1	6–9	0	1	9/10	0	1	0	1	0	
<i>cavernicolous</i> (B)	1 ^C	64–81	1	0	1	1	51–58	0	1	22–26	0	0	0	1	1	4	0	1	1	0	0	
<i>consobrinus</i> (B, M, S)	1	97–121	1	1	1	1	58–65	1	1	23–28	0	1	1–6	0	1	9/10	0	1	1	0	0	
<i>ingeri</i> (B)	C	65–76	1	1	1	1	40–43	1	1	23–27	0	0	0	0	1	8	0	1	0	1	0	
<i>matsuiai</i> (B)	C	105	1	1	1	1	51	0	1	22	1	0	0	0	0	7	0	1	0	1	0	
<i>pubisulcus</i> (B)	C	59–74	1	0	1	1	43–55	0	1	17–22	0	0	0	1	1	7–9	0	0	0	1	0	
<i>pulchellus</i> (M)	C	115	1	1	1	1	33–35	1	1	19/20	1	1	14–18	1	1	6–8	1	0	1	0	0	
<i>quadriovirgatus</i> (M, S)	C	51–71	1	1	1	1	34–42	0	1	19/20	0	1	0	0	0	0–4	0	0	0	0	1	
<i>yoshii</i> (B)	C	75–96	1	1	1	1	50–58	0	0	25–30	0	0	0	0	0	8–12	0	0	0	1	0	
<i>aurensis</i> (M)	D	92–95	0	0	0	0	45–51	1	1	18–23	0	0	0	1	1	7	0	1	1	0	0	
<i>elok</i> (M)	I	56–68	0	1	0	1	44	0	1	18/19	0	0	0	0	1	8	0	0	0	1	0	
<i>brevipalmatus</i> (M)	E	64–73	1	1	1	0	1	35–45	0	1	16–19	1	1	6/7	0	1	9/10	0	0	0	1	
<i>lateralis</i> (M, S)	L	85	1	1	1	1	60–64	0	1	21/22	?	?	0	0	1	13	0	0	0	1	0	
<i>malayanus</i> (M, B)	C	70–73	1	1	1	1	58–62	1	1	21–23	0	1	0	0	1	8–10	0	1	1	0	0	
<i>marmoratus</i> (M, J)	E	76	1	1	1	0	40–50	0	1	23/24	1	1	3–10	1	1	12–16	0	0	0	1	0	
<i>sementanjungensis</i> (M)	C	59–69	1	1	1	?	48–53	0	1	17–21	1	0	0	1	1	0	0	0	1	1	0	
<i>seribuatensis</i> (M)	C	75	1	1	1	1	28–39	0	1	19–22	1	1	42–45	0	1	42–45	1	0	0	1	0	
<i>tiomanensis</i> (M)	O	84	1	1	1	1	36–40	0	1	20–22	1	1	0	1	1	3–5	0	0	1	0	0	
<i>redimiculus</i> (P)	B	78	?	?	?	?	?	1	?	20–24	?	?	8/9	1	1	5–8	?	?	?	21		
<i>agusaniensi</i> (P)	9 ^B	70–103	1	1	1	1	46–51	0	1	23–28	0	1	3–14	0	1	7–11	0	0	1	0		
<i>annulatus</i> (P)	4 ^C	45–70	1	?	?	?	?	50–60	0	1	18–23	?	0	0	1	1	4–7	0	1	1	0	
<i>philippinicus</i> (P)	38	74–92	1	1	1	1	36–42	0	1	22–24	0	0	0	1	1	8–10	0	0	1	0	0	
<i>tauhatorium</i> (P)	16	47–69	1	1	1	1	46–58	0	1	17–21	0	0	0	1	1	4/5	0	0	1	1	0	

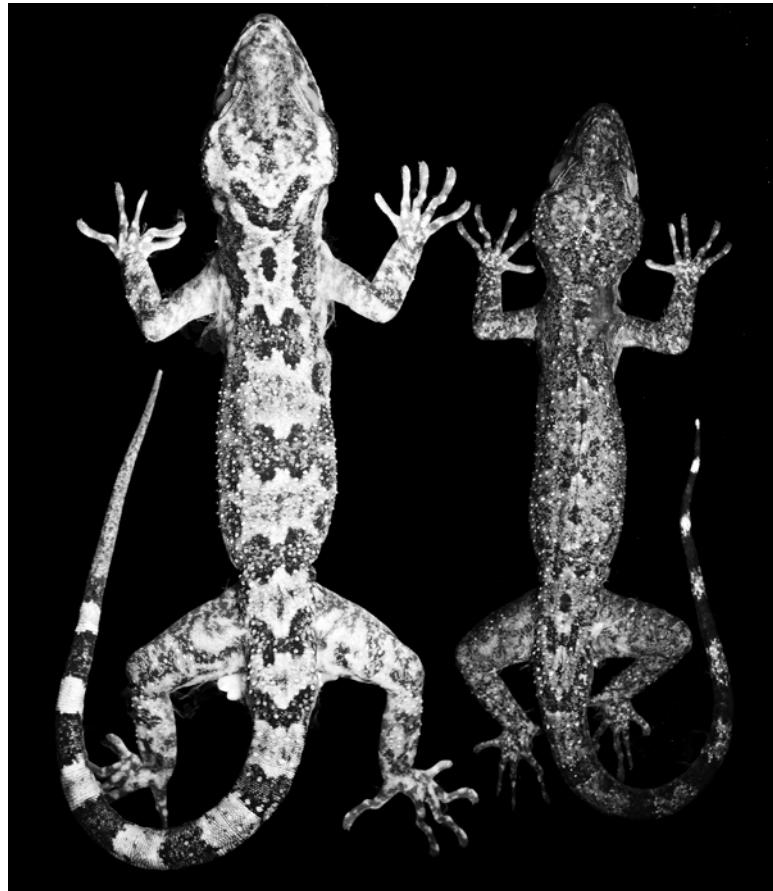


FIGURE 3. Dorsal aspect of typical sized specimens of *Cyrtodactylus annulatus* (left: KU 309364; Camiguin Sur Isl.) and *C. jambangan*, n. sp., (right: holotype PNM 9593 specimen from Pasonanca, Zamboanga City Province).

The critical comparison for the recognition of the new species is the diagnosis of the Zamboanga and Sulu populations from true *C. annulatus* (type locality from the Municipality of Bunawan, Agusan Del Sur Province, Mindanao Island), and newly designated *C. annulatus* neotype locality (Welton *et al.* 2009) of Mt. Hilonghilong, Diwata Mountains, Agusan Del Norte Province, Mindanao Island. Although morphologically similar to *C. annulatus* from throughout its range, *C. jambangan* has bright yellow canthal stripes, superciliaries, dorsal tubercles, and moderate-sized dorsolateral body tubercles, fewer precloacal pores, undifferentiated precloacals, and strongly spinose (versus moderate, domed) dorsal tuberculation. The new species is separated from *C. annulatus* by 7.9–9.5% (mean = 8.6%) uncorrected sequence divergence (Table 4) in the ND2 protein-coding mitochondrial gene region (see Table 3 for complete univariate morphometric data for *C. annulatus* and *C. jambangan*). The new species differs from all remaining Philippine species by a variety of morphological and color pattern characters (Table 2; Brown and Alcala 1978).

