Taxonomic Revision of Scaly-toed Geckos (Reptilia: Gekkonidae: Lepidodactylus) in the Northern Philippines, with Descriptions of Four New Species

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Abstract: Recent higher level phylogenetic analyses of gekkonid lizards of the genus *Lepidodactylus* uncovered an array of unrecognized species diversity, particularly within the Philippine archipelago. Novel phylogenetic analyses of multilocus data sets suggest that as many as five, previously undescribed, species-level lineages of Scaly-toed Geckos occur in just the northern portions of the archipelago. Here, we evaluate *Lepidodactylus* species diversity in the *Lepidodactylus yami–balioburius* clade and describe four new forest species from Luzon Island and surrounding minor island groups. Interestingly, these species are the first endemic *Lepidodactylus* taxa described from Luzon proper and peripheral islands. In this first review of Philippine Scaly-toed Gecko diversity in nearly half a century, we use a suite of morphological characters along with molecular data to delimit evolutionary lineages. All species described in this paper can be distinguished from congeners by an array of discrete external traits; all are also monophyletic groups, separated in our phylogenetic analyses of the mitochondrial ND2 gene. This study increases significantly the number of known Scaly-toed Geckos in the Philippines from 7 to 11, which is likely still an underestimate of the species diversity in this understudied clade.

Key words: Biodiversity; Endemism; Luzon; Philippines; Species delimitation; Taxonomy

The striking diversity of gecko species found in the Philippines has been the subject of increased attention over the past decade (Brown et al. 2008, 2009, 2011a,b, 2020; Welton et al. 2009, 2010a,b; Linkem et al. 2010; Siler et al. 2014a, 2016a, 2017; Davis et al. 2015). Of the 58 gekkonid species now recognized from this Southeast Asian country, 18 have been described since 2009 (Uetz et al. 2020). Most recent phylogenetic studies have focused largely on three genera: *Cyrtodactylus* (Welton et al. 2009, 2010a,b), *Gekko* (Brown et al. 2008, 2009, 2011a; Linkem et al. 2010), and *Pseudogekko* (Siler et al. 2014a, 2016a, 2017; Davis et al. 2015; Brown et al. 2020), whereas the diversity within a number of other gekkonid genera in the Philippines (i.e., *Hemiphyllodactylus* and *Luperosaurus*) remains poorly understood (Brown et al. 2007, 2011b, 2012a; Grismer et al. 2013; Siler et al. 2014a). The genus *Lepidodactylus* Fitzinger 1843 is one such example of a group that has received limited taxonomic attention in the Philippines in recent years; the last comprehensive taxonomic revision was over 40 yr ago (Brown and Alcala 1978). Recently, molecular phylogenetic studies have concluded that *Lepidodactylus* is closely allied with other Philippine gekkonid genera including *Gekko, Luperosaurus, Pseudogekko,* and *Ptychozoon;* all have even highlighted the paraphyletic nature of the genus with respect to the sister genera *Luperosaurus* and *Pseudogekko,* which are deeply embedded within *Lepidodactylus* (Brown et al. 2012a; Heinicke et al. 2012). However, a taxonomic reappraisal of *Lepidodactylus* species diversity in the Philippines is still lacking. Seven *Lepidodactylus* species are recognized from the archipelago with the most recent addition, *L. balioburius,* having been described 30 yr ago (Duméril and Bibron 1836; Peters 1867; Stejneger 1905; Taylor 1915, 1917, 1923; Brown and Alcala 1978; Ota and Crombie 1989).

Scaly-toed Geckos of the genus *Lepidodactylus* are small-bodied species found across Southeast Asia and Oceania. Most species appear to have limited ranges along coastal habitats (Brown and Parker 1977; Brown and Alcala 1978; Bauer and Henle 1994), except for the wide-ranging *L. lugubris,* which, presumably as a result of its parthenogenetic reproductive mode, is thought to be native throughout most of insular Southeast Asia and the Pacific (Ota et al. 1995; Radtkey et al. 1995). With 41 species of *Lepidodactylus* recognized to date, the genus represents a diverse array of gekkonid species and the Philippines in particular, with 6 endemic species (*L. aureolineatus, L. balioburius, L. christiani, L. herrei, L. labialis,* and *L. planicaudus*), and the widespread Southeast Asian taxon *L. lugubris* present, is home to one of the most varied assemblages of Scaly-toed Geckos in the world (Brown and Parker 1977; Brown and Alcala 1978; Ota and Crombie 1989; Uetz et al. 2020). Interestingly, nearly all species described to date occur in central or southern faunal regions or Pleistocene Aggerate Island Complexes of the island archipelago (PAICs; Brown and Guttman 2002; Brown et al. 2013), including Mindanao, Mindoro, and West Visayan PAICs (Brown and Parker 1977; Brown and Alcala 1978). The only exception to this is *L. balioburius* from the Batanes Island Group in the extreme northern extent of the country (Ota and Crombie 1989). Despite being the largest island in the Philippine archipelago, no species have been described from Luzon proper to date.

Over the past 15 yr, our collaborative herpetofaunal surveys across the Philippines (Brown et al. 2013) have resulted in the gradual acquisition of *Lepidodactylus* specimens from the central and northern regions of the archipelago, including across Luzon Island. Assignment of

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such individuals to known species has proven difficult because of the morphologically conserved nature of taxa within the genus. Historical recognition of taxa based on morphological characters exclusively (Brown and Parker 1977; Brown and Alcala 1978) has led to some confusion between specimens placed in *Lepidodactylus* and the closely related genus *Pseudogekko* (Kluge 1968; Brown and Alcala 1978; Siler et al. 2014a). To prevent further taxonomic inconsistencies, all *Lepidodactylus* specimens collected within the past 15 yr have been assigned to *L.* cf. *lugubris* pending in-depth morphological and phylogenetic examination.

More recently, phylogenetic studies of Old World geckos have started to shed light on species-level relationships within *Lepidodactylus* as well as how the genus fits into the larger gekkonid tree of life (Radtkey et al. 1995; Heinicke et al. 2012; Oliver et al. 2018). As of 25 yr ago, the first phylogenetic analysis inclusive of Philippine Scaly-toed Geckos provided support for the validity of *L. aureolineatus, L. herrei,* and *L. christiani* as distinct evolutionary lineages (Radtkey et al. 1995). Heinicke et al. (2012) included a single Philippine *L. lugubris* specimen collected in the Philippines in phylogenetic analyses focused on evolutionary relationships among multiple Asian gecko genera and found support for the widespread nature of this species.

Interestingly, it was not until a few years ago that Oliver et al. (2018) provided a comprehensive phylogeny including many of the recognized Philippine *Lepidodactylus* lineages. Although this most recent study omitted *L. labialis* because of a lack of genetic material, all other endemic *Lepidodactylus* species as well as a widespread sampling of *L. lugubris* were included. Despite the study's focus on higher level relationships and biogeographic history of the genus, the results highlighted that as many as six new, undescribed species may persist within the Philippines. Surprisingly, five of these divergent lineages are from the Luzon PAIC and were recovered as part of a clade with *L. balioburius* (Oliver et al. 2018) and *L. yami* from Lanyu Island, Taiwan, herein referred to as the *L. balioburius–yami* clade.

In this study, we examine all newly available vouchered specimens and genetic samples in natural history collections to evaluate and revise the *L. balioburius–yami* clade in the Philippines. We employ morphological, molecular, and geographic data sets available for all Philippine *Lepidodactylus* specimens associated with the focal clade to describe four new species from Luzon Island, Lubang Island, and the Babuyan Island Group in the northern Philippines. In doing so, we provide the first in-depth investigation of the genus *Lepidodactylus* in the Philippines in almost 50 yr and increase the country's diversity of Scaly-toed Geckos by more than one-half. In contrast to past characterizations of the northern Philippines as a region without an endemic *Lepidodactylus* fauna (Brown and Alcala 1978), we demonstrate that this biogeographic province of the Philippines is home to a diverse, poorly studied, highly distinct, endemic in situ radiation—composed of secretive forest species that may be imperiled by habitat destruction.

TAXONOMIC HISTORY

Historical Taxonomic Classifications

Lepidodactylus lugubris was first described by Duméril and Bibron (1836) as *Platydactylus lugubris* from Tahiti, Polynesia based on two female specimens. Shortly thereafter, Fitzinger (1843) described the monotypic genus *Lepidodactylus* for *L. lugubris* where the species remained until it was reassigned to *Amydosaurus lugubris* by Gray (1845) and the novel genus was sunk temporarily. The species was moved back to the genus *Platydactylus* by Cantor (1847) after examining a single *Lepidodactylus* male collected from the valley of Pinang, Malaysia. After another 20 yr, Steindachner (1867) reassigned this species again from *Platydactylus* to *Gecko*.

That same year, Peters (1867) first mentioned what are now recognized as Scaly-toed Geckos in the Philippines in describing *Gecko labialis* from Mindanao Island based on a single individual. Peters noted that the individual appeared closely related to *G. lugubris* from Tahiti (Peters 1867). The genus *Lepidodactylus* was resurrected in 1879 when *Platydactylus crepuscularis* was moved to *L. crepuscularis* in a report on geckos of New Caledonia (Sauvage 1879) and the genus expanded quickly thereafter. In an inventory of reptiles at the British Museum, Boulenger (1885) recognized the first Philippine *Lepidodactylus* when he moved both *Gecko labialis* and *Gecko lugubris* to the genus *Lepidodactylus*. At the time, only *L. labialis* was recognized from the Philippines—*L. lugubris* was not documented officially in the country for another 45 yr.

Lepidodactylus brevipes (Boettger 1897) from Samar Island and *L. planicaudus* Stejneger 1905 from Mt. Apo, Mindanao Island, were both described from single specimens based on morphological distinction from known congeners and increased the number of Philippine *Lepidodactylus* to three around the turn of the 20th century.

In the early 1900s, E.H. Taylor described several additional *Lepidodactylus* species in the Philippines, including *L. aureolineatus* Taylor 1915 from Bunauan, Mindanao Island, *L. christiani* Taylor 1917 from Mt. Kanlaon, Negros Island, *L. divergens* Taylor 1918 from Little Govenen Island, and *L. naujanensis* Taylor 1919 from Lake Naujan, Mindoro Island. Additionally, Taylor (1918) referenced a series of 17 specimens from Mindoro, Cancuman, Dipolod, Marongas, and Bubuan islands as the Solomon Island species *L. woodfordi* Boulenger 1887 because of a lack of morphological differences between those specimens and the traits listed as belonging to *L. woodfordi*.

Taylor (1922) provided the first comprehensive examination of Philippine gekkonids and in this work he recognized eight species of *Lepidodactylus* at the time: *L. aureolineatus, L. brevipes, L. christiani, L. divergens, L. labialis, L. naujanensis, L. planicaudus,* and *L. woodfordi.* The following year he described *L. herrei* Taylor 1923 based on a single specimen from Luzurriaga, Negros Province, that was described as being closely related to *L. aureolineatus,* although different in having an apparently larger body size. Following this rise in descriptions of Scaly-toed Geckos by Taylor in the 1910s and 1920s, no new species of Philippine *Lepidodactylus* were described for over 60 yr. Most work regarding the genus in the archipelago throughout the mid-20th century revolved around the validation of the nine species recognized by Taylor based on morphological features.

Specimens of *L. aureolineatus* and *L. divergens* collected by Taylor originally were re-examined by Smith (1935) and both species were collapsed into *L. lugubris* because Smith

could not find a series of morphological characters by which to separate them from *L. lugubris*. As such, *L. lugubris* was considered present in the Philippines as of 1935 (Smith 1935). Another 30 yr passed with no mention of *Lepidodactylus* in the Philippines before a checklist of amphibians and reptiles was released by Wermuth (1965) that agreed with these placements and recognized *L. lugubris* as a wide-ranging species in the Philippines.

Kluge (1968) reviewed the genus shortly after the release of this checklist and agreed with *L. divergens* being synonymous to *L. lugubris* but resurrected *L. aureolineatus* as a distinct lineage, citing that it was sufficiently distinct from *L. lugubris* to warrant its own species. The author went further and placed *L. christiani* as a species inquirenda and transferred *L. brevipes* to the genus *Pseudogekko*. Six species from the Philippines were retained by the end of the 1960s, including *L. aureolineatus, L. herrei, L. lugubris, L. naujanensis, L. planicaudus,* and *L. woodfordi*.

In the second exhaustive systematic review of Philippine gekkonids following Taylor's work in 1922, Brown and Alcala (1978) recognized four endemic species of *Lepidodactylus*—*L. aureolineatus, L. christiani, L. herrei,* and *L. planicaudus*—as well as the widespread (nonendemic) *L. lugubris*. In this review, *Lepidodactylus naujanensis* was collapsed into *L. planicaudus* on the grounds of no morphological distinction between the two species and the presence of another distinct endemic species (*L. woodfordi*) in the Philippines was considered untenable. Brown and Alcala (1978) reassigned Taylor's (1918) series of specimens to *L. lugubris*. In addition to submerging previously recognized species, the authors reported on 30 additional specimens of the poorly understood taxon *L. labialis* and, upon comparison with other *Lepidodactylus* species and *Pseudogekko brevipes*, the authors moved this species to the genus *Pseudogekko*. Brown and Alcala (1978) also named two subspecies of *L. herrei*—*L. h. herrei* and *L. h. medianus*—and asserted that *L. h. medianus* possessed scale counts between *L. h. herrei* and *L. aureolineatus* and occupied a geographic area between these two congeners.

The late 1980s brought about the descriptions of the two most recent northern Philippine (and southern Taiwan) *Lepidodactylus* additions: *L. yami* Ota 1987 from Lanyu Island, Taiwan, and *L. balioburius* from the Batanes Island Group. Although not from the Philippines, Ota (1987) considered *L. yami* to be a potential ancestral form that entered Lanyu Island from the Batanes and, upon the description of *L. balioburius,* the authors concluded that these two species may be closely related, based on shared morphological character states.

The most recent taxonomic revision to *Lepidodactylus* in the Philippines corroborated previously mentioned similarities between *Pseudogekko* and *Lepidodactylus* because Siler et al. (2014a) reverted the classification of *P. labialis* Brown and Alcala (1978), and placed the species back into the genus *Lepidodactylus,* as described originally by Boulenger (1885).

Morphological Groupings

Morphological differentiation has been the primary basis for distinguishing *Lepidodactylus* species in the Philippines for more than 150 yr. Since the first account of *L. labialis* by Peters (1867), characters such as overall body size, digit size, head size, head shape, tail size, tail shape, scansor counts, supralabial and infralabial counts, and body coloration have all been used to separate species (Peters 1867; Stejneger 1905; Taylor 1922, 1923; Brown and Parker 1977; Brown and Alcala 1978).

Brown and Parker (1977) reviewed the entire genus *Lepidodactylus* when they recognized three species groups based primarily on morphological characters (namely scansor morphology). Group I (*L. pulmilis–oorti* group), from western Indonesia, New Guinea, islands in the Torres Straits, the Solomon and Fijian islands in the Pacific, and Christmas Island in the Indian Ocean, was considered the most primitive or *Gekko*-like, and defined as containing only species with undivided toe scansors across the entirety of the toe. Group II (*L. guppyi–pulcher* group), from New Guinea, the Solomon, Admiralty, and Bismarck archipelagos, and Rotuma Island north of Fiji, was defined as species with undivided terminal toe scansors on all digits, but a varying number of divided subterminal scansors. Finally, Group III (*L. lugubris* group) contained *L. lugubris* and all members of the genus endemic to the Philippines. The authors recognized this group as the most derived, with divided terminal and subterminal toe scansors. In addition to scansor morphology, tail shape and the presence or absence of lateral flanges or spines were also described as diagnostic for group identification, with the tails on members of Groups I and II described as subcylindrical with no lateral flanges or spines, compared with flatter and broader tails with lateral flanges observed on members in Group III.

