# Additions to Philippine Slender Skinks of the Brachymeles bonitae Complex (Reptilia: Squamata: Scincidae) II: a new species from the northern Philippines 

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#### Abstract

We describe a new digitless scincid lizard of the genus Brachymeles from northern Luzon and Camiguin Norte islands in the Philippines. This species belongs to the Brachymeles bonitae Complex, and both molecular and morphological data confirm that this species is distinct from all other congeners. Formerly considered to be a single widespread species, this group of species has been the focus of recent systematic reviews. Here we describe a new species in the B. bonitae Complex, recognized currently to constitute five species. Brachymeles ilocandia sp. nov. is the second digitless and the seventeenth non-pentadactyl species in genus. The description of this species brings the total number of species in the genus to 40 , and provides new insight into unique distribution patterns of species of the northern Philippines.


Key words: Babuyan Island Group, biodiversity, ecological niche modeling, endemism, faunal region, fossorial, Luzon Island, non-pentadactyl, pentadactyl

## Introduction

The genus Brachymeles Duméril \& Bibron includes a moderate radiation of semi-fossorial (burrowing) lizards in the family Scincidae that is distributed throughout the Philippine archipelago and in limited areas of mainland and insular Southeast Asia. This genus has been the focus of numerous recent taxonomic studies, and as a result of several phylogenetic studies and examination of museum collections, alpha diversity within Brachymeles has increased dramatically over the last five years, from 15 to 39 species (for review, see Davis et al. 2014; Geheber et al. 2016). The majority of species of Brachymeles are found exclusively in the Philippines; the two exceptions include B. miriamae Heyer from Thailand and B. apus Hikida from Borneo (Heyer 1972; Hikida 1982). Though the morphology and evolutionary history of Brachymeles are both well represented in the literature, the ecology of
these species is not well known (Davis et al. 2014). Species prefer dry habitats and have been found in leaf litter, loose soil, or under decaying logs (Siler et al. 2009, 2010a,b, 2011a,b,c,d, 2012a; Davis et al. 2014). Most species are found in disturbed secondary growth lowland habitats; however, several species (B. apus, B. elerae Taylor, B. muntingkamay Siler, Rico, Duya \& Brown, and B. wrighti Taylor) inhabit mid- to high-elevation habitats (Siler 2010; Siler et al. 2009, 2011d).

With the exception of differences in limb and digit morphology, species in the genus Brachymeles have conserved body plans and pigmentation patterns. All species are slender, elongate lizards possessing relatively homogeneous brown scale coloration. Interestingly, the clade represents one of only a handful of scincid genera to possess a full spectrum of digit and limb states, from species with more robust, pentadactyl limbs to those with externally limbless bodies (Siler \& Brown 2010, 2011; Siler et al. 2011a, 2012a; Davis et al. 2014). Of the 39 currently recognized species of Brachymeles, 18 are pentadactyl (B. bicolor Gray, B. boholensis Brown \& Rabor, B. boulengeri Taylor, B. gracilis Fischer, B. hilong Brown \& Rabor, B. kadwa Siler \& Brown, B. makusog Siler, Diesmos \& Brown, B. mindorensis Brown \& Rabor, B. orientalis Brown \& Rabor, B. samad Siler, Jones, Diesmos, Diesmos \& Brown, B. schadenbergi Fischer, B. suluensis Taylor, B. talinis Brown, B. taylori Brown, B. tiboliorum Siler, Jones, Diesmos, Diesmos \& Brown, B. tungaoi Siler \& Brown, B. vindumi Siler \& Brown, and B. vulcani Siler, Jones, Diesmos, Diesmos \& Brown), 16 are non-pentadactyl and have limbs that are reduced in size and digit number (B. bicolandia Siler, Fuiten, Jones, Alcala \& Brown, B. bonitae Duméril \& Bibron, B. brevidactylus Siler, Fuiten, Jones, Alcala \& Brown, B. cebuensis Brown \& Rabor, B. cobos Siler, Fuiten, Jones, Alcala \& Brown, B. elerae, B. isangdaliri Davis, Feller, Brown \& Siler, B. libayani Siler, Fuiten, Jones, Alcala \& Brown, B. mapalanggaon Davis, Feller, Brown \& Siler, B. muntingkamay, B. paeforum Siler, Fuiten, Jones, Alcala \& Brown, B. pathfinderi Taylor, B. samarensis Brown, B. ligtas Geheber, Davis, Watters, Penrod, Feller, Davey, Ellsworth, Flanagan, Heitz, Moore, Nguyen, Roberts, Sutton, Sanguila, Brown \& Siler, B. tridactylus Brown, and B. wrighti), and five are completely limbless (B. apus, B. lukbani Siler, Balete, Diesmos \& Brown, B. minimus Brown \& Alcala, B. miriamae, and B. vermis Taylor) (Davis et al. 2014; Geheber et al. 2016). Non-pentadactyl, reducedlimbed species represent a sizeable portion of the morphological diversity observed within the genus. Of these species, one is digitless ( $B$. mapalanggaon), one is monodactyl ( $B$. isangdaliri), four are bidactyl ( $B$. bicolandia, $B$ brevidactylus, B. cobos, and B. samarensis), four are tridactyl (B. libayani, B. muntingkamay, B. paeforum, and B. tridactylus), and two are tetradactyl (B. elerae, and B. wrighti) (Davis et al. 2014). Additionally, three species have unequal numbers of fingers and toes, with $B$. cebuensis having three fingers and two toes, B. ligtas having two fingers and zero toes, and B. pathfinderi with five fingers and four toes (Siler et al. 2011c). Finally, Brachymeles bonitae sensu stricto represents an instance of both cases: some individuals have digitless limbs while others have two fingers and one toe (Davis et al. 2014).