Description of holotype. Adult male, snout–vent length 67.7 mm; head moderately long, distinct from neck, 30.3% SVL; head width 64.7% and height 41.7% head length; head triangular in dorsal aspect; lores concave; snout elongate, 41.7% head length, anterior tip rounded; eye diameter 20.6% head length, 76.3% eye–ear distance; auricular opening ovoid, longest axis 9.5% head length.

Dorsal head scalation heterogenous, scales small and granular, with tubercle density sparse medially, tubercles increasing in size and density posteriorly and laterally; superciliaries increasing in size (laterally elongated) anteriorly, with largest scales at anterodorsal margin of orbit; rostral taller than wide, divided dorsally by inverted “Y” shaped crease; rostral bordered by large, anterior internasal and smaller, paired posterior internasals, supranasals, and first supralabials; internarial distance 2.2 mm; nostrils bordered by supranasals, rostral, 2 postnasals, and first supralabials; supralabials rectangular, decreasing in size posteriorly (left/right): 9/10 to midpoint of eye, 12/12 total; infralabials 7/7 to midpoint of eye, 11/10 total; supralabials

bordered dorsally by secondary, slightly differentiated row of scales, extending to anterior margin of orbit; infralabials bordered ventrally by similar row, extending to anterior margin of orbit.

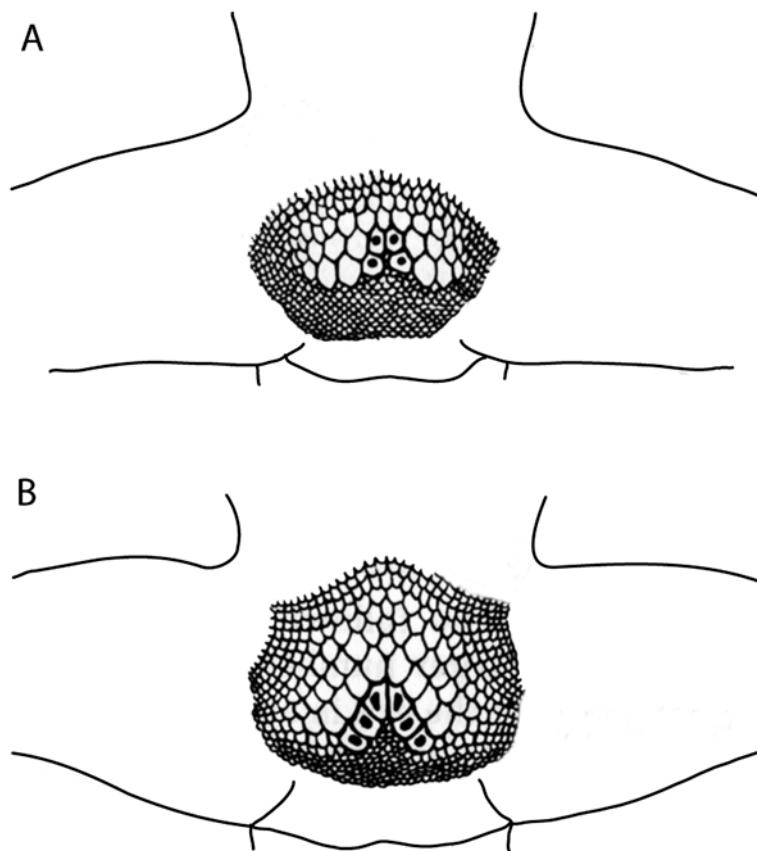


FIGURE 4. Precloacal regions of (A) *Cyrtodactylus jambangan*, n. sp., and (B) *C. annulatus* (from Taylor 1922), showing the four-pour configuration typical of *C. jambangan* and the normal condition of six pores in *C. annulatus*. Note the presence of separated lateral patches of enlarged scales on either side of the precloacal pores (anterior precloacals undifferentiated or only slightly differentiated in *C. jambangan*) versus a continuous arc of greatly enlarged precloacals in *C. annulatus*.

Ventral head sculation heterogenous; mental bordered by first infralabials, and paired postmentals, with triangular projection posteriorly; 7 differentiated gular scales posterior to postmentals; first infralabial in contact with postmental and single differentiated gular; remaining gulars heterogenous, small and granular, increasing in size in nuchal region.

Body elongate, axilla–groin distance 44.5% snout–vent length, lacking distinct ventrolateral folds; dorsal sculation granular, heterogenous, with semi-regular rows of rounded, posteriorly-oriented tubercles, increasing in protuberance (from convex to conical) and size posterior to hind limb insertions; tubercles in 17 longitudinal midbody and 27 paravertebral rows; paravertebral scales 164; transverse midbody dorsal and ventral scales 91 and 54 respectively, between lateral tubercle rows; ventral scales imbricate, slightly larger than dorsals and increasing in size medially; differentiated precloacals 4, arranged in an inverted “V” configuration pierced with enlarged pores, surrounding shallow and longitudinally short precloacal groove; two patches of enlarged scales anterolateral to precloacals (14 left, 13 right); two rows of slightly enlarged scales anterior to precloacals; three slightly enlarged scales posterior to precloacals.

Forelimbs slender, forearm and upper arm 14.3% and 12.4% snout–vent length respectively; sculation on dorsal surfaces of forelimbs heterogenous, scales larger than ventrals; tubercles absent on upper arm, sparse on forearm, less spinose than dorsal trunk tubercles; ventral sculation homogenous, lacking tubercles; fingers well developed; Fingers I and III 37.4% and 62.2% forearm length, respectively; lamellae enlarged and slightly raised, lamellae proximal to inflection larger than those distal to inflection, slight increase in size from

inflection to claw; finger number followed by subdigital lamellae (in parentheses): I (11), II (14), III (20), IV (18), V (15); all fingers clawed; claws well developed, sheathed by single dorsal and ventral scale.

TABLE 4. Summary of univariate morphological variation among mensural and meristic characters in the type series of *Cyrtodactylus jambangan*, n. sp., from Pasonanca Natural Park, Zamboanga Peninsula, western Mindanao Island, and *Cyrtodactylus annulatus* from eastern Mindanao Island (including Bunawan, the *C. annulatus* type locality). Labial scale counts were counted to below the center of the eye and bilaterally symmetrical characters are separated into left (l) and right (r) sides of the body. See Materials and Methods for character abbreviations.