Brown and Alcala (1978) dove further into Group III from Brown and Parker (1977) in the second exhaustive systematic review of Philippine gekkonids following Taylor (1922) and split Group III into two Sections: A and B. These sections are based primarily on scansor morphology again where Section A species exhibited high scansor counts (usually ≥12 scansors) across all digits, scansors covering most of each digit or at least the distal three-fourths of the digit, moderately to broadly dilated digits, webbing only at the base or basal one-fifth to one-fourth between Toes III and IV, and a tail that is slightly to moderately flattened without a broad flange of skin but often with modified, pointed scales on the lateral margin. In contrast, Section B contained species with a lower scansor count (usually <10) across all digits, scansors usually covering the distal half of each digit only, broadly dilated digits, and strongly webbed about one-fourth to one-half between Toes III and IV, and a tail that was usually broad and strongly flattened with a marginal flange of skin. Based on their grouping system, Section A of Group III originally consisted of *L. aureolineatus, L. herrei,* and *L. lugubris* while Section B consisted of *L. planicaudus* and *L. christiani*.

The late 1980s brought about the descriptions of the two newest species in Group III, *L. yami* from Lanyu Island, Taiwan, and *L. balioburius* from the Batanes Island Group. Both species were assigned to Group III, Section A based on morphology though with some reservations in both descriptions (Ota 1987; Ota and Crombie 1989). These two species are most like each other morphologically compared with all other members of Group III, and are so similar that, when describing *L. balioburius,* the authors used a suite of characters in principal component analyses to differentiate it from *L. yami* (Ota 1987; Ota and Crombie 1989).

Phylogenetic Analyses

The first phylogenetic analysis inclusive of Philippine Scaly-toed Geckos supported *Lepidodactylus aureolineatus, L. christiani,* and *L. herrei* as three valid, endemic species in the archipelago (Radtkey et al. 1995). Interestingly, despite inferences based on analyses of the mitochondrial Cytochrome b gene only and limited taxonomic sampling, Radtkey et al.'s (1995) early phylogenetic study also supported some of the same morphological grouping system set forth by Brown and Parker (1977), with *L. guppyi* (Group II species) recovered as the sister lineage to the clade containing *L. lugubris* and three included Philippine species (Group III). Ota et al. (1998) in their description of *L. vanuatuensis* used the same *L. aureolineatus* sequences from Radtkey et al. (1995) and demonstrated marked genetic divergence (p-distance ≈ 25%) between *L. guppyi* and *L. aureolineatus* for Cytochrome b, providing additional justification for the groups proposed by Brown and Parker (1977).

More recent studies including a greater diversity of Philippine gecko species have started to provide more resolution among relationships within *Lepidodactylus* as well as among other native genera (Heinicke et al. 2012; Siler et al. 2014b; Oliver et al. 2018; Wood et al. 2020). Heinicke et al. (2012) first recovered *Lepidodactylus* as a paraphyletic group inclusive of the genera *Pseudogekko* and *Luperosaurus*. More recently, Oliver et al. (2018) presented similar evidence of paraphyly within *Lepidodactylus,* sensu lato, through a robust phylogenetic analysis of six Philippine *Lepidodactylus* species and a host of other Southeast Asian gekkonids. Two clades are supported within Scaly-toed Geckos of the Philippines: (1) the *L. lugubris* clade, containing *L. lugubris, L. aureolineatus, L. herrei* (*L. h. herrei* and *L. h. medianus*), *L. planicaudus,* and an undescribed lineage referred to as *L.* sp. 5 from Zamboanga; and, (2) the *L. balioburius–yami* clade, containing *L. balioburius, L. yami, L. christiani,* and five putative new lineages from the central and northern Philippines (Oliver et al. 2018). With the exception of the inferred phylogenetic placement of *L. planicaudus,* species groups defined by Brown and Alcala (1978).

MATERIALS AND METHODS

Field Work, Sample Collection, and Specimen Preservation

We conducted fieldwork on Babuyan Claro, Batan, Bohol, Calayan, Camiguin Norte, Dalupiri, Leyte, Luzon, Mindanao, Negros, Polillo, and Sabtang islands in the Philippines. We collected specimens between 1600 and 0200 h and euthanized them via cardiac injection of nembutal or immersion in aqueous chloretone. We dissected specimens for genetic samples (liver or muscle preserved in 95% ethanol or flash frozen in liquid nitrogen), fixed them in 10% buffered formalin, and eventually transferred them to 70% ethanol. For all locality records, we used the WGS84 datum. We used the museum acronyms of Sabaj (2016).

Morphological Data

We examined 196 fluid-preserved specimens for meristic, mensural, and qualitative characters using previous taxonomic revisions by Taylor (1922) and Brown and Alcala (1978) as well as phylogenetic results from Oliver et al. (2018) to guide our identification of recognized species versus novel lineages of *Lepidodactylus* (see Appendix). Sex was determined via the presence of precloacal–precloacofemoral pores and/or by gonadal inspection. For the purposes of mensural comparisons, we used sexually mature adults only. A 20% cutoff below max snout–vent length (SVL) was used to determine sexual maturity in each lineage. SJE took all measurements to the nearest 0.1 mm with Fowler Sylvac S 235 digital calipers.

We scored all characters on the left side of the body unless otherwise noted. Characters examined were based on features used in previous *Lepidodactylus* and Southeast Asian gekkonid literature (Taylor 1922; Brown and Alcala 1978; Ota 1987; Ota and Crombie 1989; Grismer et al. 2013; Siler et al. 2014a; Eliades et al. 2019). We used a slash (/) to separate counts on the left from those on the right side of the same specimen. We used a dash for ranges of counts among specimens. Mensural characters measured include snout–vent length (SVL, distance from tip of snout to vent); axilla–groin distance (distance between posterior edge of arm insertion and anterior edge of leg insertion); tail length (distance from posterior margin of vent to tip of tail); tail width (measured at widest section of tail posterior to hemipene bulge if present); tail depth (measured from ventral to dorsal surface of tail at the same point as tail width); snout–forearm length (distance from posterior edge of arm to a point in line with the snout tip); upper arm length (measured from arm insertion point to the elbow); forearm length (measured from elbow to base of palmar surface); arm length (sum of upper arm length and forearm length); thigh length; crus length (tibia length); leg length (sum of thigh length and crus length); Finger III length (measured from base of digit to end of digit exclusive of claw); Toe IV length (measured from base of digit to end of digit exclusive of claw); head length (from tip of snout to posterior tip of mandible); head width (widest measure of head width at middle of jaw articulations); head height (measured from ventral to dorsal surface of head at jaw articulations); eye–ear distance (from the anterior edge of auricular opening [external auditory meatus] to posterior edge of orbit); eye–nostril distance (distance from anterior margin of eye to posterior margin of nostril); snout length (distance from anterior border of orbit to tip of snout); interorbital distance (distance between midline of orbits from dorsal aspect); internarial distance (from dorsal aspect between most lateral edges of nares); ear diameter (measured at widest diameter of the auricular opening); and eye diameter (at widest point).

Meristic characters counted include midbody dorsal scales (number of scales running transversely across the midbody on the dorsal surface within one eye diameter), midbody ventral scales (scales running transversely across the midbody on the ventral surface within one eye diameter), paravertebral scales (scales running longitudinally along the midbody on the dorsal surface within one eye diameter), and ventral scales (scales running longitudinally along the midbody on the ventral surface within one eye diameter); supralabials (number of enlarged supralabials, from first supralabial in contact with rostral to posterior most enlarged supralabial retaining distinct, square to rectangular shape); infralabials (number of infralabials posteriorly to the terminus of differentiation); circumorbitals (number of visible, small circumorbital scales encircling the eye); circumnasals (number of distinct scales surrounding the nostril exclusive of the rostral or supralabials); snout scales

(number of scales bordering rostral excluding supralabials and including circumnasals); Finger III total scansors (number of enlarged, total scansor rows [divided and undivided] beneath Finger III, starting just distal to point where skin between digits ends exclusive of ungual scale); Finger III first divided scansor (first row of clearly divided scansors counted from basal end of digit to distal); Finger III last divided scansor (last row of clearly divided scansors along the digit); Finger III total divided scansors (total number of clearly divided scansors on the digit); Toe IV total scansors (number of enlarged, total scansor rows [divided and undivided] beneath Toe IV, starting just distal to point where skin between digits ends exclusive of ungual scale); Toe IV first divided scansor (first row of clearly divided scansors counted from basal end of digit to distal); Toe IV last divided scansor (last row of clearly divided scansors along the digit); Toe IV total divided scansors (total number of clearly divided scansors on the digit); precloacofemoral scales bearing pores (number of differentiated, enlarged, pore-bearing scales in series anterior to the cloaca and, in some specimens, extending onto femoral regions); enlarged precloacofemoral scales without pores (total number of differentiated, enlarged, scales in series anterior to the cloaca and, in some specimens, extending onto femoral regions); and cloacal spurs (total number of enlarged scales on lateral sides of the base of tail).

Qualitative features examined include pore series continuity (continuous vs. not); pore series shape (linear, v-shaped, etc.); position of the nostril (contacting the first supralabial, rostral); cleft of the rostral (cleft vs. not); ventral scale shape; degree of webbing between Toes II and III and Toes III and IV (coded from zero to five with zero being no webbing and five being webbing between entirety of digits); and body coloration in preservative and life when photos were available. To maximize utility and comparability of color descriptions, we use color terminology and referenced codes from Köhler (2012).

Morphological Analyses

We tested for sexual dimorphism within each species using Mann–Whitney *U*-tests in R v3.6.2 (R Core Team 2019). For a single species comparison where no nonoverlapping characters were identified, we used a principal component analysis in R to differentiate species in morphospace. We followed this analysis with a series of Mann–Whitney *U*-tests in R examining particular morphological measures to provide statistical backing for noted differences between lineages.

Molecular Data

We extracted genomic DNA from liver samples of five *Lepidodactylus* specimens via high salt extraction (KU 331651, OMNH 46003, OMNH 44645, PNM 9874, PNM 9875). We amplified and sequenced a fragment of mitochondrial (mt) DNA using the Metf6 and CO1H primers from Macey et al. (1999) and PCR protocol from Welton et al. (2010a). Once sequenced, we trimmed the amplified region to 1038 bp to encompass the NADH dehydrogenase subunit 2 (ND2) gene coding region only. Resulting sequences were deposited in GenBank (Accession Numbers: MW234407–11).

Phylogenetic Analyses

We used 61 additional gekkonid ND2 sequences from Oliver et al. (2018) representing 6 described Philippine *Lepidodactylus* species, all putative lineages suggested in Oliver et al. (2018), and sequences from *Pseudogekko brevipes, Lepidodactylus guppyi,* and *Gekko mindorensis* as outgroups following higher level phylogenetic studies of gekkonid diversity (Heinicke et al. 2012; Siler et al. 2014b; Oliver et al. 2018). We trimmed all 65 total sequences to the same 1038-bp sequence length and aligned all sequences using default parameters in MUSCLE (Edgar 2004). To identify the best-fitting model of sequence evolution for each codon position of the ND2 gene we used Akaike's information criterion (AIC) in jModelTest v2.1.10 (Posada 2008). The model GTR + Γ was selected for each codon position. We used MrBayes v3.2.6 (Ronquist et al. 2012) on the Cyberinfrastructure for Phylogenetic Research (CIPRES) Science Gateway v3.3 (Miller et al. 2010) to perform partitioned Bayesian phylogenetic analyses. Two independent runs were performed for 30 million generations, both with 4 chains and default priors and a chain temperature set to 0.2. Trees were sampled every 3000 generations and the first 25% of trees were discarded as burn-in. We viewed the resulting trace plots using Tracer v1.6 (Rambaut et al. 2014) to confirm stationarity. Nodes with posterior probabilities $\geq$0.95 we considered to have strong statistical support (Erixon et al. 2003). To support the Bayesian phylogenetic approach, we also used the Poisson Tree Processes (PTP) model to generate an additional tree modeling potential species delimitation (Zhang et al. 2013). This tree was generated using default parameters with outgroups removed. We calculated uncorrected pairwise distances (p-distance) using PAUP* v4.0a (Swofford 2002).

Species Concept

Like many recent taxonomic revisions of gekkonids in the Philippines (see Siler et al. 2014a), we recognize the General Lineage Concept (de Queiroz 1998) as a continuation of the Evolutionary Species Concept (Simpson 1951, 1961; Wiley 1978). We consider lineages as distinct species based on a combination of diagnostic morphological characters, genetic distances, and in some cases, insular allopatry. Here, we have collected an extensive morphological data set that includes representatives from all described Philippine *Lepidodactylus* and use these data in combination with phylogenetic estimates (Oliver et al. 2018) to recognize only diagnosable species of Scaly-toed Geckos of the *L. balioburius–yami* clade. Although additional phenotypic and genetic variation is apparent, we refrain from describing new species without agreement between both morphological and molecular data streams.