Philippine species of Brachymeles form a monophyletic clade, suggesting in situ diversification of the genus across the archipelago (Siler \& Brown 2011; Siler et al. 2011a). Hypotheses for the high levels of Philippine diversity of plants and animals have focused on the influence of changing sea levels on species diversification (Brown et al. 2013). During Pleistocene glacial cycles, decreases in the sea level led to the formation of Philippine Aggregate Island Complexes (PAICs; Brown \& Guttman 2002; Brown \& Diesmos 2002, 2009; Fig. 1A) in which adjacent islands separated by shallow seas were connected by land bridges, allowing for faunal exchange and gene flow between islands within a single PAIC (Brown \& Diesmos 2002; Brown et al. 2002, 2009, 2013). Although this process likely contributed to the development of distinct faunal regions within the Philippines, studies suggest that species diversification patterns in Brachymeles do not follow predicted PAIC-based diversification patterns, with evidence suggesting a number of overseas dispersal events may have also taken place during the radiation of this group throughout the archipelago (Siler et al. 2011a). Furthermore, studies on radiations of other Philippine reptiles (Linkem et al. 2010, 2011; Siler et al. 2010c, 2012b, 2014; Welton et al. 2013, 2014; Brown \& Siler 2013) have also partially or fully rejected PAIC formation and fragmentation events in the generation and maintenance of species diversity. These studies suggest that additional diversification mechanisms need to be explored to accurately assess and understand the processes that have resulted in the country's diversity of Brachymeles. Regardless of the mechanisms involved, amphibian and reptile diversity in the archipelago is largely endemic (Brown et al. 2013; Diesmos et al. 2015).

The genus Brachymeles was first described in 1839 by Duméril and Bibron for the species B. bonitae, a small, elongate, limb-reduced species from Manila, on Luzon Island. To date, 11 published reviews or descriptions of the genus or species groups within the genus have improved our understanding of this unique radiation of burrowing
lizards (Taylor 1917; Brown 1956; Brown \& Rabor 1967; Brown \& Alcala 1980; Siler \& Brown 2010; Siler et al. 2011a,b,c,d, 2012a; Davis et al. 2014). Furthermore, much of the recent taxonomic resolution has been fueled by continued field surveys across the Philippines and the incorporation of genetic data into studies exploring specieslevel diversity in the genus. Guided by robust phylogenetic estimates, subsequent assessments of morphological diversity revealed many historically recognized widespread species were actually complexes of numerous distinct evolutionary lineages (Siler \& Brown 2010, 2011; Siler et al. 2011a, 2012a; Davis et al. 2014; Geheber et al. 2016). As a result, most of these complexes have now been appropriately revised to formally recognize all unique evolutionary lineages (four species of the $B$. boulengeri Complex [Siler \& Brown 2010], five species of the $B$. bonitae Complex [Davis et al. 2014; Geheber et al. 2016], seven species of the B. gracilis Complex [Siler et al. 2012a], nine species of the B. samarensis Complex [Siler et al. 2011b], two species of the B. schadenbergi Complex [Siler \& Brown 2010], and three species of the B. talinis Complex [Siler \& Brown 2010]).


FIGURE 1. (A) Map of the Philippines islands, with labels for islands discussed in the study, the five recognized major PAICs, major island groups, and additional deep-water islands provided for reference. Current islands in the Philippines are shown in medium grey to black; light gray areas enclosed in black 120 m bathymetric contours indicate the hypothesized maximum extent of land during the mid- to late Pleistocene. Vouchered localities for Brachymeles ilocandia sp. nov. marked by red circles. (B) Mapped output of Maxent results as the mean ecological niche model of suitable climatic conditions for Brachymeles ilocandia sp. nov. projected across the known distribution of the genus throughout the Philippines. Values corresponding to the likelihood of climatic suitability are included for scale and interpretation of heat map color-coding. Values are logistic-transformed for ease of interpretation on a scale of $0-1$, according to the default Maxent output settings (ENM analysis and projection performed by NAH and MP).