	<i>jambangan</i>	<i>jambangan</i>	<i>annulatus</i>	<i>annulatus</i>
	Male (N=10)	Female (N=10)	Male (N=4)	Female (N=6)
Snout-vent length	60.4–72.3 (67.1 ± 3.8)	61.2–81.5 (71.1 ± 5.9)	68.8–79.4 (74.1 ± 5.6)	59.3–80.5 (67.3 ± 8.3)
Lamellae of Finger 3	17–20 (18 ± 0.9)	16–22 (18 ± 1.7)	17–21 (19 ± 1.0)	15–18 (17 ± 1.2)
Lamellae of Toe 4	20–23 (21 ± 1.0)	20–24 (22 ± 1.3)	20–22 (21 ± 1.0)	17–21 (19 ± 1.5)
Finger 1 length	2.7–3.7 (3.3 ± 0.4)	2.6–4.1 (3.4 ± 0.4)	3.2–4.1 (3.8 ± 0.4)	2.6–4.0 (3.2 ± 0.6)
Finger 3 length	4.3–6.0 (5.4 ± 0.5)	4.4–7.0 (5.5 ± 0.6)	4.0–6.2 (5.3 ± 1.1)	4.0–5.9 (5.0 ± 0.8)
Toe 1 length	2.9–3.7 (3.2 ± 0.3)	2.5–3.9 (3.4 ± 0.4)	3.0–3.9 (3.4 ± 0.4)	2.0–3.8 (3.2 ± 0.7)
Toe 4 length	6.8–9.0 (7.8 ± 0.7)	6.9–10.3 (8.6 ± 1.1)	6.6–9.7 (8.1 ± 1.4)	5.5–8.7 (7.4 ± 1.2)
Supralabials (l)	8–11 (9 ± 1.0)	8–10 (9 ± 0.7)	8–10 (9 ± 1.0)	7–10 (9 ± 1.2)
Supralabials (r)	8–10 (9 ± 0.6)	8–10 (9 ± 0.6)	8–10 (9 ± 1.0)	7–10 (9 ± 0.8)
Infralabials (l)	6–8 (7 ± 0.5)	7–8 (7 ± 0.3)	7–8 (7 ± 1.0)	7–8 (8 ± 0.5)
Infralabials (r)	6–8 (7 ± 0.6)	6–8 (7 ± 0.5)	7–8 (7 ± 1.0)	7–8 (7 ± 0.5)
Precloacals (l)	2 or 3 (2.2 ± 0.4)	N/A	2 or 3	N/A
Precloacals (r)	0–2 (1.2 ± 0.6)	N/A	3	N/A
Total precloacals	2–5 (3.4 ± 0.8)	N/A	5 or 6	N/A
Midbody dorsals	75–91 (87 ± 4.6)	86–96 (93 ± 3.1)	87–95 (91 ± 3.7)	81–91 (85 ± 4.0)
Midbody tubercles	17–19 (18 ± 0.6)	16–18 (17 ± 0.9)	14–16 (15.5 ± 1.3)	14–16 (15 ± 1.0)
Midbody ventrals	48–59 (53 ± 3.6)	50–63 (57 ± 4.6)	49–54 (51 ± 2.5)	50–60 (53 ± 3.7)
Paravertebrals	144–174 (161 ± 8.4)	150–170 (163 ± 6.2)	124–166 (152 ± 18.9)	137–163 (151 ± 12.5)
Paravertebral tubercles	25–30 (27 ± 1.8)	23–31 (27 ± 2.7)	17–27 (24 ± 4.7)	21–28 (24 ± 2.4)
Eue-narial distance	5.9–7.4 (6.5 ± 0.5)	6.0–8.1 (7.0 ± 0.6)	5.4–7.7 (6.7 ± 1.1)	4.6–7.5 (6.0 ± 1.1)
Eye-tympanum distance	5.3–6.5 (5.6 ± 0.4)	5.8–7.7 (6.4 ± 0.6)	5.4–6.6 (6.0 ± 0.5)	5.0–6.4 (5.7 ± 0.6)
Interorbital distance	2.2–3.0 (2.6 ± 0.2)	2.4–3.7 (3.0 ± 0.4)	2.9–3.9 (3.3 ± 0.5)	2.6–3.4 (2.9 ± 0.3)
Snout length	6.3–8.7 (7.8 ± 0.8)	7.1–9.5 (8.4 ± 0.7)	6.5–9.3 (8.2 ± 1.3)	5.5–8.9 (7.0 ± 1.4)
Internarial distance	1.9–2.5 (2.2 ± 0.2)	2.0–3.0 (2.5 ± 0.3)	2.2–2.5 (2.4 ± 0.1)	2.1–2.6 (2.3 ± 0.2)
Eye diameter	3.8–4.6 (4.2 ± 0.3)	3.7–5.1 (4.5 ± 0.5)	4.3–4.8 (4.6 ± 0.2)	3.6–5.2 (4.3 ± 0.6)
Upper arm length	6.8–9.9 (7.8 ± 0.9)	6.9–10.7 (9.0 ± 1.0)	6.2–9.6 (7.9 ± 1.5)	5.1–10.4 (7.4 ± 2.2)
Forearm length	8.1–9.8 (9.0 ± 0.6)	8.2–10.8 (9.6 ± 0.8)	8.6–11.1 (10.1 ± 1.2)	7.6–11.5 (9.4 ± 1.4)
Femur length	10.4–12.8 (11.7 ± 0.9)	9.5–14.9 (12.4 ± 1.4)	11.4–13.3 (12.6 ± 0.9)	9.0–13.6 (11.6 ± 1.7)
Tibia length	9.4–11.1 (10.3 ± 0.5)	8.7–13.6 (10.9 ± 1.2)	10.2–13.0 (11.4 ± 1.3)	9.5–13.1 (10.7 ± 1.4)
Axilla-groin distance	26.3–32.8 (29.3 ± 2.3)	27.7–34.6 (32.0 ± 2.1)	26.3–31.2 (31.6 ± 4.1)	26.0–36.8 (29.9 ± 4.5)
Transverse bands	3–5 (3 ± 0.7)	3–4 (3 ± 0.3)	3	3–4 (3 ± 0.4)
Postcloacal tubercles	2–5 (4 ± 0.9)	2–4 (4 ± 0.7)	2–4 (3 ± 1.2)	2–4 (3 ± 1.0)
Postementals	6–9 (7 ± 1.0)	6–9 (8 ± 1.2)	8–10 (9 ± 1.0)	6–11 (8 ± 1.9)