Results

Morphology

Although we acknowledge that sample sizes are small for three of the four species described in this study, we have examined large series ($\geq$9 individuals) of all described Philippine *Lepidodactylus* species for comparative purposes. Each of the three lineages with small sample sizes are identified readily based on suites of multiple, nonoverlapping differences in meristic and mensural characters from each

TABLE 1.—Summary of morphological characters in Philippine species of *Lepidodactylus*. In parentheses, mean ± one standard deviation follows ranges.

	aureolineatus (4 m, 4 f)	*babuyanensis* (17 m, 23 f)	*balioburius* (7 m, 9 f)	*bakingibut* (1 m, 1 f)	*bisakol* (3 m, 2 f)	*christiani* (10 m, 2 f)
Snout–vent length (SVL)	32.7–37.8 (35.6 ± 1.9)	31.9–39.3 (35.1 ± 1.9)	28.1–35.0 (32.4 ± 1.8)	35.9, 37.7	34.5–39.2 (36.9 ± 1.7)	33.1–39.0 (36.2 ± 1.8)
Axilla–groin distance/SVL	45.0–53.1% (47.0 ± 3.2%)	43.5–55.4% (50.9 ± 2.7%)	39.8–53.2% (48.0 ± 3.7%)	49.3, 49.6%	47.3–54.2% (50.4 ± 3.3%)	41.6–52.5% (48.4 ± 2.7%)
Snout–forearm length/SVL	37.9–41.5% (39.8 ± 1.3%)	31.0–39.8% (34.0 ± 2.0%)	34.6–40.1% (37.0 ± 1.4%)	34.5, 35.4%	35.1–39.1% (36.6 ± 1.6%)	34.9–41.4% (37.9 ± 1.9%)
Total arm length/SVL	22.3–25.7% (24.3 ± 1.2%)	18.7–23.3% (20.7 ± 1.2%)	18.3–24.4% (20.9 ± 1.7%)	21.2%	18.1–29.6% (21.2 ± 4.7%)	20.9–28.1% (24.4 ± 1.9%)
Total leg length/SVL	28.7–32.4% (30.5 ± 1.1%)	23.4–31.4% (27.9 ± 1.6%)	25.4–28.7% (27.1 ± 1.2%)	27.6, 28.7%	26.3–31.9% (28.2 ± 2.2%)	26.2–32.0% (29.1 ± 1.8%)
Midbody dorsal scales	16–20 (17.9 ± 1.3)	16–21 (18.7 ± 1.8)	20–24 (21.3 ± 1.9)	19, 22	20–24 (21.8 ± 2.0)	18–22 (20.1 ± 1.3)
Midbody ventral scales	9–14 (12.6 ± 1.8)	9–13 (11.0 ± 1.1)	10–16 (12.1 ± 1.7)	14, 16 (7.4 ± 1.1)	15–17 (16.2 ± 0.8)	12–14 (12.8 ± 0.8)
Total pores (in males)	25–31 (27.5 ± 2.5)	18–23 (20.7 ± 1.5)	19–23 (21.1 ± 1.5)	25	23–27 (25.0 ± 2.8)	20–27 (24.3 ± 2.3)
Circumnasal scales	3	3 or 4	4	4	4	4
Rostral contacting nares	yes	no	no	no	no	no

	herrei herrei (6 m, 2 f)	*herrei medianus* (8 m, 3 f)	*labialis* (8 m, 7 f)	*lugubris* (1 m, 14 f)	*nakahiwalay* (1 m, 1 f)	*planicaudus* (5 m, 17 f)
Snout–vent length (SVL)	41.6–50.8 (46.0 ± 2.6)	38.1–44.7 (41.4 ± 2.2)	42.5–52.8 (47.9 ± 3.2)	36.1–44.0 (39.7 ± 2.3)	40.6, 40.8	29.1–37.6 (32.2 ± 2.5)
Axilla–groin distance/SVL	45.2–50.8% (47.8 ± 2.0%)	42.3–54.7% (46.6 ± 3.4%)	45.9–56.4% (50.8 ± 2.7%)	39.6–51.8% (45.2 ± 3.7%)	51.2, 52.2%	33.9–50.5% (43.4 ± 4.7%)
Snout–forearm length/SVL	31.3–38.4% (36.8 ± 2.3%)	35.2–43.2% (38.8 ± 2.5%)	31.5–38.1% (34.8 ± 2.1%)	34.5–43.1% (38.9 ± 2.4%)	34.2, 34.3%	32.2–39.6% (37.3 ± 2.0%)
Total arm length/SVL	20.8–23.8% (22.3 ± 1.1%)	20.0–24.7% (22.6 ± 1.4%)	20.2–26.5% (23.9 ± 1.7%)	19.1–25.6% (22.9 ± 2.0%)	18.1, 20.2%	16.2–22.0% (20.0 ± 1.6%)
Total leg length/SVL	26.6–31.3% (28.7 ± 1.5%)	28.2–32.9% (30.3 ± 1.5%)	25.5–31.8% (27.9 ± 1.6%)	26.0–33.0% (29.5 ± 1.9%)	23.5, 26.1%	24.8–30.9% (27.1 ± 1.6%)
Midbody dorsal scales	9–11 (9.9 ± 0.8)	11–14 (12.5 ± 1)	18–24 (20.5 ± 1.9)	16–22 (19.1 ± 2.0)	22, 23	17–27 (20.8 ± 2.6)
Midbody ventral scales	9–11 (10 ± 0.8)	9–12 (10.7 ± 1.0)	9–12 (10.2 ± 0.7)	10–15 (12.5 ± 1.4)	14, 16	11–16 (13.8 ± 1.4)
Total pores (in males)	31–37 (34.2 ± 1.9)	33–39 (36.7 ± 2.1)	11–13 (12 ± 0.8)	32	23	18–23 (20.3 ± 2.2)
Circumnasal scales	3	3 or 4	3	3	4	3
Rostral contacting nares	yes	yes	yes	yes	no	yes

other and all other known Philippine species (Table 1). No species examined in this study exhibited sexual dimorphism based on SVL. One lineage represented with an expansive sample size from the Batanes Island chain can be separated from all Philippine species except *L. balioburius* based on nonoverlapping morphological features. For this lineage, a principal component analysis (PCA; Fig. 1) weighted most heavily by SVL for PC1 and eye diameter for PC2 offers explicit distinction between its members and those of *L. balioburius* (see Ota and Crombie 1989 for previous use of PCA to distinguish species in *Lepidodactylus*). Additionally, we found that multiple body size measures including SVL, axilla–groin distance, total arm length, and total leg length all differed significantly between the two lineages. Features used most commonly to discern *Lepidodactylus* species boundaries include body and head lengths, axilla–groin distance, and body, supra or infralabial, digital, and pore-bearing scale counts (Brown and Parker 1977; Brown and Alcala 1978; Siler et al. 2014a).

Phylogenetics

Discrete differences observed in ranges of morphological characters parallel results of Bayesian phylogenetic analyses (Fig. 2). The additional tree from PTP species delimitation procedures produced results similar to our analyses of morphological data and Bayesian phylogenetic analyses,

although PTP proposed more extensive splitting than our most liberal interpretation based on morphology (Fig. 2). This additional delimiting is not unexpected given this model's basis on the phylogenetic species concept, and its explicit goal of inferring the smallest possible units of phylogenetic interrelatedness (Zhang et al. 2013).
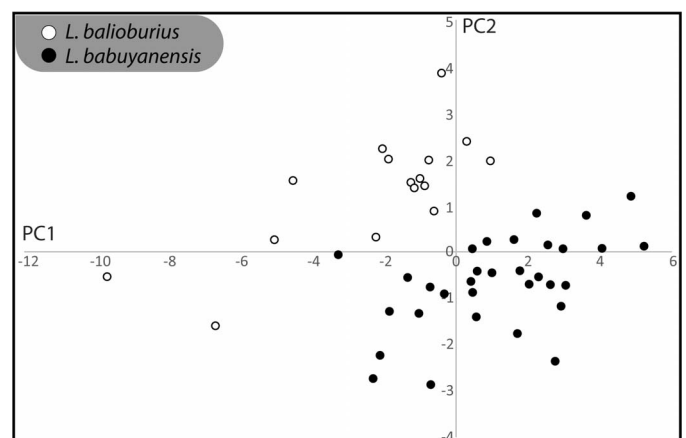

FIG. 1.—Two-dimensional principal component analysis comparing 21 meristic morphological features of adult *Lepidodactylus balioburius* and *L. babuyanensis* specimens.
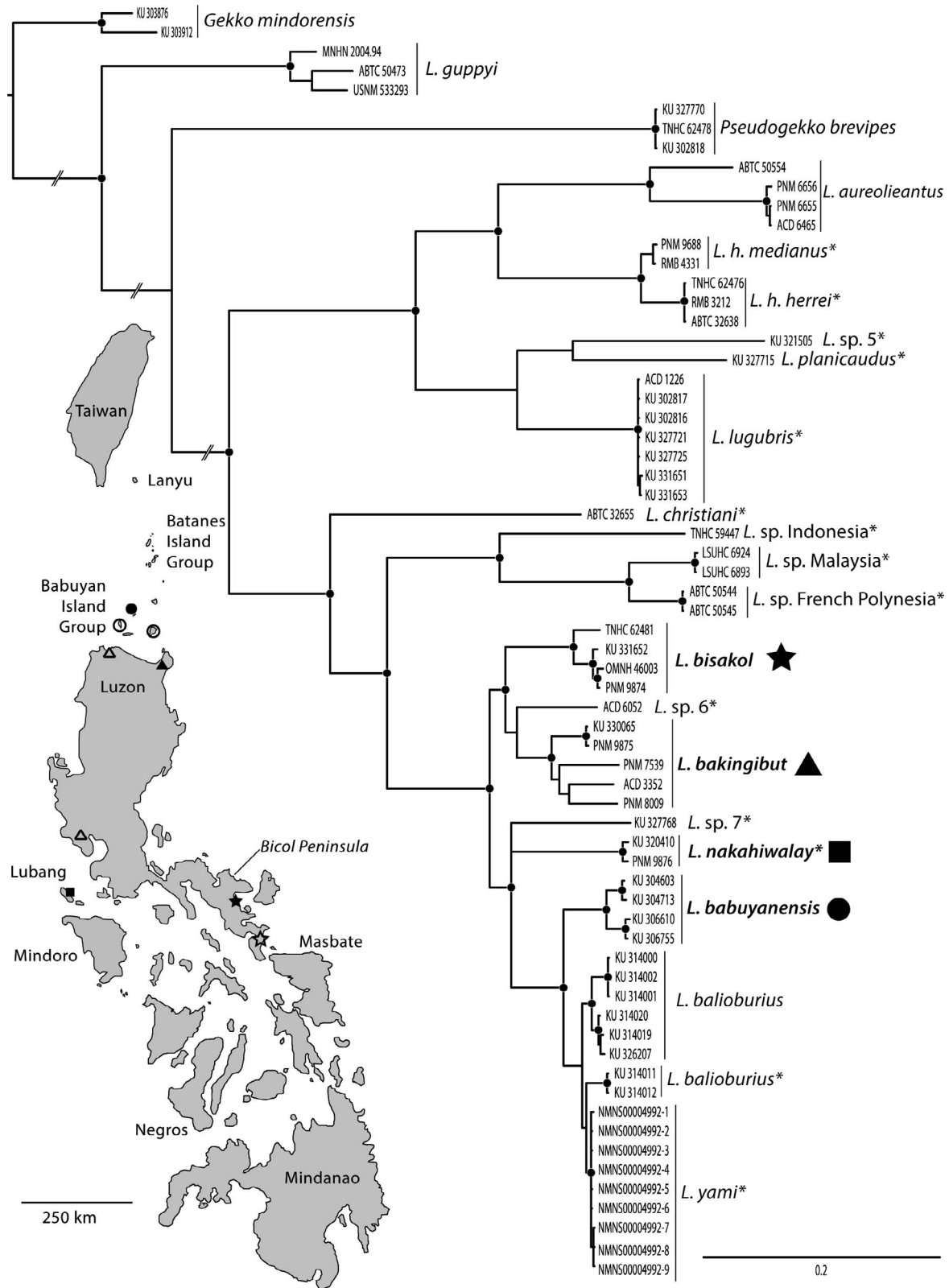
FIG. 2.—Maximum clade credibility topology resulting from Bayesian analysis of the mitochondrial ND2 coding region for geckos of the genus *Lepidodactylus*. *Gekko mindorensis*, *Lepidodactylus guppyi*, and *Pseudogekko brevipes* samples were used as outgroups following higher level phylogenetic analyses (Oliver et al. 2018). Black circles at nodes indicate Bayesian posterior probabilities ≥0.95; nodes shown without circles were supported by posterior probabilities <0.95. Asterisks following taxonomic names on the topology denote lineages delimited in Poisson Tree Processes (PTP) modeling analysis; taxa without asterisks were subdivided by PTP analysis. A reduced map of the Philippine islands is presented on the bottom left, showing the location of type localities of the four species described herein by shapes matching those denoted on the topology. Filled shapes denote type localities while open shapes represent paratypes and/or referred specimens.

Uncorrected pairwise sequence divergences show minimal variability within species described here (0.12–3.9% mtDNA divergence at ND2), whereas interspecific divergences are substantially higher (approximately ≥10%). The exception to this general level of interspecific divergence lies within lineages found on island chains north of Luzon, including *Lepidodactylus yami, L. balioburius,* and a novel lineage from the Babuyan Island Group described herein. Although the novel species is differentiated readily from the two previously described species (6.2–7.7% mtDNA divergence), genetic divergence is less apparent between the Lanyu Island and Batanes Island chain lineages (1.7–2.7% mtDNA divergence). Interestingly, while describing *L. balioburius,* Ota and Crombie (1989) had some difficulty in identifying distinct diagnostic characters between it and *L. yami* and had to use a suite of characters in differentiation. We were only able to examine two juvenile *L. yami* specimens for comparisons of morphological character state differences, so we are unable to definitively evaluate the validity of *L. balioburius* as distinct from *L. yami;* we hold evaluation of these two named species in abeyance and follow Ota and Crombie (1989) in recognizing both taxa until a comprehensive analysis of phenotypic variation is forthcoming.

Taxonomic Conclusions

Following examination of morphological data and consideration of molecular phylogenetic estimates, we recognize four lineages, unambiguously characterized by unique, nonoverlapping suites of diagnostic morphological character state differences (Table 1) and which are distinct, genetically divergent clades (Fig. 2). All four novel lineages occur on Luzon Island, Lubang Island, or the Babuyan Island Group, all of which are part of (or geographically associated with) the Luzon PAIC in the northern Philippines.

Species Accounts

Lepidodactylus **bisakol** sp. nov.
(Table 1; Figs. 3A, 4)

Lepidodactylus sp. 1: Oliver et al. 2018:4.

Holotype.—PNM 9874 (formerly OMNH 46002; NAH Field No. 479), adult male, collected 17 March 2017 at 365 m on Mt. Mayon, Sitio Nagsipit, Barangay Mariroc, Municipality of Tabaco, Albay Province, Luzon Island, Philippines (13.30558°, 123.68898°), by N.A. Huron and J.B. Fernandez.

Paratype (Paratopotype).—OMNH 46003 (NAH Field No. 480), adult male, collected 14 March 2017 by N.A. Huron and J.B. Fernandez.

Other paratypes.—KU 331652 (RMB Field No. 13781), adult female, collected 16 January 2011 at 51 m in residential area on house walls in Barangay Tanawan, Municipality of Malinao, Albay Province, Luzon Island, Philippines (13.40534°, 123.67683°), by RMB. TNHC 62481 (RMB Field No. 4028), adult female, collected 23 November 2001 at 10 m in hilly and selectively logged primary rainforest near Bulusan Lake, on Mt. Bulusan, Barangay San Rogue, Municipality of Irosin, Sorsogon Province, Luzon Island, Philippines (12.752104°, 124.096736°), by RMB and B.R. Fernandez. KU 347921 (RMB Field No. 23234), adult male, and KU 348462 (RMB Field No. 23233), juvenile, collected

FIG. 3.—Photographic plate of (A) *Lepidodactylus bisakol* (holotype PNM 9874), (B) *Lepidodactylus bakingibut* (paratype KU 330065), and (C) *Lepidodactylus babuyanensis* (paratype OMNH 46977) in life. A color version of this figure is available online.

4 February 2017 at 260 m on Mt. Cawayan, Barangay Cawayan, Municipality of Irosin, Sorsogon Province, Luzon Island, Philippines (12.6968°, 124.0827°), by RMB and J.B. Fernandez. KU 346536 (RMB Field No. 24027), juvenile, collected 4 August 2017 at 643 m on Mt. Jormahan, Barangay Cogon, Municipality of Irosin, Sorsogon Province, Luzon Island, Philippines (12.76116°, 124.0036°), by RMB, J.B. Fernandez, M. Buehler, and C. Tracy. KU 346537 (RMB Field No. 24672), juvenile, collected 11 August 2017 at 82 m near Bayugin Falls, Barangay San Francisco, Municipality of Bulusan, Sorsogon Province, Luzon Island, Philippines (12.7586°, 124.11996°), RMB, J.B. Fernandez, M. Buehler, and C. Tracy.