With the exception of the historically recognized distribution of B. talinis spanning from the southernmost islands of the Mindanao Faunal Region in the Philippines to the Babuyan Island Complex north of the Luzon Faunal Region (Fig. 1A; Siler \& Brown 2010; Siler et al. 2011a), B. bonitae was recognized as having one of the largest distributions of any species within the genus, with populations found throughout much of the central and northern Philippines and spanning multiple PAICs (Siler et al. 2011a; Davis et al. 2014; Geheber et al. 2016). However, recent investigations focused on this widespread species have clarified the distributions of true $B$. bonitae and the closely related tridactyl species $B$. tridactylus, and recognized three additional lineages within the species complex (Davis et al. 2014; Geheber et al. 2016). Currently, the B. bonitae Complex comprises five recognized species: B. bonitae, B. isangdaliri, B. ligtas, B. mapalanggaon, and B. tridactylus. Of these species, both $B$. tridactylus and true $B$. bonitae are known from a number of sites within the Philippines; however, based on our current understanding of their natural histories, B. isangdaliri, B. mapalanggaon, and B. ligtas have limited ranges (Davis et al. 2014; Geheber et al. 2016). Due to the secretive and semi-fossorial nature of these skinks, it is likely that additional, undescribed diversity exists within the complex (Davis et al. 2014; Geheber et al. 2016).

In this paper, we describe a new digitless species of Brachymeles in the B. bonitae Complex from Luzon Island, discuss its potential distribution, comment on its natural history and ecology, and provide the first illustrations of its diagnostic head scale patterns.

## Materials and methods

Field work, sample collection, and specimen preservation. Fieldwork was conducted on Camiguin Norte, Catanduanes, Lubang, Luzon, Marinduque, Masbate, Mindoro, Polillo, Sibuyan, and Tablas islands, all in the Philippines (Fig. 1A), between 1991 and 2012. Specimens were collected during the day, euthanized with MS-222, dissected for tissue samples (liver preserved in $95 \%$ ethanol), fixed in $10 \%$ formalin, and eventually ( $<2 \mathrm{mo}$ ) transferred to $70 \%$ ethanol. Specimens are deposited in U.S. and Philippine museum collections (see Acknowledgments and Specimens Examined). Museum abbreviations for specimens examined follow those from Sabaj Pérez (2014).

Morphological data. We examined fluid-preserved specimens (Appendix I) for variation in qualitative, meristic (scale counts) and mensural (measurements) characters. Sex was determined by gonadal inspection, and measurements were taken to the nearest 0.1 mm with digital calipers by CDS. X-rays were taken with a company cabinet X-ray on Kodak MIN-R 2000 film exposed at 5 milliamperes and 30 volts for 1 minute 15 seconds.

Meristic and mensural characters were chosen based on Siler et al. (2009a, 2010a,b): snout-vent length (SVL), axilla-groin distance (AGD), total length (TotL), midbody width (MBW), midbody height (MBH), tail length (TL), tail width (TW), head length (HL), head width (HW), snout-forearm length (SnFa), eye diameter (ED), eye-nares distance (END), snout length (SNL), fore-limb length (FLL), hind limb length (HLL), midbody scale-row count (MBSR), paravertebral scale-row count (PVSR), axilla-groin scale-row count (AGSR), supralabial count (SL), infralabial count (IFL), supraciliary count (SC), and supraocular count (SO). Additionally, we counted the number of presacral vertebrae (PSV) from X-ray images of specimens. In the description, ranges are followed by mean $\pm$ standard deviation in parentheses.