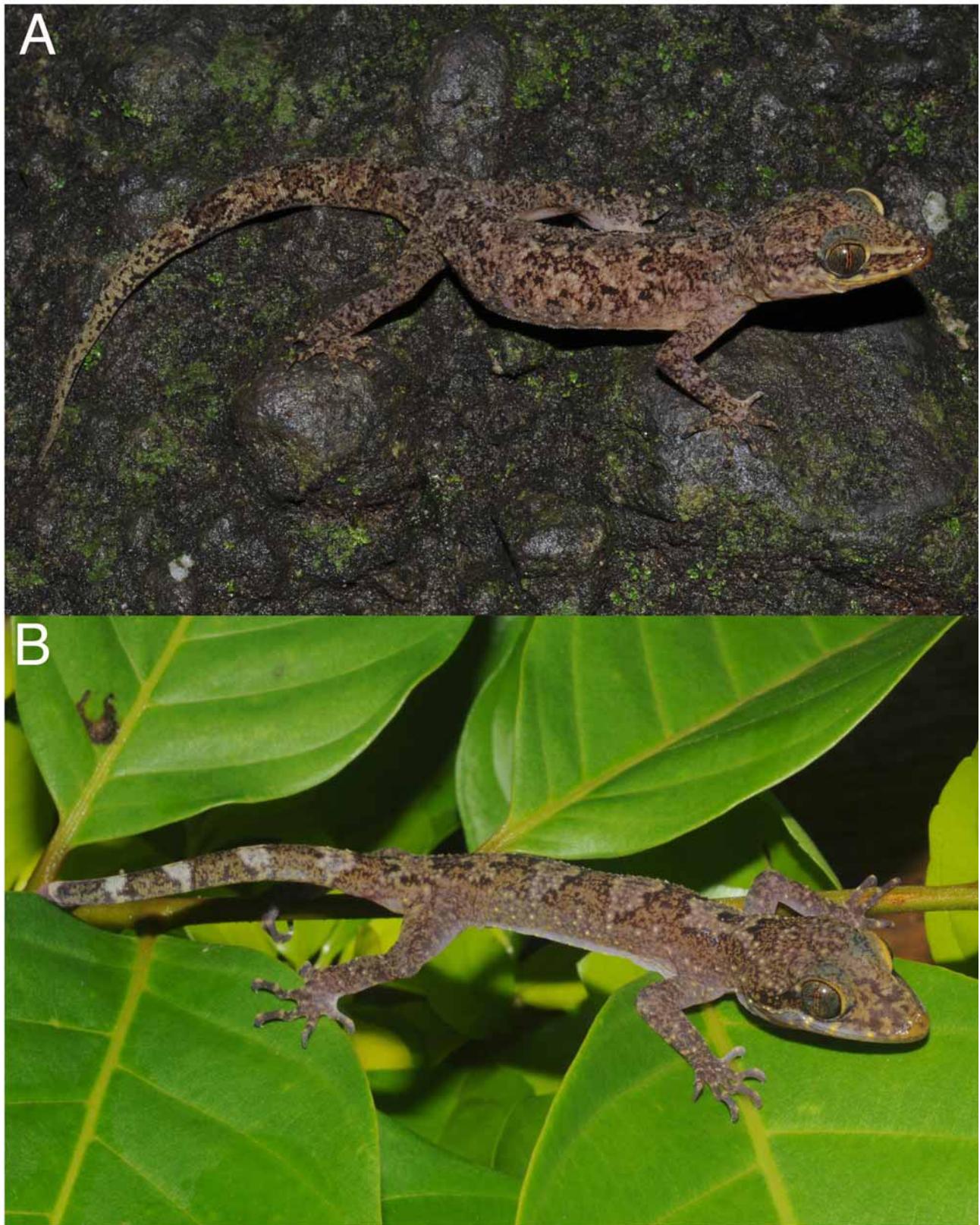


FIGURE 5. Photographs of *Cyrtodactylus jambangan*, n. sp., in life: typical muted, marbled color pattern of (A) adults (holotype PNM 9593) and (B) more strikingly patterned contrasting coloration of juveniles (KU 314812).

Hind limbs relatively robust, limb diameter at insertion twice that of forelimb; femur long, 16.8% snout–vent length; dorsal hindlimb scalation heterogenous, scales increasing in size distally, with tubercles regularly

distributed, increasing in size and becoming more spinose distally; ventral scalation heterogenous, increasing in size distally, lacking tubercles; right limb with two conspicuous patches dorsally, lacking scales or tubercles (possibly resulting from injury); enlarged femoral scales (and pores) absent; toes well developed, relatively longer than those on manus; Toes I and IV 31.2% and 85.4% tibia length, respectively; lamellae enlarged and slightly raised, lamellae proximal to inflection larger than those distal to inflection, slight increase in size from inflection to claw; toe number followed by subdigital lamellae (in parentheses): I (12), II (16), III (20), IV (23), V (22); all toes clawed; claws well developed, sheathed by single dorsal and ventral scale.

Tail original, length 78.2 mm, width and height 5.6 and 4.8 mm at base respectively, tapering abruptly posterior to hemipenal bulge, then gradually to terminus; 7 annuli discernable dorsally through lateral margins, posterior to which whorls cannot be distinguished, owing to absence of differentiated scales associated with annuli; tubercles smaller and less spinose than those of trunk; enlarged medial subcaudal scales absent; 1 enlarged post-cloacal tubercle present on each side of cloaca; anterior margin of hemipenal bulge with paired, laterally expanded, postcloacal glandular openings.

Measurements of holotype (in mm). Snout–vent length 67.7; lamellae under Finger III 20; lamellae under Toe IV 23; Finger I length 3.6; Finger III length 6.0; Toe I length 3.3; Toe IV length 9.0; eye–narial distance 6.5; eye–ear distance 5.6; interorbital distance 2.6; snout length 8.6; internarial distance 2.2; eye diameter 4.2; upper arm length 8.4; upper arm length 9.7; femur length 11.4; tibia length 10.5; hand length 9.1; foot length 10.9; axilla–groin distance 10.1; tail length 84.6.

Coloration of holotype in preservative. Dorsal ground coloration (of head, neck, body, limbs, and tail) dark brown, with irregularly shaped dark gray to lavender transverse dorsal bands, varying from irregular dark gray blotches anteriorly, to a single medial blotch followed posteriorly by a “V-shaped” marking in the nuchal region, to three conspicuous, “butterfly-shaped” patterns interspersed with three irregularly shaped transverse blotches throughout the trunk, and becoming less-defined laterally; supralabials with four conspicuous light tan to white blotches (left and right) irregularly distributed between the second and twelfth scales; light gray band bordered by dark brown extends from posterior margin of eye to auricular opening; trunk tubercles primarily light tan to cream; limbs mottled, with dark gray and dark brown, lacking distinct bands; digits with light tan to cream blotches at joints; tail more conspicuously banded than trunk, with dark brown ground coloration fading to white at the terminus of tail, overlain with 10 dark gray to black bands.

Ventral portions of head, trunk, and limbs tan, darkening at margins of ventrolateral tubercle row; hands and feet tan, fingers and toes slightly darker; subcaudal coloration cream with increased dark speckling through anterior third; seven discernable white bands posteriorly.

Color Variation. Our sample of 36 males, 52 females, and 26 juveniles exhibits minimal color variation. Four adult males (KU 314794, 314796, 314813, and 314825) and four adult females (KU 314804, 314823–24, and 314831) are darker, with dorsal bands through the axilla-groin region of higher contrast to the lighter ground color. One adult male (KU 314815) and two adult females (KU 314822, and 314827) are lighter, with distinct dorsal banding, and light brown to light gray ground color overlaid by medium to dark gray band. One adult male (KU 314805) and one adult female (KU 314795) lack a defined “V-shaped” blotch spanning the posterior dorsum of the head and nuchal region. Three adult males (KU 314794, 314805, and 314835) lack the conspicuous blotch medially in the nuchal region. All other specimens have color and patterning consistent with the holotype. Additionally, nine adult males (KU 314781, 314784–85, 314789, 314791, 314797, 314803, 314812, and 314836), 19 adult females (KU 314778–80, 314787–88, 314790, 314792, 314798, 314808–09, 314816–19, 314820–21, 314829, 314832, and 314834), and 10 juveniles (KU 314782–83, 314883, 314799–802, 314807, 314786, and 314814) show similar trends in variation, with one adult male (KU 314797), two adult females (KU 314816 and 314832), and two juveniles (KU 314814 and 314833) with a darker overall coloration and more highly defined dorsal banding. Four adult males (KU 314781, 314784, 314789, and 314803) and 13 adult females (KU 314734, 314779–80, 314790, 314792, 314798, 314809, 314817–21, and 314829) have a light gray ground color with dark gray, well-defined dorsal banding. Regenerated tails have highly variable dark speckling overlaying a medium gray ground color, to a completely dark brown dorsal coloration.