Diagnosis.—*Lepidodactylus bisakol* can be distinguished from congeners by the following combination of characters: (1) body size moderate (SVL 34.5–39.2 mm); (2) thigh length
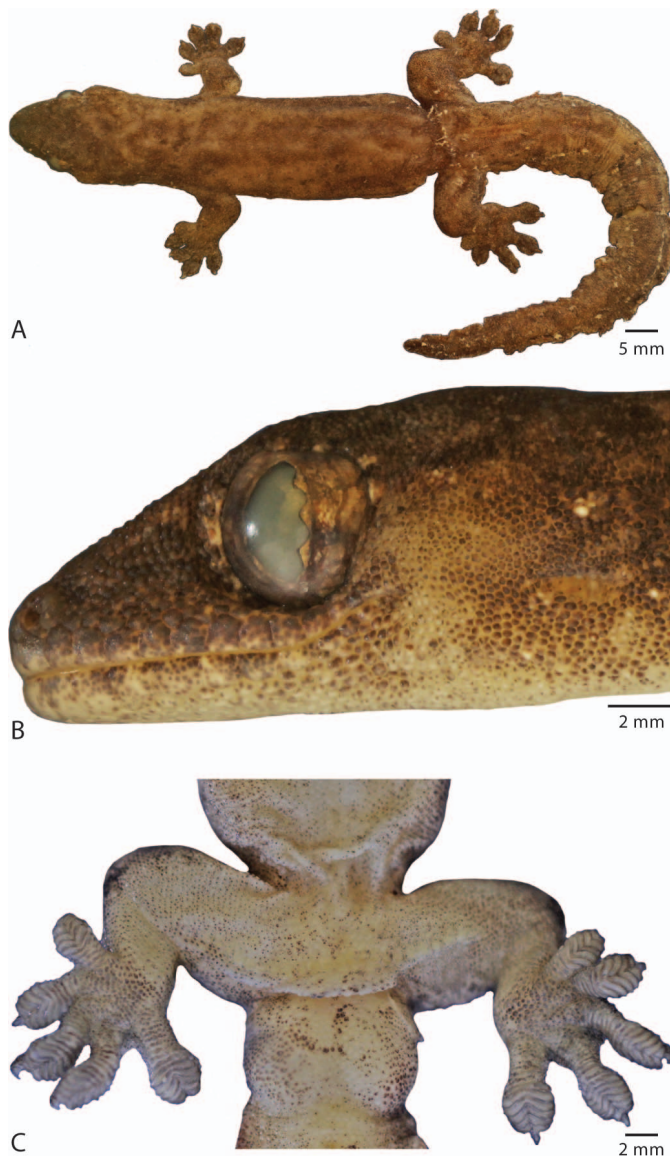
Fig. 4.—Dorsal body (A), head (B), and cloacal region (C) of the holotype of *Lepidodactylus bisakol*. A color version of this figure is available online.

moderate, 13.9–15.4% SVL; (3) total leg length moderate, 26.3–31.9% SVL; (4) head width moderate, 61.2–69.5% head length; (5) snout length short, 32.7–45.3% head length; (6) paravertebral scale count within one eye diameter 21–23; (7) midbody ventral scale count within one eye diameter 15–17; (8) ventral scale count within one eye diameter 15–18; (9) circumnasal scales 4; (10) precloacofemoral pores in males 23–27; (11) pore series shape linear; and (12) rostral scale not in contact with nostril.

Comparisons.—Characters distinguishing *Lepidodactylus bisakol* from all other species of Philippine *Lepidodactylus* are summarized in Table 1 and additional comprehensive comparisons are available in Supplemental Table 1 (available online). This new species most closely resembles *L. lugubris;* however, it differs in several characters, including having more circumnasal scales (4 vs. 3), fewer Toe IV total scansors (9–11 vs. 12–18), fewer precloacofemoral pores in males (23–27 vs. 32), a linear pore series shape (vs. v-shaped) and a rostral scale that does not contact the nostril (vs. in contact).

Considering all other Philippine congeners, *L. bisakol* can be distinguished readily from *L. aureolineatus, L. herrei herrei, L. herrei medianus, L. labialis,* and *L. planicaudus* by having a rostral scale separated from the nostril (vs. in contact); from *L. h. herrei* and *L. h. medianus* by having more midbody dorsal scales (20–24 vs. <15); from *L. babuyanensis, L. h. herrei, L. h. medianus, L. nakahiwalay,* and *L. bakingibut* by having more paravertebral scales (21–23 vs. <21); from *L. aureolineatus, L. babuyanensis, L. christiani, L. h. herrei, L. h. medianus,* and *L. labialis* by having more midbody ventral scales (15–17 vs. <15); from *L. aureolineatus, L. babuyanensis, L. h. herrei, L. h. medianus,* and *L. labialis* by having more ventral scales (15–18 vs. <15); from *L. bakingibut* by having more supralabial scales (13 vs. 11–12); from *L. aureolineatus, L. h. herrei, L. labialis,* and *L. planicaudus* by having more circumnasal scales (4 vs. 3); from *L. nakahiwalay* by having more total scansors on Finger III (9–12 vs. 7); from *L. h. herrei, L. h. medianus,* and *L. labialis* by having a moderate number of precloacofemoral pores (23–27 vs. <14 [*L. labialis*], >30 [*L. h. herrei, L. h. medianus*]); from *L. labialis* by having a linear pore series shape (vs. v-shaped), a rostral scale that is not cleft (vs. cleft), more webbing between Toes II and III (1–2 vs. 0), and more cloacal spurs (1–2 vs. 0); from *L. labialis* and *L. balioburius* by having more webbing between Toes III and IV (2–3 vs. >2); from *L. nakahiwalay* by having a larger relative snout–forearm length (35.1–39.1% SVL vs. <34.4%), relative crus length (12.3–16.5% SVL vs. 11.8%), and relative total leg length (26.3–31.9% SVL vs. <26.2%); from *L. bakingibut* by having a smaller eye–nostril distance relative to head length (23.4–30.5% head length vs. >32.3%); and from *L. aureolineatus, L. h. herrei,* and *L. h. medianus* by having a greater eye diameter relative to head length (21.8–25.3% head length vs. <21.7%).

Description of holotype.—Adult male in good condition; small incision in ventral surface from retrieval of genetic sample. Body moderate, SVL 36.8 mm, axilla–groin distance 47.3% SVL; limbs well-developed, moderately slender; tail original, wide, somewhat ornamental; margins of limbs smooth, lacking cutaneous flaps or dermal folds; trunk lacking ventrolateral cutaneous fold.

Head moderate in size, largely undifferentiated from neck as a result of hypertrophied temporal musculature; snout rounded in dorsal and lateral aspects; head length 29.6% SVL, 209.7% head height; head width 68.8% head length, 144.2% head height; snout length 37.6% head length, 54.7% head width; dorsal surfaces of head homogeneous, with only slight prefrontal and interorbital concavities present; auricular opening large, ovoid, angled slightly anteroventrally and posterodorsally, positioned anterior to temporal swellings on either side of head; eye moderate; pupil vertical, margin straight; nostril contacting first supralabial, not contacting rostral; limbs and digits moderate in length, and moderately slender; legs longer than arms, thighs moderately thicker compared with brachium; thigh length 112.5% crus length; leg length 27.7% SVL, 136.0% arm length.

Rostral somewhat rectangular in anterior view, not cleft, bordered laterally by first supralabials, posterolaterally by anterior-most enlarged circumnasals, and posteriorly by two additional scales (= four snout scales); nostril surrounded by first supralabial and four equally sized enlarged circum-

nasals; supranasals separated by four heterogeneously sized median scales.

Total number of differentiated supralabials 13/12; total number of differentiated infralabials 11/12, bordered ventrally by slightly enlarged chin and undifferentiated gular scales; total number of chin scales between second and third infralabials eight; number of enlarged scale rows adjacent to chin scales one or two until fourth or fifth infralabials; patch of enlarged gular scales on anterior end of gular region continuing to a point in line with fifth infralabial on both sides.

Dorsal cephalic scales fairly homogeneous in size, shape, disposition, and distribution; cephalic scalation slightly convex, primarily round scales; prefrontal and interorbital depressions slight; undifferentiated posterior head scales slightly convex; gular and throat scales small, oval, rounded, and nonimbricate, making a moderately sharp transition in scalation toward posterior end of neck on ventral surface, with enlarged rounded, hexagonal, nonoverlapping scales; circumorbitals 38 (L). Dorsal body scales round, convex, juxtaposed, relatively homogeneous in size; dorsals gradually transition to subimbricate to nonoverlapping ventrals along lateral body surface; midbody dorsal scales within one eye diameter 21; paravertebral scales within one eye diameter 21; midbody ventral scales within one eye diameter 16; ventral scales within one eye diameter 16; scales on dorsal surfaces of limbs undifferentiated from dorsals; scales on dorsal surfaces of hands and feet similar to dorsal limb scales; ventral body scales flat, rounded, hexagonal, subimbricate to nonoverlapping, much larger than dorsal body scales, relatively homogeneous in size. Enlarged precloacofemoral pore-bearing scales in a continuous, linear row 23; rectangular patch of moderately enlarged precloacal scales directly posterior to pore series and anterior to cloacal opening.

Digits moderately expanded and covered on palmar surface proximally with undivided bowed scansors and distally with divided scansors; total scansors on Finger III 10, first divided scansor on Finger III scansor eight, last divided scansor on Finger III scansor 10; total scansors on Toe IV 10, first divided scansor on Toe IV scansor eight, last divided scansor on Toe IV scansor 10; webbing between Toes II and III two, between Toes III and IV two.

Tail round, wide, length moderate, 113.9% SVL; tail width 196.8% tail diameter; intermittent enlarged scales resembling spikes present along lateral sides; caudals slightly convex, much more subrectangular than dorsals, subcaudals much more rectangular than ventrals; ventrolateral ridge with intermittent, enlarged, imbricate scales present; cloacal spurs at base of tail two.

Coloration of holotype in preservative.—Dorsal surfaces of body, limbs, and tail Glaucous (Color 272) mottled with faint patches of Hair Brown (Color 277); posterior regions of head similar in color to body but transitions to Raw Umber (Color 280) anteriorly toward snout; ventral surfaces of head body and limbs Smoke Gray (Color 266) with small specks of Hair Brown (Color 277) present; ventral surface of tail shows similar coloration to body, however with increased Hair Brown (Color 277) present; base coloration of tail gradually transitions from Smoke Gray (Color 266) to Sepia (Color 279) posteriorly.

Coloration of paratype in life.—Based on photograph of PNM 9874 in life (Fig. 3A). Dorsal surface of body Smoke

Gray (Color 267) mottled with speckles of Smoky White (Color 261) to Sepia (Color 279) forming weak chevron patterning; dorsolateral coloration and dorsal surface of limbs darker than dorsal body surface, closer to Fuscus (Color 283) with speckles of Drab-Gray (Color 256) and Smoky White (Color 261); dorsal surface of head Fuscus (Color 283) with patches of Drab-Gray (Color 256) and Smoky White (Color 261); post orbital stripe Smoky White (Color 261) continues to a point in line with anterior edge of forelimb; faint stripe of Smoky White (Color 261) extending horizontally across head between center of eyes; dorsal surface of tail Fuscus (Color 283) with patches ranging from Smoky White (Color 261) to Smoke Gray (Color 267); tail coloration mostly Smoky White (Color 261) along lateral surfaces.

Measurements and scale counts of holotype (in mm).—Snout–vent length 36.8; axilla–groin distance 17.4; tail length 41.9; tail width 6.1; tail depth 3.1; snout–forearm length 14.4; upper arm length 3.0; forearm length 4.5; thigh length 5.4; crus length 4.8; Finger III length 2.6; Toe IV length 2.7; head length 10.9; head width 7.5; head height 5.2; eye–ear distance 3.3; eye–nostril distance 3.2; snout length 4.1; interorbital distance 1.2; internarial distance 1.6; ear diameter 0.4; eye diameter 2.4; midbody dorsal scales 21; paravertebral scales 21; midbody ventral scales 16; ventral scales 16; supralabials 13; infralabials 11; circumorbital scales 38; circumnasals 4; snout scales 4; chin scales 8; Finger III total scansors 10; Finger III divided scansors 3; Toe IV total scansors 10; Toe IV divided scansors 4; precloacofemoral pores 23; cloacal spurs 2.

Variation.—Intraspecific variation among characters recorded is summarized in Table 1. Among the five specimens examined, we observed variation in the number of midbody dorsal, paravertebral, midbody ventral, ventral, infralabial, circumorbital, snout, and chin scales, Finger III total scansors, Finger III divided scansors, Toe IV total scansors, Toe IV divided scansors, and precloacofemoral pores in males (Supplemental Table 1).

Distribution.—*Lepidodactylus bisakol* is known from two sites approximately 80 km apart in southern portions of the Bicol Peninsula. We anticipate that additional populations exist in suitable habitat throughout Albay and Sorsogon provinces. Future surveys could discover additional populations further north in the Bicol in Camarines Sur or Camarines Norte provinces.

Ecology and natural history.—*Lepidodactylus bisakol* has been found in disturbed and secondary growth habitats. In some regions of its known range, substantial habitat degradation has occurred with agricultural fields fragmenting remaining forest patches. In Albay Province, individuals were observed on small tree branches and large shrubs along stream systems at low elevations on Mt. Mayon. Individuals of this species have also been found in residential areas on artificial buildings. This species is known to co-occur with the widespread *L. lugubris* in sympatry within the Municipality of Malinao, Albay Province and it may be sympatric with *L. lugubris* across most of its range. This is the first example of sympatric *Lepidodactylus* species on or near Luzon Island to date.

Etymology.—The specific epithet is chosen in reference to the biogeographically and culturally distinct Bicol Region of southern Luzon Island (Albay, Camarines Norte, Camar-

ines Sur, Catanduañes, and Sorsogon provinces). The cultural diversity on the peninsula is home to a diverse group of indigenous dialects, which are referred to collectively as the Bisakol languages. This unique subfaunal region in the northern Philippines is home to a growing number of endemic vertebrates. Suggested common name: Bicol Scaly-toed Geckos.

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Lepidodactylus **bakingibut** sp. nov.
(Table 1; Figs. 3B, 5)

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Lepidodactylus cf. *lugubris:* Brown et al. 2013:52, their fig. 50.
Lepidodactylus sp. 2: Oliver et al. 2018:4.

Holotype.—PNM 9875 (formerly KU 330066; RMB Field No. 14886), adult male, collected 15 July 2011 at 685 m on Mt. Cagua, Barangay Magrafil, Municipality of Gonzaga, Cagayan Province, Luzon Island, Philippines (18.236°, 122.104°), by J.B. Fernandez, L.J. Welton, C.H. Oliveros, and RMB.

Paratype.—KU 330065 (RMB Field No. 14765), adult female, collected 12 July 2011, at 785 m on Mt. Cagua, Barangay Magrafil, Municipality of Gonzaga, Cagayan Province, Luzon Island, Philippines (18.219°, 122.111°), by J.B. Fernandez, L.J. Welton, C.H. Oliveros, and RMB.