Generally, a greater level of definition in dorsal banding is present in female and juveniles; these

specimens have greater contrast in dorsal banding; a few individuals nearly lack dorsal bands all together (KU 314799, 314801, and 314802). Ventral coloration is less variable except on the tail. Original tails are similarly colored with speckling increasing from the anterior margin of the tail to the terminus, with the tail tip being nearly black. Dorsal, light-colored bands extend through venter, becoming lighter in color and more defined towards terminus of tail. One adult male (KU 314825) has speckling at the base and the tip of the tail, a cream ground color throughout, and lacks dark patterning in between. All others exhibit increasing amounts of dark speckling over a light to medium gray ground color from the anterior margin of the tail to the terminus.

Morphological variation. Summaries of univariate morphological variation in the series are presented in Table 3. Our series shows minimal morphological variation between males and females. However, females are generally larger and more robust (the largest specimen, KU 314831, is female with SVL = 81.5).

Color in life. *Cyrtodactylus jambangan* has light yellow to gold dorsal tubercles through the axilla–groin region, a yellow canthal stripe, bright yellow superciliaries, and a variable dorsal banding pattern. All three characters are in contrast to observations of true *C. annulatus*, which has regular, distinct, and brightly contrasting dorsal bands through the axilla–groin region, more pattern variation, and also lacks bright yellow canthal stripe and superciliaries (see Fig. 5).

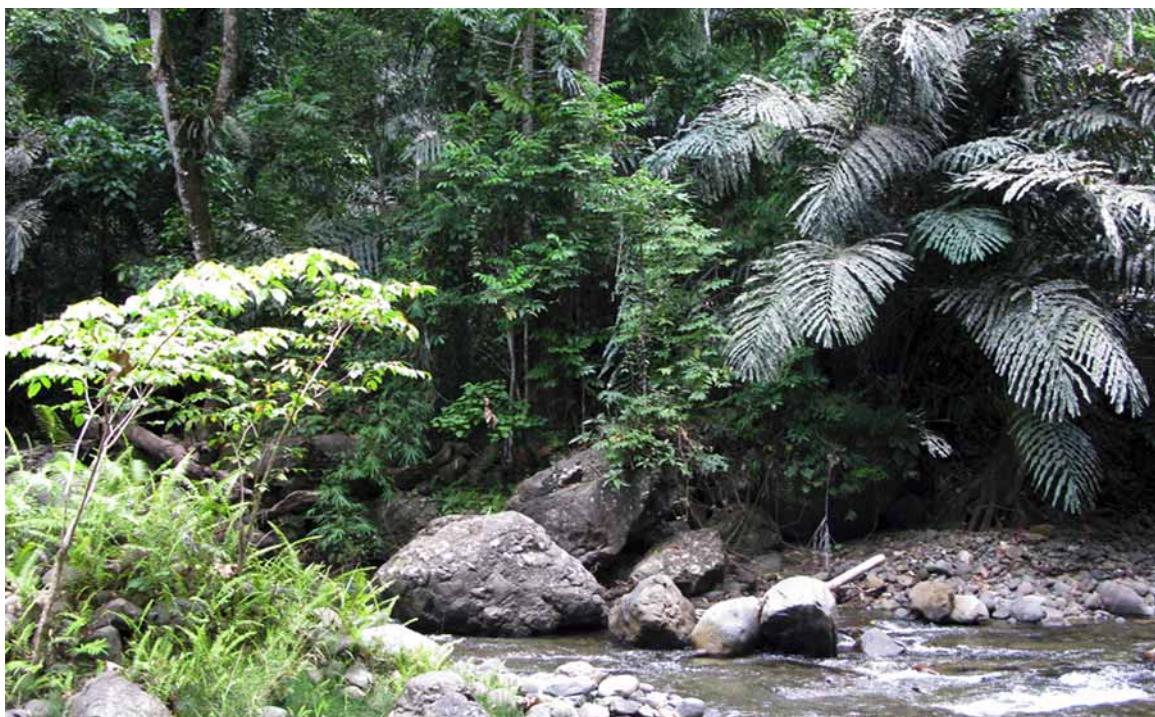


FIGURE 6. Preferred riparian habitat characteristics of *C. jambangan*, n. sp., along the Tumaga River, 90 m above sea level, Pasonanca Natural Park, Zamboanga City Province, Mindanao.

Ecology and natural history. The new species is found at low and mid-elevations in riparian habitats (gallery forests) along streams. We encountered *C. jambangan* specimens on trunks of trees, rocks, and overhanging exposed root masses on the banks of rivers and streams.

Distribution. The distribution of the new species includes Pasonanca Natural Park, Zamboanga Peninsula, extreme western Mindanao Island, and adjacent Sulu Archipelago islands to the southwest (Fig. 1). Other localities in the Sulu Archipelago where Taylor (1922a) observed this species include Basilan, Great Santa Cruz, Teipono, Tamuk, Cancuman, Dipolod, Bitinan, Jolo, Tulian, Tawitawi, Papahag, Bongao, Buban Islands of the Tapiantana and Taipan Island Groups.

Etymology. The specific epithet is derived from the term *Jambangan*—the ancient name for the Zamboanga City area. Sulu and Zamboanga folklore suggest that the name was bestowed upon the Zamboanga City area by the immigrant Subanons (“People of the River”) who arrived in western Mindanao

and the Sulu archipelago in approximately 1200 A.D., after traveling by boat through the Sulu Archipelago, from what is now Indonesia. *Jambangan* means “The Land of Flowers,” a name presumably used in reference to the natural beauty of the area surrounding Zamboanga City.

Discussion

The description of *Cyrtodactylus jambangan* brings the total number of endemic Philippine *Cyrtodactylus* species to six (including the newly described species from Palawan, *C. tautbatorum*; Welton *et al.* 2009). This is likely to be an underestimate of the species diversity in the archipelago. In addition to the suspected presence of numerous endemics inhabiting deep-water islands that remain unsurveyed, full realization of Philippine *Cyrtodactylus* diversity may only come to fruition through more attentiveness to the widespread species *C. philippinicus* and *C. annulatus*. *Cyrtodactylus philippinicus* has a range encompassing most of the Philippines (Brown & Alcala 1978; Brown *et al.* 1996, 2000c). This widespread taxon may be expected to harbor numerous undiagnosed species but evaluation of this expectation remains a potentiality. Phylogeographic studies of this widespread taxon should provide an illustrative test of the expectation of PAIC-level structuring of the genetic underpinnings of biodiversity in this complex. Continued analysis of both genetic and morphological data will be necessary to fully resolve the taxonomic status of *C. philippinicus*. In the case of *C. annulatus*, remaining populations referred to this taxon span two PAICs (Visayan and Mindanao geologic platforms) and other small, deep water islands (Siquijor, Camiguin Sur), and might be expected to represent two or more evolutionary lineages (Brown & Diesmos 2002, 2009; Gaulke *et al.* 2007). However, our sequence data suggest that they form a clade with relatively little intraspecific divergence (Table 5) suggesting that a relatively recent set of dispersal events may have given rise to present day distributions (Fig. 1). Thus, we are confident in assigning the Visayan and Mindanao faunal region populations to this widespread, morphologically homogenous single species. We examined specimens from the area surrounding Mt. Malingdang (Zamboanga del Norte Province, western Mindanao; Fig. 1) and scored these for the diagnostic characters distinguishing *C. annulatus* and *C. jambangan*. These specimens, four males (CAS-SU 23500, 23504, 23508, 23511), five females (CAS-SU 23503, 23509–10, 23512, 23514), and nine juveniles (CAS-SU 23501–502, 23505–507, 23513, 23515, 23535–36, all collected 28 April–7 May, 1959) are clearly *C. annulatus* as defined here and in our recent redescription of *C. annulatus* (Welton *et al.* 2009). The possibility that *C. annulatus* and *C. jambangan* may occur in sympatry in the northern portions of the Zamboanga Peninsula (or that their ranges may abut at the base of the peninsula but not substantially overlap) will require further field study for confirmation.