Referred specimens.—PNM 7539 (RMB Field No. 4273), collected in Barangay Pancian, Municipality of Pagudpud, Ilocos Norte Province (on the boundary with Cagayan Province), Luzon Island, Philippines. PNM 8009 (ACD Field No. 1129), collected on Mt. Natib, Barangay Tala, Municipality of Orani, Bataan Province, Luzon Island, Philippines. ACD Field No. 3352, collected on Luzon Island (specific locality unknown; deposited at PNM). Although genetic data are available for these specimens (Fig. 2; Appendix; Oliver et al. 2018), morphological data were not available at the time of this investigation. As such, we assign these individuals to *L.* cf. *bakingibut* pending morphological data collection but designate them as paratypes.

Diagnosis.—*Lepidodactylus bakingibut* can be distinguished from congeners by the following combination of characters: (1) body size moderate (SVL 35.9–37.7 mm); (2) snout–forearm length moderate, 34.5–35.4% SVL; (3) forearm length moderate, 10.9–11.4% SVL; (4) thigh length moderate, 13.8–14.5% SVL; (5) crus length moderate, 13.8–14.2% SVL; (6) total leg length moderate, 27.6–28.7% SVL; (7) Finger III length long, 32.9–35.0% total arm length; (8) Toe IV length long, 35.0–39.4% total leg length; (9) head length moderate, 25.6–27.1% SVL; (10) head width moderate, 63.7–69.6% head length; (11) head height narrow, 36.3–37.0% head length; (12) eye–ear distance short, 23.5–26.1% head length; (13) snout length moderate, 41.2–42.4% head length; (14) eye diameter small, 21.6–22.8% head length; (15) midbody ventral scale count within one eye diameter 14–16; (16) ventral scale count within one eye diameter 16; (17) circumnasal scales 4; (18) Finger III total scansors 9; (19) Toe IV total scansors 9; (20) precloacofemoral pores in males 25; (21) rostral scale not in contact with nostril; and (22) webbing between Toes II and III minimal.

Comparisons.—Characters distinguishing *Lepidodactylus bakingibut* from all other species of Philippine *Lepidodactylus* are summarized in Table 1 and additional comprehensive comparisons are available in Supplemental
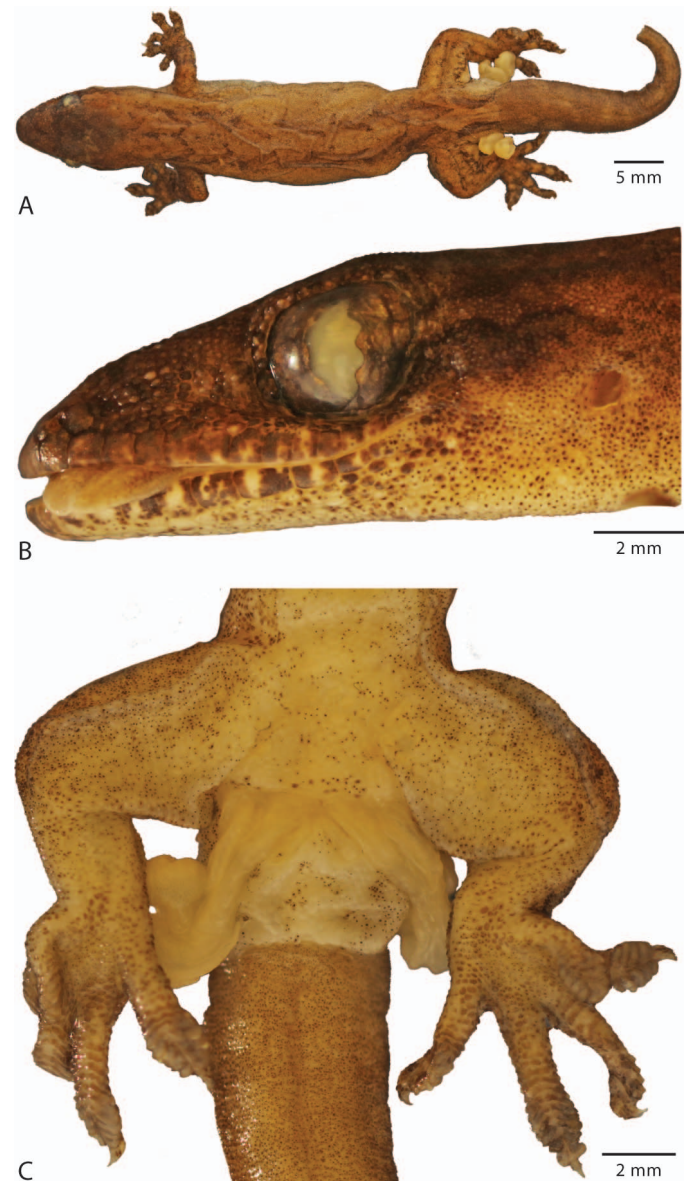

Fig. 5.—Dorsal body (A), head (B), and cloacal region (C) of the holotype of *Lepidodactylus bakingibut*. A color version of this figure is available online.

Table 1. The new species most closely resembles *L. babuyanensis;* however, it differs in several characters, including having more midbody ventral scales (14–16 vs. 9–13), more ventral scales (16 vs. 8–12), more precloacofemoral pores (25 vs. 18–23), and a smaller thigh length relative to crus length (100.0–102.0% crus length vs. 103.8–120.8%).

Considering all other Philippine congeners, *L. bakingibut* can be distinguished readily from *L. aureolineatus, L. herrei herrei, L. herrei medianus, L. labialis, L. lugubris,* and *L. planicaudus* by having a rostral scale separated from the nostril (vs. contacting); from *L. h. herrei* and *L. h. medianus* by having more midbody dorsal scales (19–22 vs. <15); from *L. bisakol, L. h. herrei, L. h. medianus, L. labialis,* and *L. nakahiwalay* by having a moderate number of paravertebral scales (17 or 18 vs. <16 [*L. h. herrei, L. h. medianus*], >18 [*L. bisakol, L. labialis, L. nakahiwalay*]); from *L. h. herrei, L. h. medianus,* and *L. labialis* by having more midbody ventral

scales (14–16 vs. <13); from *L. aureolineatus, L. christiani, L. h. herrei, L. h. medianus, L. labialis, L. nakahiwalay,* and *L. lugubris* by having more ventral scales (16 vs. <16); from *L. bisakol* and *L. labialis* by having fewer supralabials (11–12 vs. >13); from *L. aureolineatus, L. christiani,* and *L. h. herrei* by having more circumorbital scales (32–35 vs. <31); from *L. aureolineatus, L. h. herrei, L. labialis, L. lugubris,* and *L. planicaudus* by having more circumnasal scales (4 vs. 3); from *L. balioburius, L. h. herrei, L. h. medianus, L. labialis, L. lugubris, L. nakahiwalay,* and *L. planicaudus* by having a moderate number of precloacofemoral pores (25 vs. <24 [*L. labialis, L. nakahiwalay, L. planicaudus*], >30 [*L. h. herrei, L. h. medianus, L. lugubris*]); from *L. labialis* and *L. lugubris* by having a linear pore series (vs. v-shaped); from *L. labialis* by having a rostral scale not cleft (vs. cleft) and more cloacal spurs (1 or 2 vs. 0); from *L. aureolineatus, L. christiani, L. h. herrei, L. labialis,* and *L. planicaudus* by having minimal webbing between Toes II and III (1 vs. 0 [*L. labialis*], >1 [*L. aureolineatus, L. christiani, L. h. herrei, L. planicaudus*]); from *L. aureolineatus, L. balioburius,* and *L. labialis* by having more webbing between Toes III and IV (3 vs. <3); from *L. aureolineatus, L. christiani,* and *L. h. herrei* by having a larger axilla–groin distance relative to head length (182.4–193.5% head length vs. <177.9%); from *L. aureolineatus, L. balioburius, L. christiani, L. h. herrei, L. h. medianus, L. nakahiwalay,* and *L. planicaudus* by having a larger crus length relative to head length (51.0–55.4% head length vs. <50.5%); and from *L. aureolineatus, L. balioburius, L. bisakol, L. christiani, L. h. herrei, L. h. medianus,* and *L. planicaudus* by having a larger eye–nostril distance relative to head length (32.4–34.8% head length vs. <31.7%).

Description of holotype.—Adult male in good condition; small incision in ventral surface from retrieval of genetic sample, hemipenes inverted from preservation. Body small, SVL 37.7 mm, axilla–groin distance 49.3% SVL; limbs well-developed, moderately slender; tail regenerated, narrow; margins of limbs smooth, lacking cutaneous flaps or dermal folds; trunk lacking ventrolateral cutaneous fold.

Head moderate in size, largely undifferentiated from neck as a result of hypertrophied temporal musculature; snout rounded in dorsal and lateral aspects; head length 27.1% SVL, 275.7% head height; head width 63.7% head length, 175.7% head height; snout length 41.2% head length, 64.6% head width; dorsal surfaces of head homogeneous, with only slight prefrontal and interorbital concavities present; auricular opening large, slightly ovoid, elongated ventrally and dorsally, positioned toward posterior-most point on either side of head; eye moderate; pupil vertical, margin straight; nostril contacting first supralabial, not contacting rostral; limbs and digits moderate in length, and moderately slender; legs longer than arms, thighs moderately thicker compared with brachium; thigh length 100.0% crus length; leg length 27.6% SVL, 130.0% arm length.

Rostral somewhat pentagonal in anterior view, not cleft, bordered laterally by first supralabials, posterolaterally by anterior-most enlarged circumnasals, and posteriorly by three additional scales (= five snout scales); nostril surrounded by first labial and four equally sized enlarged circumnasals; supranasals separated by four heterogeneously sized median scales.

Total number of differentiated supralabials 12/13; total number of differentiated infralabials 11/11, bordered ven-trally by slightly enlarged chin and undifferentiated gular scales; total number of chin scales between second and third infralabials 9; number of enlarged scale rows adjacent to chin scales one or two until sixth infralabials; patch of enlarged gular scales on anterior end of gular region continuing to a point in line with third infralabial on both sides.

Dorsal cephalic scales fairly homogeneous in size, shape, disposition, and distribution; cephalic scalation slightly convex, primarily round scales; prefrontal and interorbital depressions slight; undifferentiated posterior head scales slightly convex; gular and throat scales small, oval, rounded, and nonimbricate, making a somewhat gradual transition in scalation toward posterior end of neck on ventral surface, with enlarged rounded, hexagonal, nonoverlapping scales; circumorbitals 32 (L). Dorsal body scales round, convex, juxtaposed, relatively homogeneous in size; dorsals gradually transition to flat, subimbricate to nonoverlapping ventrals along lateral body surface; midbody dorsal scales within one eye diameter 22; paravertebral scales within one eye diameter 17; midbody ventral scales within one eye diameter 14; ventral scales within one eye diameter 16; scales on dorsal surfaces of limbs undifferentiated from dorsals; scales on dorsal surfaces of hands and feet similar to dorsal limb scales; ventral body scales flat, rounded, hexagonal, subimbricate to nonoverlapping, much larger than dorsal body scales, relatively homogeneous in size. Enlarged precloacofemoral pore-bearing scales in a continuous, linear row 25; triangular patch of moderately enlarged precloacal scales directly anterior to cloacal opening.

Digits moderately expanded and covered on palmar surface proximally with undivided bowed scansors and distally with divided scansors; total scansors on Finger III nine, first divided scansor on Finger III scansor seven, last divided scansor on Finger III scansor nine; total scansors on Toe IV nine, first divided scansor on Toe IV scansor six, last divided scansor on Toe IV scansor nine; webbing between Toes II and III one, between Toes III and IV three.

Tail round, narrow, regenerated, length short, 50.1% SVL; tail width 170.0% tail depth; caudals slightly convex, similar in shape to dorsals, subcaudals fairly heterogeneous in shape, more rectangular than ventrals; ventrolateral ridge present but poorly defined; singular cloacal spur at base of tail.

Coloration of paratype in preservative.—Dorsal surfaces of body and limbs Glaucous (Color 272) with broken chevron patterning of Hair Brown (Color 277) running posteriorly from back of head to base of tail; dorsal surface of tail Sepia (Color 279) with small patches of Glaucous (Color 272); posterior regions of head similar in color to body but transitions to Raw Umber (Color 280) anteriorly toward snout; infralabial scale line Raw Umber (Color 280) with speckling of Smoke Gray (Color 266); ventral surface of head, body and limbs Smoke Gray (Color 266) with light speckling of Hair Brown (Color 277); ventral surface of tail Grayish Horn Color (Color 268).

Coloration of paratype in life.—Based on photograph of KU 330065 in life (Fig. 3B). Dorsal surfaces of body and limbs Smoke Gray (Color 267) with irregular chevron patterning of Grayish Horn Color (Color 268) on body from posterior end of head through to end of tail; dorsal surface of head Smoke Gray (Color 267) with speckling of Smoky White (Color 261) to Sepia (Color 286); post orbital stripe of Olive Clay Color (Color 85) runs to a point in line with the

anterior edge of the forelimb; post orbital stripe has faint border of Smoky White (Color 261) above and Sepia (Color 286) below; three spots of Sepia (Color 286) present on dorsolateral surface just anterior to, even with, and posterior to forelimb insertion point; two similar dots of Sepia (Color 286) present even with, and just posterior to, hind limb insertion point; intermittent patches of Sepia (Color 286) present on dorsolateral edges of tail.

Measurements and scale counts of holotype (in mm).—Snout–vent length 37.7; axilla–groin distance 18.6; tail length 18.9; tail width 5.1; tail depth 3.0; snout–forearm length 13.0; upper arm length 3.9; forearm length 4.1; thigh length 5.2; crus length 5.2; Finger III length 2.8; Toe IV length 4.1; head length 10.2; head width 6.5; head height 3.7; eye–ear distance 2.4; eye–nostril distance 3.3; snout length 4.2; interorbital distance 1.4; internarial distance 1.5; ear diameter 0.6; eye diameter 2.2; midbody dorsal scales 22; paravertebral scales 17; midbody ventral scales 14; ventral scales 16; supralabials 12; infralabials 11; circumorbital scales 32; circumnasals 4; snout scales 5; chin scales 9; Finger III total scansors 9; Finger III divided scansors 3; Toe IV total scansors 9; Toe IV divided scansors 3; precloacofemoral pores 25; cloacal spurs 1.

Variation.—Morphometric variation is summarized in Table 1. Among the two specimens examined, we observed variation in the number of midbody dorsal, paravertebral ventral, midbody ventral, supralabial, infralabial, and circumorbital scales, as well as Toe IV divided scansors (Supplemental Table 1).

Distribution.—*Lepidodactylus bakingibut* is known to occur on Mt. Cagua in Cagayan Province along the northernmost extent of the Sierra Madre mountain range, and likely also occurs in north-central and northwestern Luzon Island. Individuals of this lineage have been observed in Kalinga and Ilocos Norte provinces; therefore, *L. bakingibut* may be more widespread across the northern extent of the island. Such a distribution across northern Luzon Island has been observed in other squamate reptiles in the Philippines (i.e., *Brachymeles ilocandia;* Siler et al. 2016b).

Ecology and natural history.—The type specimens for this species were both found in mixed primary and secondary-growth rainforest at mid- to high elevation on Mt. Cagua. Other specimens for which only genetic data were available have been observed in lower elevation habitats converted for agricultural and residential purposes.

Etymology.—The name is based on terms in the dominant Ilocano dialect of northern Luzon Island, and chosen in recognition of the biogeographically and culturally distinct region in the northern Philippines. The specific epithet is derived from the Ilocano terms "bákir," meaning forest, and "alibut," meaning lizard or gecko, in reference to the observed habitat preferences of the new species. Suggested common name: Ilocano Scaly-toed Geckos.