TABLE 5. Uncorrected pairwise sequence divergences (%) within diagonal (bold for emphasis) and between (below diagonal) the members of the *Cyrtodactylus annulatus* (*C. annulatus*, *C. tautbatorum*, and *C. jambangan*, n. sp.) complex and outgroup *C. baluensis*. For simplicity, a single sequence from one specimen of *C. baluensis* was designated as outgroup in the Phylogenetic analysis (Fig. 2) and intraspecific divergences within *C. baluensis* were not calculated. Entries include range (with means \pm 1 S.D. in parentheses).

	<i>C. baluensis</i>	<i>C. tautbatorum</i>	<i>C. jambangan</i>	<i>C. annulatus</i>
<i>C. baluensis</i>	—			
<i>C. tautbatorum</i>	15.4–16.0 (15.7 \pm 0.1)	0.0		
<i>C. jambangan</i>	15.6–16.9 (16.1 \pm 0.1)	11.4–11.8 (11.5 \pm 0.0)	0.1–1.3 (0.8 \pm 0.4)	
<i>C. annulatus</i>	15.0–16.5 (15.7 \pm 0.1)	11.4–12.3 (11.8 \pm 0.0)	7.9–9.5 (8.6 \pm 0.1)	0.1–4.3 (3.2 \pm 0.9)

The total number of *Cyrtodactylus jambangan* specimens consists of 112 individuals from our eight sites in the Zamboanga City area, two sites on Basilan, and two additional collection areas on New Govenen, and Jolo islands. However, we anticipate (based on Taylor 1922a, b) that the new species is present at many additional localities throughout the Sulu Archipelago. Our impression is that the new species is very common at the type locality, and probably not threatened by forest disturbance, especially given the protection

conferred by the Zamboanga City Water District and Pasonanca Natural Park. Taylor (1922a:46) described the new species as “one of the commonest species in the Sulu Archipelago.”

Other gekkonids encountered during our work in southwestern Mindanao include *Gekko gecko*, *Gehyra mutilata*, *Hemidactylus frenatus*, *H. platyurus*, *Hemiphyllodactylus typus*, and *Luperosaurus joloensis*. As mentioned previously, the single Zamboanga record for *Perochirus ateles* (Duméril, 1856; Boulenger, 1885; Taylor 1922a; Brown & Alcala 1978) has never been verified, but can not yet be discounted due to the paucity of recent field work in western Mindanao.

As with many localities throughout the Philippines, the island of Mindanao requires additional survey work before species diversity can be understood with reasonable certainty. Continued faunal surveys are sorely needed on southern and southeastern Mindanao because, at present, a lack of basic biodiversity data greatly hinders conservation efforts.

We encourage field workers to focus on diverse habitat types when surveying for gekkonid diversity in the Philippines. In our experience, gekkonids often have highly specific microhabitat preferences. In addition to forests, non-forested areas, and riparian corridors (in lowland and montane regions), field workers should target limestone forests and caves (Tri *et al.* 2008). These habitats are patchily distributed and, as such, promote evolutionary divergence (Brown & Alcala 2000; Roesler *et al.* 2006; Siler *et al.* 2007, 2009). Karsts are also increasingly under threat from overexploitation by humans (Clements *et al.* 2006). We are aware of at least one additional karst gekkonid species in the Philippines presently awaiting description (Linkem *et al.* in press).

Finally, the large islands of Mindanao, Palawan, and Luzon possess distinct upland geological components (isolated mountain ranges) now separated by low elevation. We expect that more comprehensive herpetological surveys of the large islands of the Philippines will show fine-scale differentiation and the presence of numerous montane endemic species (Brown *et al.* 2000a,b, 2007, 2008, in press b).

Acknowledgments

For the loans of specimens we thank A. Resetar (FMNH), J. Vindum (CAS), J. Rosado (MCZ), and T. LaDuc (TNHC; museum abbreviations follow Leviton *et al.* 1985). Support for fieldwork was provided by the University of Kansas and the National Science Foundation (DEB 0743491 to RMB). We thank the Protected Areas and Wildlife Bureau of the Department of the Environment and Natural Resources (DENR) for facilitating research and export permits for this and related studies. We also thank J. Fernandez, V. and M. Yngente, and J. Phenix for assistance in the field and Municipal and Provincial DENR authorities of Zamboanga City for assistance with permits and facilitating our work in Zamboanga. We greatly appreciate the support of Pasonanca Natural Park and Zamboanga City Water District management for their tremendous logistical support. Special thanks are due to Pasonanca Protected Area Superintendent M. Delacruz, Chief Zamboanga City Water District engineer A. Braulio, and DENR Natural Resource Officers L. Narag, and E. Toribio for assisting in all aspects of our survey work in Pasonanca.

References

- Batuwita, S. & Bahir, M.M. (2005) Description of five new species of *Cyrtodactylus* (Reptilia: Gekkonidae) from Sri Lanka. *Raffles Bulletin of Zoology*, 12, 351–380.
- Bauer, A.M. (2003) Description of seven new *Cyrtodactylus* (Squamata: Gekkonidae) with a key to the species of Myanmar. *Proceedings of the California Academy of Sciences*, 54, 463–498.
- Boulenger, G.A. (1885) *Catalogue of the Lizards in the British Museum (Natural History)*. Second edition. Vol. I. *Geckonidae, Eublepharidae, Uroplatidae, Pygopodidae, Agamidae*. British Museum (Natural History), London, England, 436 pp
- Brown, R.M. (1999) New species of parachute gecko (Squamata; Gekkonidae; Genus *Ptychozoon*) from northeastern Thailand and Central Vietnam. *Copeia*, 1999, 990–1001.
- Brown, R.M. & Alcala, A.C. (2000) Geckos, cave frogs, and small land-bridge islands in the Visayan sea. *Haring Ibon*,