<center>

Lepidodactylus **nakahiwalay** sp. nov.
(Table 1; Fig. 6)

</center>

Lepidodactylus sp. 3: Oliver et al. 2018:4.

Holotype.—PNM 9876 (formerly KU 320411; CDS Field No. 3931), adult male, collected 29 April 2009 at 98 m in Sitio Dangay, Barangay Vigo, Municipality of Lubang,
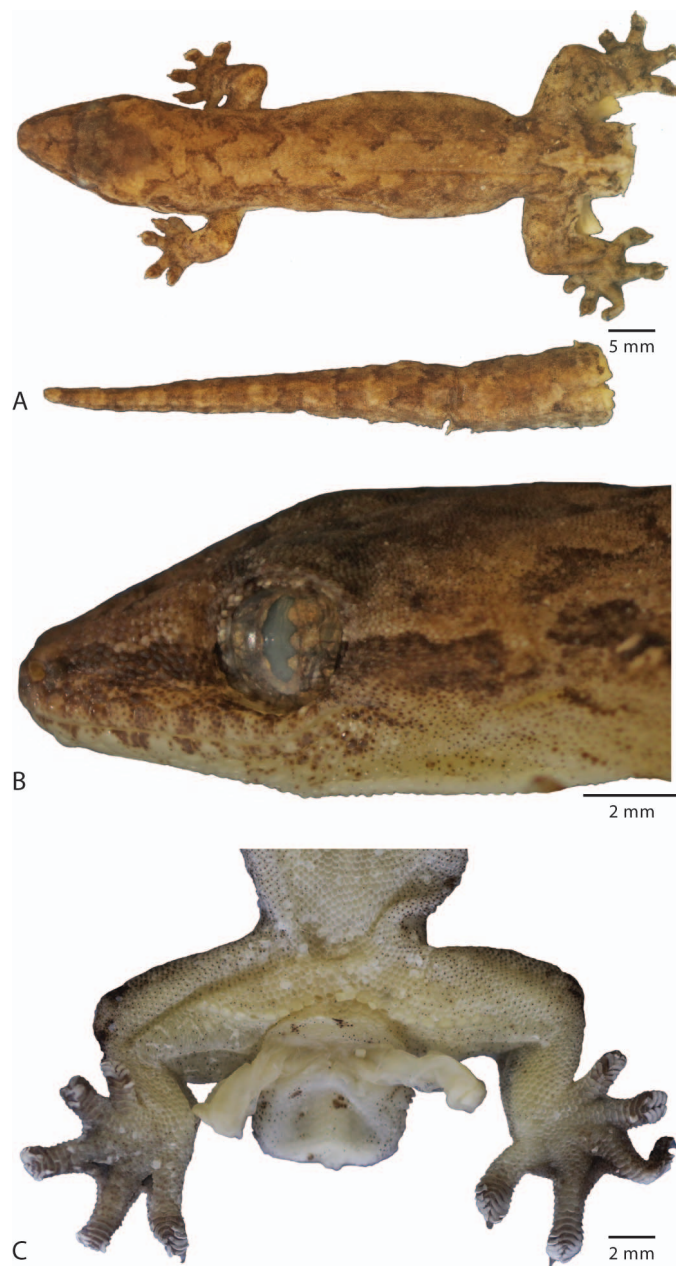

Fig. 6.—Dorsal body (A), head (B), and cloacal region (C) of the holotype of *Lepidodactylus nakahiwalay*. A color version of this figure is available online.

Occidental Mindoro Province, Lubang Island, Philippines (13.78304°, 120.17246°), by CDS, J.B. Fernandez, and RMB.

Paratype (paratopotype).—KU 320410 (CDS Field No. 3930), adult female, collected 29 April 2009 by CDS, J.B. Fernandez, and RMB.

Diagnosis.—*Lepidodactylus nakahiwalay* can be distinguished from congeners by the following combination of characters: (1) body size moderate to large (SVL 40.6–40.8 mm); (2) snout–forearm length moderate, 34.2–34.3% SVL; (3) total arm length short, 18.1–20.2% SVL; (4) crus length moderate, 11.8% SVL; (5) total leg length moderate, 23.5–26.1% SVL; (6) Finger III length long, 29.7–35.4% total arm length; (7) Toe IV length moderate, 33.0–36.5% total leg length; (8) head length moderate, 26.4–26.5% SVL; (9) head width moderate, 67.3–69.4% head length; (10) snout length

long, 43.5–44.9% head length; (11) eye diameter large, 22.4–25.0% head length; (12) midbody dorsal scale count within one eye diameter 22 or 23; (13) paravertebral scale count within one eye diameter 19 or 20; (14) midbody ventral scale count within one eye diameter 14–16; (15) circumnasal scales 4; (16) Finger III total scansors 7; (17) Toe IV total scansors 8 or 9; (18) precloacofemoral pores in males 23; and (19) rostral scale not in contact with nostril.

Comparisons.—Characters distinguishing *Lepidodactylus nakahiwalay* from all other Philippine species of *Lepidodactylus* are summarized in Table 1 and additional comprehensive comparisons are available in Supplemental Table 1. The new species most closely resembles *L. bisakol;* however, it differs in several characters, including having fewer paravertebral scales (19–20 vs. 21–23), a smaller relative snout–forearm length (34.2–34.3% SVL vs. 35.1–39.1%), relative crus length (11.8% SVL vs. 12.3–16.5%), and relative total leg length (23.5–26.1% SVL vs. 26.3–31.9%), a larger Toe IV length relative to total leg length (33.0–36.5% leg length vs. 25.7–32.7%), and a larger head width relative to head height (178.6–180.0% head height vs. 144.2–176.3%).

Considering all other Philippine congeners, *L. nakahiwalay* can be distinguished readily from *L. aureolineatus, L. herrei herrei, L. herrei medianus, L. labialis, L. lugubris,* and *L. planicaudus* by having a rostral scale separated from the nostril (vs. contacting); from *L. aureolineatus, L. balioburius, L. h. herrei,* and *L. h. medianus* by having more midbody dorsal scales (22 or 23 vs. <22); from *L. h. herrei, L. h. medianus,* and *L. bakingibut* by having more paravertebral scales (19 or 20 vs. <19); from *L. babuyanensis, L. h. herrei, L. h. medianus,* and *L. labialis* by having more midbody ventral scales (14–16 vs. <14); from *L. bakingibut* by having fewer ventral scales (12–15 vs. 16); from *L. aureolineatus, L. christiani,* and *L. h. herrei* by having more circumorbital scales (31–34 vs. <31); from *L. aureolineatus, L. h. herrei, L. labialis, L. lugubris,* and *L. planicaudus* by having more circumnasal scales (4 vs. 3); from *L. aureolineatus, L. balioburius, L. h. herrei, L. h. medianus, L. labialis, L. lugubris,* and *L. bakingibut* by having fewer total scansors on Finger III (7 vs. >7); from *L. aureolineatus, L. h. herrei, L. h. medianus, L. labialis,* and *L. lugubris* by having fewer total scansors on Toe IV (8 or 9 vs. >9); from *L. aureolineatus, L. h. herrei, L. h. medianus, L. labialis, L. lugubris,* and *L. bakingibut* by having a moderate number of precloacofemoral pores in males (23 vs. <14 [*L. labialis*], >24 [*L. aureolineatus, L. h. herrei, L. h. medianus, L. lugubris, L. bakingibut*]); from *L. labialis* and *L. lugubris* by having a linear pore series shape (vs. v-shaped); from *L. labialis* by having no cleft on the rostral scale (vs. cleft), more webbing between Toes II and III (1 or 2 vs. 0), and more cloacal spurs (2 or 3 vs. 0); from *L. aureolineatus, L. christiani, L. h. herrei, L. h. medianus, L. lugubris,* and *L. planicaudus* by having a larger axilla–groin distance relative to head length (193.5–198.1% head length vs. <188.2%); from *L. aureolineatus, L. balioburius, L. christiani, L. h. medianus, L. bakingibut,* and *L. lugubris* by having a smaller relative snout–forearm length (34.2–34.3% SVL vs. >34.4%); from *L. aureolineatus, L. balioburius, L. christiani, L. h. herrei, L. h. medianus, L. lugubris,* and *L. planicaudus* by having a larger relative head length (26.4–26.5% SVL vs. <26.4%); from *L. aureolineatus, L. h. herrei, L. h. medianus, L. lugubris, L. bakingibut,* and *L.*

planicaudus by having a larger snout length relative to head length (43.5–44.9% head length vs. <43.3%).

Description of holotype.—Adult male in good condition; large incision in ventral surface from retrieval of genetic sample, hemipenes inverted from preservation. Body moderate, SVL 40.6 mm, axilla–groin distance 52.2% SVL; limbs well-developed, moderately slender; tail original, detached; margins of limbs smooth, lacking cutaneous flaps or dermal folds; trunk lacking ventrolateral cutaneous fold.

Head moderate in size, largely undifferentiated from neck as a result of hypertrophied temporal musculature; snout rounded in dorsal and lateral aspects; head length 26.4% SVL, 267.5% head height; head width 67.3% head length, 180.0% head height; snout length 44.9% head length, 66.7% head width; dorsal surfaces of head homogeneous, with only slight prefrontal and interorbital concavities present; auricular opening large, elongated, angled anteroventrally and posterodorsally, positioned anterior to temporal swellings on either side of head; eye moderate; pupil vertical, margin straight; nostril contacting first supralabial, not contacting rostral; limbs and digits moderate in length, and moderately slender; legs longer than arms, thighs moderately thicker compared with brachium; thigh length 120.8% crus length; leg length 26.1% SVL, 129.3% arm length.

Rostral somewhat rectangular in anterior view, not cleft, bordered laterally by first supralabials, posterolaterally by anterior-most enlarged circumnasals, and posteriorly by three additional scales (= five snout scales); nostril surrounded by first labial and four equally sized enlarged circumnasals; supranasals separated by four heterogeneously sized median scales.

Total number of differentiated supralabials 14/13; total number of differentiated infralabials 12/12, bordered ventrally by slightly enlarged chin and undifferentiated gular scales; total number of chin scales between second and third infralabials 9; number of enlarged scale rows adjacent to chin scales one or two until fourth infralabials; patch of enlarged gular scales on anterior end of gular region continuing to a point in line with third infralabial on both sides.

Dorsal cephalic scales fairly homogeneous in size, shape, disposition, and distribution; cephalic scalation slightly convex, primarily round scales; prefrontal and interorbital depressions slight; undifferentiated posterior head scales slightly convex; gular and throat scales small, oval, rounded, and nonimbricate, making a moderately sharp transition in scalation toward posterior end of neck on ventral surface, with enlarged rounded, hexagonal, nonoverlapping scales; circumorbitals 31 (L). Dorsal body scales round, convex, juxtaposed, relatively homogeneous in size; dorsals sharply transition to flat, nonoverlapping ventrals along lateral body surface; midbody dorsal scales within one eye diameter 22; paravertebral scales within one eye diameter 19; midbody ventral scales within one eye diameter 16; ventral scales within one eye diameter 15; scales on dorsal surfaces of limbs undifferentiated from dorsals; scales on dorsal surfaces of hands and feet similar to dorsal limb scales; ventral body scales flat, rounded, hexagonal, nonoverlapping, much larger than dorsal body scales, relatively homogeneous in size. Enlarged precloacofemoral pore-bearing scales in a continuous, linear row 23; rectangular patch of moderately enlarged precloacal scales directly posterior to pore series and anterior to cloacal opening.

Digits moderately expanded and covered on palmar surface proximally with undivided bowed scansors and distally with divided scansors; total scansors on Finger III seven, first divided scansor on Finger III scansor three, last divided scansor on Finger III scansor seven; total scansors on Toe IV eight, first divided scansor on Toe IV scansor six, last divided scansor on Toe IV scansor eight; webbing between Toes II and III two, between Toes III and IV three.

Tail moderately round, detached, length moderate, 100.2% SVL; tail width 156.3% tail depth; caudals slightly convex, much more subrectangular than dorsals, subcaudals much more rectangular than ventrals; ventrolateral ridge with intermittent, enlarged, imbricate scales present; cloacal spurs at base of tail three.

Coloration of holotype in preservative.—Dorsal surface of body and limbs Grayish Horn Color (Color 268) with chevron patterning of Brownish Olive (Color 276) and Raw Umber (Color 280) running dorsolaterally on both sides of spine; dorsal surface of head Grayish Horn Color (Color 268) with tear-drop shaped spot of Hair Brown (Color 277) present between eyes that extends to a point in line with back of the head; dorsal surface of tail Grayish Horn Color (Color 268) with moderate striping of Brownish Olive (Color 276); ventral surface of body and limbs Smoky White (Color 261) with light speckling of Smoke Gray (Color 266) present; ventral surface of tail has a base color of Smoky White (Color 261) but gradually transitions to Smoke Gray (Color 266) base color with Brownish Olive striping (Color 276) on posterior half of tail.

Measurements and scale counts of holotype (in mm).—Snout–vent length 40.6; axilla–groin distance 21.2; tail length 40.7; tail width 5.0; tail depth 3.2; snout–forearm length 13.9; upper arm length 4.0; forearm length 4.2; thigh length 5.8; crus length 4.8; Finger III length 2.9; Toe IV length 3.5; head length 10.7; head width 7.2; head height 4.0; eye–ear distance 3.5; eye–nostril distance 3.6; snout length 4.8; interorbital distance 1.7; internarial distance 1.6; ear diameter 0.4; eye diameter 2.4; midbody dorsal scales 22; paravertebral scales 19; midbody ventral scales 16; ventral scales 15; supralabials 14; infralabials 12; circumorbital scales 31; circumnasals 4; snout scales 5; chin scales 9; Finger III total scansors 7; Finger III divided scansors 5; Toe IV total scansors 8; Toe IV divided scansors 3; precloacofemoral pores 23; cloacal spurs 3.

Variation.—Variation in mensural and meristic characters is summarized in Table 1. Among the two specimens examined, we observed variation in the number of midbody dorsal, paravertebral, midbody ventral, ventral, supralabial, infralabial, circumorbital, snout, and chin scales, Finger divided III scansors, Toe IV total scansors, and Toe IV divided scansors (Supplemental Table 1).

Distribution.—*Lepidodactylus nakahiwalay* occurs on Lubang Island in the Occidental Mindoro Province. This lineage may occur throughout the Lubang Island Group and may be found on surrounding Ambil, Cabra, and Golo islands; however, current distribution is restricted to Lubang Island exclusively. It is unlikely that this lineage expands beyond the Lubang Island Group; examination of a *Lepidodactylus* specimen from Subic Bay on nearby Luzon Island suggests evolutionary distinction between localities.

Ecology and natural history.—*Lepidodactylus nakahiwalay* has only been observed in well-established secondary-
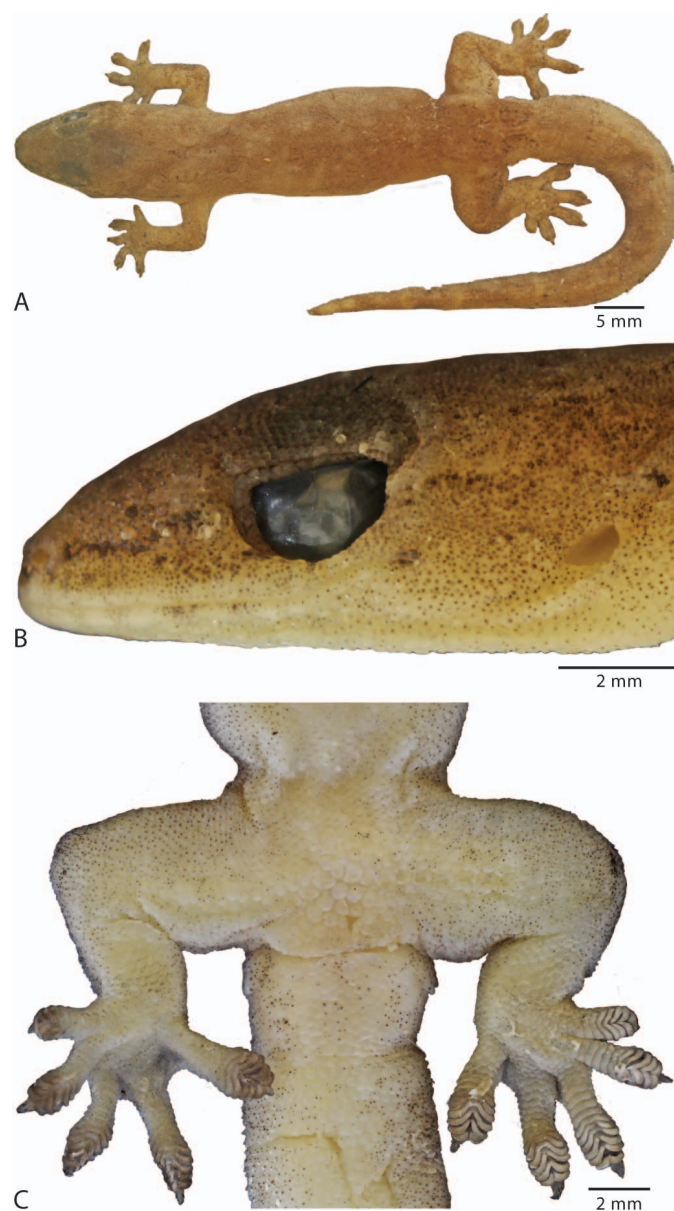

FIG. 7.—Dorsal body (A), head (B), and cloacal region (C) of the holotype of *Lepidodactylus babuyanensis*. A color version of this figure is available online.

growth rainforest habitats and has yet to be observed in more disturbed agricultural or residential areas along the coasts of the island. Like other members of the genus, this arboreal species was observed primarily on small branches or trunks of trees in the forest as well as along small stream systems.

Etymology.—The specific epithet is derived from the Tagalog term for isolated and is in reference to the biogeographically distinct and isolated island of Lubang, which is believed to be surrounded by deep-ocean channels and never in historical contact with surrounding paleoisland landmasses. Suggested common name: Lubang Scaly-toed Geckos.

*Lepidodactylus **babuyanensis*** sp. nov.
(Table 1; Figs. 3C, 7)

Lepidodactylus sp. 4: Oliver et al. 2018:4.

Holotype.—PNM 9877 (formerly OMNH 46971; CDS Field No. 9198), adult male, collected 27 May 2018 at 72 m

in Barangay Magsidel, Municipality of Calayan, Cagayan Province, Calayan Island, Philippines (19.27482°, 121.44701°), by CDS, K. Wang, J. Brown, E.D. Ellsworth, and S.N. Smith.

Paratypes (paratopotypes).—OMNH 46977, 46978, 46979, 46982, 46989 adult males, OMNH 46980, 46981, 46983 46993, 47001 adult females collected 26 May 2018; OMNH 46970, adult male, OMNH 46972, 46973 adult females collected 27 May 2018; OMNH 47002 juvenile, OMNH 46974 subadult female, OMNH 46985 adult male, OMNH 46975, OMNH 46976, 46984, 46986, 46987, 46988, adult females collected 28 May 2018; OMNH 46992 adult male, OMNH 46990, 46991 adult females collected 29 May 2018; OMNH 47004 adult female collected 31 May 2018; OMNH 47005 adult female collected 31 May 2018; OMNH 47006 adult female collected 1 June 2018; OMNH 47007 subadult male collected 1 June 2018; OMNH 46994 subadult male, OMNH 47003 adult female collected 2 June 2018; OMNH 46996 subadult female, OMNH 46997, 46998, 46999, 47000, adult males, OMNH 46995 adult female collected 3 June 2018 by CDS, K. Wang, J. Brown, E.D. Ellsworth, and S.N. Smith.

Other paratypes.—KU 304603 (RMB Field No. 5723) subadult male, collected 6 March 2006, KU 304713 (RMB Field No. 5834) subadult female, collected 9 March 2006 in Barangay Balatabat, Municipality of Calayan, Cagayan Province, Camiguin Norte Island, Philippines. KU 306610 (RMB Field No. 6359), subadult male, collected 13 September 2006, KU 306755 (RMB Field No. 6388), juvenile, collected 15 September 2006, at Nipa Creek, Municipality of Calayan, Cagayan Province, Dalupiri Island, Philippines by J.B. Fernandez.

Diagnosis.—*Lepidodactylus babuyanensis* can be distinguished from congeners by the following combination of characters: (1) body size small (SVL 31.9–39.3 mm); (2) snout–forearm length short, 31.0–39.8% SVL; (3) total arm length short, 18.7–23.3% SVL; (4) total leg length short, 23.4–31.4% SVL; (5) head length short, 24.7–31.9% SVL; (6) Finger III divided scansors 3; (7) precloacofemoral pores in males 18–23; and (8) rostral scale not in contact with the nostril.

Comparisons.—Characters distinguishing *Lepidodactylus babuyanensis* from all other Philippine species of *Lepidodactylus* are summarized in Table 1 and additional comprehensive comparisons are available in Supplemental Table 1. The new species appears to be quite cryptic in phenotype when compared with *L. balioburius*, with little distinction observed among morphometric characters traditionally employed in systematic studies of the genus. However, examination of robust series of both *L. babuyanensis* ($n = 40$) and *L. balioburius* ($n = 16$) reveal that *L. babuyanensis* has tendencies toward being a larger species compared with *L. balioburius*, including a larger body size (maximum SVL 39.3 mm, mean SVL 35.1 mm vs. 35.0 mm, 32.4 mm), a larger relative axilla–groin distance (55.4% SVL, 50.9% SVL vs. 53.2%, 48.0%), a larger axilla–groin distance relative to snout–forearm length (174.0% snout–forearm length, 150.3% snout–forearm length vs. 144.3%, 129.8%), and a smaller eye diameter relative to head length (22% head length, 20.2% head length vs. 23.5%, 21.5%). Additionally, principal component analysis does recover some degree of

separation between these lineages, primarily based on body size (Fig. 1).

Considering all other Philippine congeners, *L. babuyanensis* can be distinguished readily from *L. aureolineatus, L. herrei herrei, L. herrei medianus, L. labialis, L. lugubris,* and *L. planicaudus* by having a rostral scale separated from the nostril (vs. contacting); from *L. h. herrei* and *L. h. medianus* by having more midbody dorsal scales (15–22 vs. <15); from *L. h. herrei* and *L. bisakol* by having a moderate number of paravertebral scales (15–20 vs. <13 [*L. h. herrei*], >20 [*L. bisakol*]); from *L. bisakol, L. nakahiwalay,* and *L. bakingibut* by having fewer midbody ventral scales (9–13 vs. >13); from *L. bisakol* and *L. bakingibut* by having fewer ventral scales (8–12 vs. >14); from *L. lugubris* by having fewer total scansors on Finger III (7–11 vs. >11); from *L. h. herrei* and *L. planicaudus* by having fewer divided scansors on Finger III (3 vs. >3); from *L. aureolineatus, L. h. herrei, L. h. medianus, L. lugubris, L. labialis,* and *L. bakingibut* by having a moderate number of precloacofemoral pores (18–23 vs. <14 [*L. labialis*], >24 [*L. aureolineatus, L. h. herrei, L. h. medianus, L. lugubris, L. bakingibut*]); from *L. labialis* and *L. lugubris* by having a linear pore series shape (vs. v-shaped); from *L. labialis* by having no cleft on the rostral scale (vs. cleft) and more webbing between Toes III and IV (1–3 vs. 0); from *L. bakingibut* by having a larger thigh length relative to crus length (103.8–120.8% crus length vs. 100.0–102.0%); and from *L. christiani* by having a larger Finger III length relative to total arm length (21.7–35.5% arm length vs. <21.4%).

Description of holotype.—Adult male in good condition; large incision in ventral surface from retrieval of genetic sample. Body small, SVL 37.3 mm, axilla–groin distance 50.1% SVL; limbs well-developed, moderately slender; tail original; margins of limbs smooth, lacking cutaneous flaps or dermal folds; trunk lacking ventrolateral cutaneous fold.

Head moderate in size, largely undifferentiated from neck as a result of hypertrophied temporal musculature; snout rounded in dorsal and lateral aspects; head length 26.8% SVL, 285.7% head height; head width 70.0% head length, 200.0% head height; snout length 42.0% head length, 60.0% head width; dorsal surfaces of head homogeneous, prefrontal and interorbital concavities absent; auricular opening large, ovoid, angled slightly anteroventrally and posterodorsally, positioned anterior to temporal swellings on either side of head; eye small; pupil vertical, margin straight; nostril contacting first supralabial, not contacting rostral; limbs and digits moderate in length, and moderately slender; legs longer than arms, thighs moderately thicker compared with brachium; thigh length 104.1% crus length; leg length 26.8% SVL, 128.2% arm length.

Rostral pentagonal in anterior view, not cleft, bordered laterally by first supralabials, posterolaterally by anterior-most enlarged circumnasals, and posteriorly by four heterogeneously sized additional scales (= six snout scales); nostril surrounded by first labial and four equally sized enlarged circumnasals; supranasals separated by four homogeneously sized median scales.

Total number of differentiated supralabials 13/12; total number of differentiated infralabials 12/11, bordered ventrally by slightly enlarged chin and undifferentiated gular scales; total number of chin scales between second and third

infralabials 10; number of enlarged scale rows adjacent to chin scales one until second or third infralabials.

Dorsal cephalic scales fairly homogeneous in size, shape, disposition, and distribution; cephalic scalation slightly convex, primarily round scales; prefrontal and interorbital depressions slight; undifferentiated posterior head scales slightly convex, slightly smaller than cephalic scales; gular and throat scales small, oval, rounded, and nonimbricate, making a gradual transition in scalation toward posterior end of neck on ventral surface, with enlarged rounded, hexagonal, nonoverlapping scales; circumorbitals 31 (L). Dorsal body scales round, slightly convex, juxtaposed, relatively homogeneous in size; dorsals sharply transition to flat, nonoverlapping ventrals along lateral body surface; midbody dorsal scales within one eye diameter 18; paravertebral scales within one eye diameter 17; midbody ventral scales within one eye diameter 10; ventral scales within one eye diameter 10; scales on dorsal surfaces of limbs undifferentiated from dorsals; scales on dorsal surfaces of hands and feet similar to dorsal limb scales; ventral body scales flat, rounded, elongated, subimbricate to nonoverlapping, much larger than dorsal body scales, relatively homogeneous in size. Enlarged precloacofemoral pore-bearing scales in a continuous, linear row 20; triangular patch of moderately enlarged precloacal scales directly posterior to pore series and anterior to cloacal opening.

Digits moderately expanded and covered on palmar surface proximally with undivided bowed scansors and distally with divided scansors; total scansors on Finger III nine, first divided scansor on Finger III scansor seven, last divided scansor on Finger III scansor nine; total scansors on Toe IV seven, first divided scansor on Toe IV scansor five, last divided scansor on Toe IV scansor seven; webbing between Toes II and III two, between Toes III and IV three.

Tail moderately round, wide, length long, 119.3% SVL; tail width 143.3% tail depth; caudals slightly convex, subimbricate to overlapping, much more rectangular than dorsals, subcaudals much more rectangular than ventrals, anterior to posterior in direction; ventrolateral ridge with intermittent, enlarged, imbricate scales present; cloacal spurs at base of tail three.

Coloration of holotype in preservative.—Dorsal surface of body, limbs, and tail a mix of Smoke Gray (Color 266) and Grayish Horn (Color 268); dorsal surface of head similar in coloration to body except for large spot of Sepia (Color 279) extending a point in line with back of the eyes to a point in line with back of head; ventral surface of head, body, limbs, and tail all Smoky White (Color 261).

Coloration of paratype in life.—Based on photograph of OMNH 46977 in life (Fig. 3C). Dorsal surface of head, body, limbs, and tail mostly Drab (Color 19) to Smoke Gray (Color 266) with minimal speckling of Olive-Brown (Color 278) and Sepia (Color 279); very faint chevron patterning present along dorsal surface; faint post orbital stripe of Cream Color (Color 12) with minimal speckling of Sepia (Color 286) extends to a point in line with the posterior end of the head.

Measurements and scale counts of holotype (in mm).—Snout–vent length 37.3; axilla–groin distance 18.7; tail length 44.5; tail width 4.3; tail depth 3.0; snout–forearm length 11.8; upper arm length 3.8; forearm length 4.0; thigh length 5.1; crus length 4.9; Finger III length 2.4; Toe IV

length 3.4; head length 10.0; head width 7.0; head height 3.5; eye–ear distance 2.6; eye–nostril distance 2.9; snout length 4.2; interorbital distance 1.4; internarial distance 1.4; ear diameter 0.7; eye diameter 2.0; midbody dorsal scales 18; paravertebral scales 17; midbody ventral scales 10; ventral scales 10; supralabials 13; infralabials 12; circumorbital scales 31; circumnasals 4; snout scales 6; chin scales 10; Finger III total scansors 9; Finger III divided scansors 3; Toe IV total scansors 7; Toe IV divided scansors 3; precloacofemoral pores 20; cloacal spurs 3.

Variation.—Morphometric variation within this series is summarized in Table 1. Among the 40 specimens examined, we observed variation in the number of midbody dorsal, paravertebral, midbody ventral, ventral, supralabial, infralabial, circumorbital, snout, and chin scales, Finger III total scansors, Toe IV total scansors, and precloacofemoral pores in males (Supplemental Table 1).

Distribution.—*Lepidodactylus babuyanensis* occurs throughout the Babuyan Island Group in Cagayan Province. Individuals have been collected from Calayan, Camiguin Norte, and Dalupiri islands and we anticipate this lineage also inhabits Fuga and Babuyan islands.

Ecology and natural history.—*Lepidodactylus babuyanensis* has been found in patchwork secondary-growth rainforest habitat on multiple islands in the Babuyan Island Group. This species appears to be common in secondary-growth habitats, particularly on Calayan Island, where a large series of individuals were observed during our recent biodiversity surveys. *Lycodon alcalai* is a known predator of this species at least on Calayan Island (Griffing et al. 2019).

Etymology.—The specific epithet is chosen in reference to the biogeographically unique Babuyan Island Group of the northern Philippines, located in the Luzon Strait. The small archipelago is composed of five major islands (Babuyan Claro, Calayan, Camiguin Norte, Dalupiri, and Fuga), as well as associated small islets (Fig. 8). The Babuyan Island Group is surrounded by deep-ocean channels and believed to have never been in historical contact with surrounding paleoisland landmasses. As such, the island group is home to a number of endemic vertebrate species. Suggested common name: Babuyan Scaly-toed Geckos.