- Brown, R.M. & Diesmos, A.C. (2001 [2002]) Application of lineage-based species concepts to oceanic island frog populations: the effects of differing taxonomic philosophies on the estimation of Philippine biodiversity. *The Silliman Journal*, 42, 133–162.
- Brown, R.M. & Diesmos, A.C. (2009) Philippines, Biology. In: Gillespie, R. & Clague, D. (Eds.). *Encyclopedia of Islands*, University of California Press, Berkeley, California, pp. 723–732.
- Brown, R.M., Diesmos, A.C. & Alcala, A.C. (2001 [2002]) The state of philippine herpetology and the challenges for the next decade. *The Silliman Journal*, 42, 18–87.
- Brown, R.M., Diesmos, A.C. & Duya, M.V. (2007) A new *Luperosaurus* (Squamata: Gekkonidae) from the Sierra Madre of Luzon Island, Philippines. *Raffles Bulletin of Zoology*, 55, 167–174.
- Brown, R.M., Diesmos, A.C., Duya, M.V. Garcia, H.J.D. & Rico, E.L. (In press b) A new forest gecko (Squamata; Gekkonidae; Genus *Luperosaurus*) from Mt. Mantalingajan, southern Palawan Island, Philippines. *Journal of Herpetology*.
- Brown, R.M., Ferner, J.W. & Diesmos, A.C. (1997) Definition of the Philippine Parachute Gecko, *Ptychozoon intermedium* Taylor 1915 (Reptilia: Lacertilia: Gekkonidae): redescription, designation of a neotype, and comparisons with related species. *Herpetologica*, 53, 357–373.
- Brown, R.M., Ferner, J.W., Sison, R.V., Gonzales, P.C., & Kennedy, R.S. 1996. Amphibians and reptiles of the Zambales Mountains of Luzon Island, Republic of the Philippines. *Herpetological Natural History*, 4, 1–22.
- Brown, R.M. & Guttman, S.I. (2002) Phylogenetic systematics of the *Rana signata* complex of Philippine and Bornean stream frogs: reconsideration Huxley's modification of Wallace's Line at the Oriental-Australian faunal zone interface. *Biological Journal of the Linnean Society*, 76, 393–461.
- Brown, R.M., McGuire, J.A. & Diesmos, A.C. (2000a) Status of some Philippine frogs related to *Rana everetti* (Anura: Ranidae), description of a new species, and resurrection of *Rana igorota* (Taylor 1922). *Herpetologica*, 56, 81–104.
- Brown, R.M., McGuire, J.A. Ferner, J.W. Icarangal, N. & Kennedy, R.S. (2000c) Amphibians and reptiles of Luzon Island, II: Preliminary report on the herpetofauna of Aurora Memorial National Park, Philippines. *Hamadryad*, 25, 175–195.
- Brown, R.M., Oliveros, C. Siler, C.D. & Diesmos, A.C. (2008) A new *Gekko* from the Babuyan Islands, northern Philippines. *Herpetologica*, 64, 305–320.
- Brown, R.M., Oliveros, C. Siler, C.D. & Diesmos, A.C. (2009) Phylogeny of *Gekko* from the northern Philippines, and description of a new species from Calayan Island. *Journal of Herpetology*, 43, 620–635.
- Brown, R.M., Supriatna, J. & Ota, H. (2000b) Discovery of a new species of *Luperosaurus* (Squamata; Gekkonidae) from Sulawesi, with a phylogenetic analysis of the genus and comments on the status of *L. serraticaudus*. *Copeia*, 2000, 191–209.
- Brown, W.C. & Alcala, A.C. (1978) Philippine Lizards of the Family Gekkonidae. *Silliman University Press*, Dumaguete City, pp. 1–146.
- Clements, R., Sodhi, N., Schilthuizen, N. & Ng, P.K.L. (2006) Limestone karsts of Southeast Asia: Imperiled arks of biodiversity. *Bioscience*, 56, 733–742.
- de Queiroz, K. (1998) The general lineage concept of species, species criteria, and the process of speciation. In: Howard, D.J. & Berlocher, S.H. (Eds.), *Endless Forms: Species and Speciation*. Oxford University Press, New York, New York, U.S.A., pp. 57–75.
- de Queiroz, K. (1999) The general lineage concept of species and the defining properties of the species category. In: Wilson, R.A. (Ed.), *Species: New Interdisciplinary Essays*. Massachusetts Institute of Technology Press, Cambridge, Massachusetts, U.S.A., pp. 49–89.
- Duméril, A.H.A. (1856) Description des reptiles nouveaux ou imparfaitement connus de la collection du Muséum d'Histoire Naturelle et remarques sur la classification et les caractères des reptiles. *Archives du Muséum Histoire Natural, Paris*, 8, 438–588.
- Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32, 1792–1797.
- Evans, B.J., Brown, R.M. McGuire, J.A., Supriatna, J. Andayani, N., Diesmos, A.C., Iskandar, D., Melnick, D.J. & Cannatella, D.C. (2003) Phylogenetics of Fanged Frogs: Testing Biogeographical Hypotheses at the Interface of Asian and Australian Faunal Zones. *Systematic Biology*, 52, 794–819.
- Esselstyn, J.A., Garcia, H.J.D., Saulog, M.G. & Heaney, L.R. (2008) A new species of *Desmalopex* (Pteropodidae) from the Philippines, with a phylogenetic analysis of the Pteropodini. *Journal of Mammalogy*, 89, 815–825.
- Gaulke, M., Roesler, H. & Brown, R.M. (2007) A new species of *Luperosaurus* (Squamata: Gekkonidae) from Panay Island, Philippines, with comments on the taxonomic status of *Luperosaurus cumingii* (Gray, 1845). *Copeia*, 2007, 413–425.
- Grismer, L.L. (2005) New species of bent-toed gecko (*Cyrtodactylus* Gray 1827) from Pulau Aur, Johor, West Malaysia. *Journal of Herpetology*, 39, 424–432.
- Grismer, L.L., Onn, C.K., Grismer, J.L., Wood, P.L. & Belabut, D. (2008) Three new species of *Cyrtodactylus*