DISCUSSION

The four species described here bring the total number of recognized Scaly-toed Geckos endemic to the Philippines to 11. Interestingly, *Lepidodactylus bisakol* and *L. bakingibut* represent the first endemic species described from Luzon Island proper, with *L. babuyanensis* and *L. nakahiwalay* described from small, peripheral, deep-water islands in close proximity to the Luzon PAIC (Calayan, Camiguin Norte, and Dalupiri islands, to the north in the Babuyan Island Group or Lubang Island to the southwest). In addition to the Batan–Sabtang endemic (*L. balioburius*), the Orchid Island population (*L. yami*), plus probable species *L.* sp. 6 and *L.* sp. 7, this entire clade of as many as eight species has gone nearly unstudied over the past half century (Brown and Alcala 1978; Ota 1987; Ota and Crombie 1989). These findings, of endemic Luzon PAIC taxa, stand in contrast to the earlier characterization of the Luzon fauna region as a biogeographic entity with no native *Lepidodactylus* fauna (Brown and Alcala 1978). In addition to the members of this
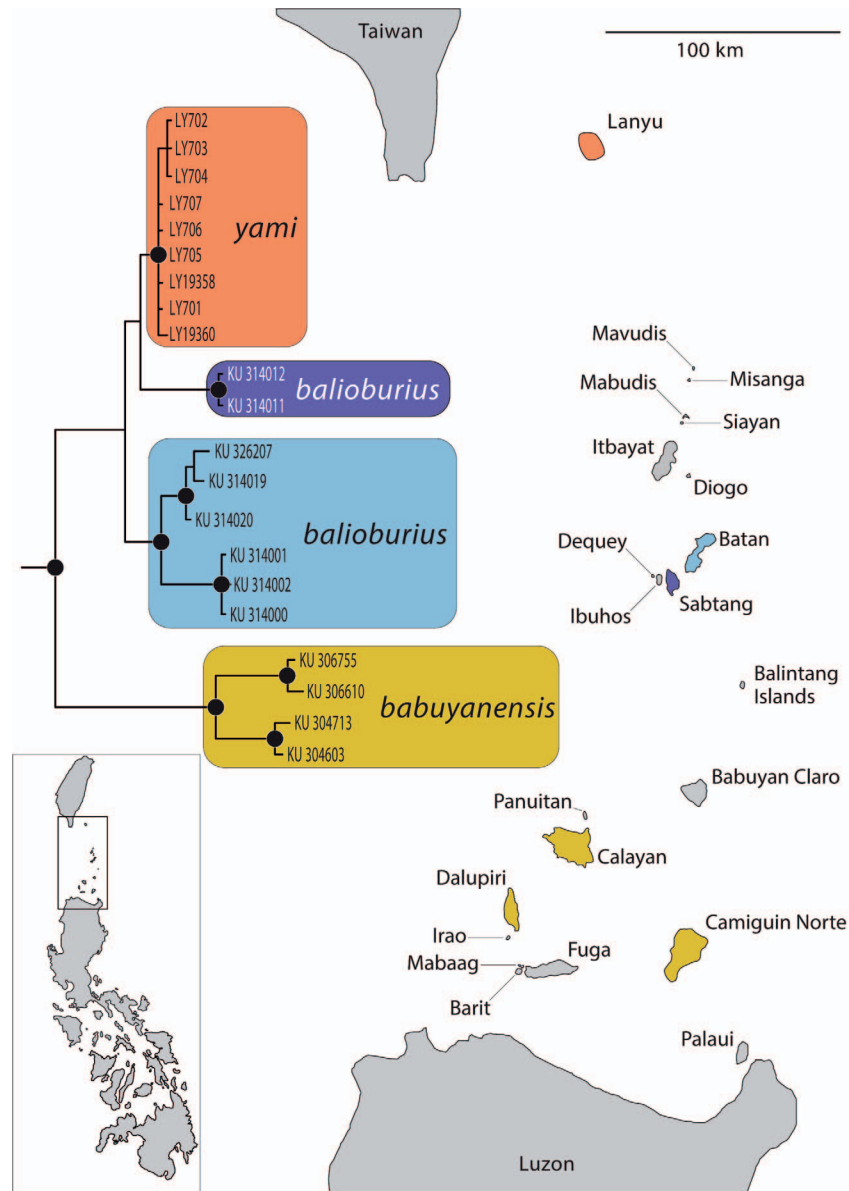
Fɪɢ. 8.—Island distributions of sampled individuals of *Lepidodactylus babuyanensis, L. balioburius,* and *L. yami* across the northern Philippines and southern Taiwan. Color-coded clades correspond to the islands of specimen origination. Note the nonmonophyly of *L. balioburius* populations from neighboring Batan and Sabtang islands. Asterisks following taxonomic names on the topology denote lineages delimited in Poisson Tree Processes (PTP) modeling analysis; taxa without asterisks were subdivided by PTP analysis. A color version of this figure is available online.

novel clade characterized here we anticipate that, with targeted field work (Brown et al. 2012b, 2013; Devan-Song and Brown 2012) focused on *Lepidodactylus* microhabitats, and collection of genetic and phenotypic data, the large, geographically complex island of Luzon will eventually be recognized as home to greater—as of yet unsampled and unrecognized—species diversity (Siler et al. 2011, 2014a; Brown et al. 2011b, 2013, 2020).

Phylogenetic studies suggest that all four species described here are members of Brown and Parker's morphological Group III (1977), and two distinct phenotypic groups of *Lepidodactylus* do exist in the archipelago, as first recognized by Brown and Alcala (1978). However, phylogenetic evidence suggests that splitting Philippine *Lepidodactylus* into two sections, based on morphological characters alone, may lead to erroneous understandings of relationships. As opposed to retaining the Sections A and B of Brown and Alcala (1978), we recognize instead the *L. lugubris* and *L. yami–balioburius* clades. Based on our phylogenetic results, the *L. lugubris* clade contains *L. aureolineatus, L. herrei, L. lugubris,* and *L. planicaudus,* whereas the *L. yami–balioburius* clade contains the two namesake species, *L. christiani,* and all four lineages described here. We abstain from placing *L. labialis* into either clade, pending future availability of vouchered genetic material (Sanguila et al. 2016).

Although phylogenetic relationships within the *L. yami–balioburius* clade are clearer following this study, several uncertainties remain; these warrant further investigation. Oliver et al. (2018) provided genetic evidence for additional lineages in the *L. yami–balioburius* clade (*L.* sp. 6) and even from other nearby and distant insular nations (Fig. 2).

Lepidodactylus sp. 6, for example, from Bulacan Province likely represents yet another distinct lineage from Luzon. However, at the time of this study, we were unable to obtain specimens of these putative lineages for examination of phenotypic variation and, therefore, cannot draw conclusions on their validity as potential species.

Additionally, one individual previously assigned to *L.* sp. 3 (KU 327768; Oliver et al. 2018) from Subic Bay on Luzon Island shows ~13% sequence divergence at the mitochondrial ND2 gene from the two *L. nakahiwalay* type specimens. Furthermore, phylogenetic analyses failed to show strong support for the Subic Bay and Lubang Island populations as a monophyletic group. Unfortunately, because of the availability of a single specimen only from the Subic Bay population, we are not able to evaluate fully the distinctiveness of this lineage and reference it as *L.* sp. 7 pending the collection of additional vouchered material. Given this individual's genetic divergence and the recognized biogeographic distinctiveness of this region of Luzon Island from the deep-ocean island of Lubang (Brown and Diesmos 2009; Devan-Song and Brown 2012), it would not be surprising if the population from Subic is a distinct species.

Finally, although *L. babuyanensis* is genetically distinct from both *L. yami* and *L. balioburius,* the latter two species show limited genetic differentiation from each other (<2.7%). Further complicating this situation, two individuals from Sabtang Island in the Batanes Island chain, assigned to *L. balioburius* (KU 314011, 314012), exhibit less genetic distance from *L. yami* ($\approx$ 2.0–2.1%) than they do from other members of *L. balioburius* from Batan Island ($\approx$ 3.0–3.9%; Fig. 2). This is particularly puzzling because Sabtang is located <5 km away from Batan (the type locality of *L. balioburius*) and is >170 km away from Lanyu (the type locality of *L. yami;* Fig. 8). Ota and Crombie (1989) struggled to find a single morphological trait to distinguish the two species and, instead, relied on a suite of traits for their diagnosis of *L. balioburius.* Now with phylogenetic evidence, the distinction between *L. yami* and *L. balioburius* is even less clear. In the description of *L. balioburius* (Ota and Crombie 1989), type specimens were examined from Batan Island only; our expanded sampling and examinations of specimens from throughout the Batanes and Babuyan Islands may find the two to be conspecific. We could not address the validity of *L. balioburius* and *L. yami* as distinct entities at this time because of our limited sample size for *L. yami.*

A biogeographic link between Luzon and Lanyu herpetofauna has been documented previously in skinks (Ota and Huang 2000) and even another gekkonid species in *Gekko kikuchii* (Siler et al. 2014c). Interestingly, both examples are believed to be conspecific with individuals from Luzon Island and possible recent introductions (Ota and Huang 2000; Siler et al. 2014c). The presence of *L. yami* on Lanyu Island, a potential conspecific in *L. balioburius* in the Batanes Islands, and a discreet species in *L. babuyanensis* in the Babuyan Island chain provides an intriguing opportunity to study the dispersal and speciation of herpetofauna across deep ocean barriers in this intervening biogeographic region (Fig. 8). Along with untangling taxonomic relationships between *L. yami* and *L. balioburius,* future studies could examine the directionality with which gekkonid species have moved historically between the Philippines and Taiwan and investigate modalities of faunal exchange between deep-oceanic geographic barriers (Siler et al. 2014c).

Despite this investigation, clarifying a small number of taxonomic uncertainties among Philippine *Lepidodactylus,* new systematic issues need further scrutiny to comprehend fully the relationships among Scaly-toed Geckos in the Philippines. Currently recognized taxa need further validation, and putative, novel lineages suggested by genetic data, should be explored. With >20 gekkonid species having been described from the Philippines in the past decade alone (Uetz et al. 2020), our understanding of species diversity is improving rapidly, but still leaves many questions (Brown et al. 2020). Greater insight into Philippine gekkonid evolutionary lineage diversity will allow for novel, higher level phylogenetic analyses (Wood et al. 2020), which must further explore relationships among the genera *Lepidodactylus, Luperosaurus,* and *Pseudogekko.* In depth, densely sampled future studies of these focal clades provide particularly promising opportunities for improving our understanding of reptile diversification patterns across the complex landscape of the Philippine archipelago.

Supplemental Material

Supplemental material associated with this article can be found online at https://doi.org/10.1655/HERPMONO GRAPHS-D-19-00014.S1.

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APPENDIX

Specimens Examined

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

Lepidodactylus aureolineatus (9).—MINDANAO ISLAND, Agusan Province, Bunauan (MCZ R–26109–R–26117).

Lepidodactylus babuyanensis (42).—CALAYAN ISLAND, Cagayan Province, Municipality of Calayan, Barangay Magsidel (Holotype PNM 9877, formerly OMNH 46971), (Paratopotypes OMNH 46970–47003); Sitio Longog (Paratypes OMNH 47004–47007); CAMIGUIN NORTE ISLAND, Cagayan Province, Municipality of Calayan, Barangay Balatabat (Paratypes KU 304603, 304713); DALUPIRI ISLAND, Cagayan Province, Municipality of Calayan, Nipa Creek (Paratypes KU 306610, 306755).

Lepidodactylus bakingibut (2).—LUZON ISLAND, Cagayan Province, Municipality of Gonzaga, Barangay Magrafil, Mt. Cagua, (Holotype PNM 9875, formerly KU 330066), (Paratype KU 330065).

Lepidodactylus balioburius (22).—BATAN ISLAND, Batanes Province, Municipality of Basco (KU 314000–314008), Municipality of Ivana (KU 314019, 314020), Municipality of Mahatao (KU 326207); SABTANG ISLAND, Batanes Province, Municipality of Sabtang (KU 314009–314018).

Lepidodactylus bisakol (8).—LUZON ISLAND, Albay Province, Municipality of Tabaco, Barangay Mariroc, Sitio Nagsipit (Holotype PNM 9874, formerly OMNH 46002), (Paratopotype OMNH 46003), Municipality of Malinao, Barangay Tanawan (Paratype KU 331652); Sorsogon Province, Municipality of Irosin, Barangay San Rogue, Bulusan Lake, on Mt. Bulusan (Paratype TNHC 62481); Barangay Cawayan, Mt. Cawayan (Paratypes KU 347921, 348462); Barangay Cogon, Mt. Jormahan (Paratype KU 346536); Municipality of Bulusan, Barangay San Francisco, Bayugin Falls (Paratype KU 346537).

Lepidodactylus christiani (14).—NEGROS ISLAND, Negros Oriental Province (CAS–SUR 24246–24250, CAS 129326, 129335, 129351, 129352, 133058, 133059), Municipality of Sibulan (CAS 128877–128879).

Lepidodactylus herrei herrei (18).—NEGROS ISLAND, Negros Oriental Province (CAS 129297, 129298, 129353–129355, 129376, 129377, 132661–132667, 132675); Municipality of Valencia, Barangay Bongbong, Cuernos de Negros Mountain Range, Mt. Talinis (KU 327769, TNHC 62476, 62477).

Lepidodactylus herrei medianus (16).—CEBU ISLAND, Cebu Province, Cebu City (CAS–SUR 27302, CAS 125239–125242, 140036, 140037), Municipality of Carmen (CAS–SUR 24813, CAS 131821), Municipality of Dalaguete (CAS 128434, 129047, 129063, 129064), Municipality of Minglanilla (CAS 185693); PORO ISLAND, Cebu Province, Municipality of Poro (CAS 125126, 125127).

Lepidodactylus labialis (15).—MINDANAO ISLAND, Agusan del Norte Province, Municipality of Cabadbaran (CAS 133209, 133210, 133238, 133243, 133258, 133314–133317, 133329, 133338, 133339, 133353–133356, 133790).

Lepidodactylus lugubris (20).—GREAT AND LITTLE GOVENEN ISLANDS, Basilan Province (MCZ R–26087, R–26088, R–26092, R–26093, R–85747–R–85750); BASILAN ISLAND, Basilan Province (CAS 60507,

60508, 60510, 60513–60518, 60520); LUZON ISLAND, Albay Province, Municipality of Malinao (KU 331651, 331653).

Lepidodactylus nakahiwalay (2).—LUBANG ISLAND, Occidental Mindoro Province, Municipality of Lubang, Barangay Vigo, Sitio Dangay (Holotype PNM 9876, formerly KU 320411), (Paratopotype KU 320410).

Lepidodactylus planicaudus (15).—MINDANAO ISLAND, Cotobato or Sulturan Kudarat Province, Tatayan to Saub, Cotobato coast (MCZ R–26094–R–26099, R–26101, R–26102, R–163938, R–163939, R–163941, R–163943–R–163945); Davao del Sur Province, Mt. Apo (KU 327715).

Lepidodactylus yami (2).—*TAIWAN*, LANYU ISLAND, Imoro (USNM 267944), Lung Men (USNM 291811).

Lepidodactylus sp. 7 (1).—LUZON ISLAND, Zambales Province, Municipality of Olongapo, Subic Bay (KU 327768).