- (Squamata: Gekkonidae) from Peninsular Malaysia. *Zootaxa*, 1921, 1–23.
- Grismer, L.L., & Ahmad, N. (2008) A new insular species of *Cyrtodactylus* (Squamata: Gekkonidae) from the Langkawi Archipelago, Kedah, Peninsular Malaysia. *Zootaxa*, 1924, 53–68.
- Grismer, L.L. & Leong, T.M. (2005) New Species of *Cyrtodactylus* (Squamata: Gekkonidae) from southern Peninsular Malaysia. *Journal of Herpetology*, 39, 584–591.
- Hayden, C.J., Brown, R.M., Gillespie, G., Setiadi, M.I., Linkem, C.W., Iskandar, D.T., Umilaela, Bickford, D.P., Riyanto, A., Mumpuni & McGuire, J.A. (2008) A new species of bent-toed gecko *Cyrtodactylus* Gray, 1827, (Squamata: Gekkonidae) from the island of Sulawesi, Indonesia. *Herpetologica*, 64, 109–120.
- Kraus, F. (2008) Taxonomic partitioning of *Cyrtodactylus louisiadensis* (Lacertilia: Gekkonidae) from Papua New Guinea. *Zootaxa*, 1883, 1–27.
- Leviton, A.E., Gibbs, Jr., R.H., Heal, E. & Dawson, C.E. (1985) Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia*, 1985, 802–821.
- Linkem, C.W., McGuire, J.A., Hayden, C.J., Setiadi, M.I., Bickford, D.P. & Brown, R.M. (2008) A new species of bent-toe gecko (Gekkonidae: *Cyrtodactylus*) from Sulawesi Island, Eastern Indonesia. *Herpetologica*, 64, 232–242.
- Linkem, C.W., C.D Siler, A.C. Diesmos & Brown, R.M. (In press) A new species of *Gekko* (Squamata: Gekkonidae) from central Luzon Island, Philippines. *Zootaxa*.
- Macey, J.R., Wang, Y., Ananjeva, N.B., Larson, A. & Papenfuss, T.J. (1999) Vicariant patterns of fragmentation among Gekkonid lizards of the genus *Teratoscincus* produced by the Indian collision: A molecular phylogenetic perspective and an area cladogram for central Asia. *Molecular Phylogenetics and Evolution*, 12, 320–332.
- Maddison, D.R. & Maddison, W.P. (2005) *MacClade: analysis of phylogeny and character evolution*. Vers. 4.08. Sinauer, Sunderland, Massachusetts, 223 pp.
- Manthey, U. & Grossman, W. (1997) *Amphibien und Reptilien sudostasiens*. Natur und Tier-Verlag, Berlin, Germany, 512 pp.
- Ota, H. & Crombie, R.I. (1989) A new lizard of the genus *Lepidodactylus* (Reptilia: Gekkonidae) from Batan Island, Philippines. *Proceedings of the Biological Society of Washington*, 102, 559–567.
- Ota, H. Lue, K.-Y., Chen, S.-H. & Brown, W.C. (1989) Taxonomic status of the Taiwanese *Gekko*, with comments on the synonymy of *Luperosaurus amissus* (Taylor). *Journal of Herpetology*, 23, 76–78.
- Posada, D. & Crandall, K.A. (1998) Modeltest: testing the model of DNA substitution. *Bioinformatics*, 14, 817–818.
- Rambaut, A. & Drummond, A.J. (2007) Tracer v1.4. Available from <http://beast.bio.ed.ac.uk/Tracer>.
- Roesler, H., Siler, C.D., Brown, R.M., Demegillo, A.D. & Gaulke, M. (2006) *Gekko ernstkelleri* sp. n.—a new gekkonid lizard from Panay Island, Philippines. *Salamandra*, 42, 197–211.
- Ronquist, F. & Huelsenbeck, J.P. (2003) MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19, 1572–1574.
- Siler, C.D., Linkem, C.W., Diesmos, A.C. & Alcala, A.C. (2007) New Species of the genus *Platymantis* (Amphibia; Anura; Ranidae) from Panay Island, Philippines. *Herpetologica*, 63, 351–36.
- Siler, C.D., Diesmos, A.C., Alcala, A.C. & Brown, R.M. (2009) A new species of limestone forest frogs, genus *Platymantis* (Amphibia; Anura; Ceratobatrachidae) from Samar Island, Philippines. *Herpetologica*, 65, 92–105.
- Siler, C.D., Oaks, J.R., Esselstyn, J.A., Diesmos, A.C. & Brown, R.M. (In press) Phylogeny and biogeography of Philippine bent-toed geckos (Gekkonidae: *Cyrtodactylus*) contradict a prevailing model of Pleistocene diversification. *Molecular Phylogenetics and Evolution*.
- Simpson, G.G. (1961) *Principles of animal taxonomy*. Columbia University Press, New York, New York, U.S.A, 290 pp.
- Stamatakis, A. (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22, 2688–2690.
- Swofford, D.L. (2002) PAUP*. *Phylogenetic analysis using parsimony (*and other methods)*. Ver 4.0. Sinauer Associates, Sunderland, MA.
- Taylor, E.H. (1922a) *The lizards of the Philippine Islands*. Philippine Bureau of Science, Manila, Philippines, 269 pp.
- Taylor, E.H. (1922b) Additions to the herpetological fauna of the Philippine Islands, I. *Philippine Journal of Science*, 21, 161–206.
- TIGR Reptile database (2009) <http://www.reptile-database.org/>. (Accessed August 2009).
- Tri, N.V., Grismer, L.L. & Grismer, J.L. (2008) A new endemic cave dwelling species of *Cyrtodactylus* Gray, 1827 (Squamata: Gekkonidae) in Kien Giang Biosphere Reserve, Southwestern Vietnam. *Zootaxa*, 1967, 53–62.
- Welton, L.J., Siler, C.D., Diesmos, A.C. & Brown, R.M. (2009) A new bent-toed Gekko (Genus *Cyrtodactylus*) from southern Palawan Island, Philippines and clarification of the taxonomic status of *C. annulatus*. *Herpetologica*, 65:328–343.
- Wiley, E.O. (1978) The evolutionary species concept reconsidered. *Systematic Zoology*, 21, 17–26.
- Yumul, G., Dimalanta, C., Queaño, K & Marquez, E. (2009) Philippines, geology. *Encyclopedia of Islands* (ed. by R. Gillespie & D. Calgue), Pp. 732–738. University of California Press, Berkeley.

Specimens examined

All specimens except *Cyrtodactylus baluensis* are from The Philippines.

Cyrtodactylus annulatus (65 specimens): Cebu Island, Cebu Province, Minglanilla area Dipterocarp forest: CAS SUR 139048; Taptap Barrio, Cebu City: CAS SUR 142063; 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; 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; Bohol Island, Bohol Province, Municipality of Camern, Barangay Riverside: TNHC 56467.

Cyrtodactylus agusanensis (7 specimens): Dinagat Island, Surigao del Norte Province, Loreto, Barangay Esparanza: KU 305564–65; Mindanao Island, Agusan del Norte Province, Tagibo River, S. side of Mt. Hilonghilong: CAS SUR 133424–26; Tagibo & Dayadian RVS, S. side Mt. Hilonghilong: CAS SUR 133506; Samar Island, Eastern Samar Province, Taft, Barangay San Rafael, Taft Forest: KU 305566.

Cyrtodactylus baluensis (7 specimens): Malaysia, Borneo Island, Sabah Province, Lahad Datu District: FMNH 246203, 246205, 230090, and 246204; Tenom District: FMNH 243734, and 243746; Mt. Kinabalu: SP 6891.

Cyrtodactylus tautbatorum (Welton et al. 2009) (16 specimens): Palawan Island, Palawan Province, Municipality of Brooke's Point, Barangay Mainit, Mainit Falls: PNM 9507–14, KU 309318–25.

Cyrtodactylus philippinicus (29 specimens): Bohol Island, Bohol Province, Municipality of Baler, just outside Raja Sikatuna National Park: PNM 9544; Luzon Island, Albay Province, Mt. Malinao: PNM 9548–51; Quezon Province, Quezon National Park: PNM 9553–54, and KU 307452; Zambales Province, Ilanin Forest, "Nav-Mag" area, SBMA Naval Base: PNM 9555; Luzon Island, Camarines del Sur Province, Naga: KU 305571; Sorsogon Province, Municipality of Irosin, Barangay San Roque, ridge above Bulusan Lake, Mt. Bulusan: PNM 9552; Mindoro Island, Occidental Mindoro Province, Sablayan, Barangay Batong Buhay Batulai, Mt. Siburan: KU 303866, 303870, 303873–75, 303879, 303881–83, 303886, 303888–89, 303892–94, 303898; Negros Island, Oriental Negros Province, Mt. Talinis: PNM 9547; Sibuyan Island, Romblon Province, edge of Guiting-guiting National Park: PNM 9545.

Cyrtodactylus jambangan: See holotype and paratypes section.