Distribution model. We estimated the geographic distribution of the new species using ecological niche modeling (ENM) that searches for associations between species' presence and environmental conditions (Soberón \& Peterson 2005). We used the SDMtoolbox (v1.1c; Brown 2014) package in ArcMap (v10.2; ESRI 2013) to generate a minimum convex polygon that included the 13 known localities of occurrence for B. ilocandia sp. nov. and used the polygon to limit the extent of the environmental data input in the model (Barve et al. 2011). To characterize the environment, we downloaded 19 bioclimatic variables at 30 arc-seconds resolution (approximately 1 km ; Hijmans et al. 2005) derived from weather station data from the 1950-2000 period and ran a correlation analysis to remove highly correlated variables, thus limiting collinearity in our dataset. As a result, we retained five variables to run the ecological niche model: annual mean temperature ( BIO 1 ), mean diurnal range ( BIO ), isothermality (BIO3), annual precipitation (BIO12), and precipitation of driest month (BIO14). All pairs of variables had a correlation coefficient below 0.7, except for two: BIO12 - BIO14 (|r$\left.{ }^{2} \mid=0.8\right)$ and BIO12 -BIO2 ( $\left|\mathrm{r}^{2}\right|$ $=0.82$ ). To generate the niche model and estimate potential distribution, we used the Maxent maximum entropy algorithm (v3.3.3k; Phillips et al. 2006, Phillips \& Dudík 2008) with the default settings except for the number of
replicates, which we modified from the default (one) to five replicates. Each of these five models was built with a different subset of occurrences split into two groups: one larger subset for model calibration and one smaller subset for model performance evaluation with five-fold cross-validation (Hijmans 2012). The replicates were trained at the geographic extent encompassing all known occurrences for B. ilocandia sp. nov. and projected at the extent of the entire Philippine archipelago known to possess species of Brachymeles to estimate the potential distribution of the species in the region (Brown \& Rabor 1967; Siler \& Brown 2010; Davis et al. 2014). We used the average of Maxent suitability scores of the five replicates to map the potential distribution of the species. To assess the model predictive accuracy of each replicate, we examined omission error, representing the proportion of presences (used for model validation) that are incorrectly predicted absent by the model. Omission error is calculated by converting the continuous Maxent suitability values to presence-absence; all values below the lowest value associated with a presence (from the training dataset; "lowest presence threshold"; Pearson et al. 2007) are assigned a value of zero (absent) and all at or above that value are assigned a value of one (present).

Species concept. For this study, we apply the General Lineage Concept of species (de Queiroz 1998, 1999), as an extension of the Evolutionary Species Concept (Simpson 1961; Wiley 1978; Frost \& Hillis 1990). We consider phenotypically divergent populations as distinct lineages, especially if such populations are allopatric. In this study we diagnose a new species based on diagnostic character differences in non-overlapping morphological character states.

Research experience in the undergraduate classroom. As part of the Spring 2015 Herpetology Course (BIOL 4083) taught by CDS at the University of Oklahoma, students took part in a semester long, small group writing assignment, with each group assigned a distinct lineage of Brachymeles to describe under a structured writing and mentoring program (Siler et al. unpublished data). Detailed description of this course project has been made freely available at http://www.webcitation.org/6hEkRmogM (Watters \& Siler 2016).

## Taxonomic account

## Brachymeles ilocandia sp. nov.

(Figs. 2, 3)

Brachymeles bonitae Duméril \& Bibron 1839; Taylor 1917; Brown 1956:5; Brown \& Rabor 1967:526; Brown \& Alcala 1970; Brown \& Alcala 1980:20; Davis et al. 2014; Geheber et al. 2016.

Holotype. PNM 9819 (RMB Field No. 7324, formerly KU 308004), adult female, collected under a decaying log in secondary-growth forest on 10 February 2007, Sitio Kauringan, Barangay Balatubat, Municipality of Calayan, Cagayan Province, Camiguin Norte Island, Philippines ( $18.902^{\circ} \mathrm{N}, 121.908^{\circ}$ E; WGS $84 ; 303 \mathrm{~m}$ elev.), by J. Fernandez.

Paratypes (Paratopotypes). One adult female (KU 307967), collected on 8 February 2006 in Sitio Kauringan, Barangay Balatubat, Municipality of Calayan, Cagayan Province, Camiguin Norte Island, Philippines, by J. Fernandez and RMB. Four adult females, collected under a decaying log in secondary-growth forest on 11 February 2007 (KU 308019, 308020), 12 February 2007 (KU 308027), and 14 February 2007 (KU 308030) in Sitio Kauringan, Barangay Balatubat, Municipality of Calayan, Cagayan Province, Camiguin Norte Island, Philippines, by J. Fernandez and C. Oliveros.

Paratypes. One adult female (CAS 61377), collected in 1920 in Nayon, Ifugao Subprovince, Mountain Province, Luzon Island, Philippines. One adult female (FMNH 259449), collected on 10 March 2001 in Kalinga Province, Luzon Island, Philippines, by RMB and ACD. One adult female (KU 304567), collected on 5 March 2006 in "Limandok," Barangay Balatabat, Municipality of Calayan, Cagayan Province, Camiguin Norte Island, Philippines ( $18.92927^{\circ}$ N, $121.89881^{\circ}$ E; WGS 84; 403 m elev.), by J. Fernandez and RMB.

Diagnosis. Following recent taxonomic revisions of Brachymeles (Siler et al. 2011; Davis et al. 2014; Geheber et al. 2016) the new species is assigned to the $B$. bonitae Complex based on the following suite of morphological characters: (1) limbs present, (2) non-pentadactyl, (3) fore-limbs with $0-3$ fingers, (4) hind limbs with $0-2$ toes, (5) paravertebral scale rows $\geq 91$, (6) presacral vertebrae 47-53, (7) supraoculars four, (8) enlarged, differentiated nuchals present, (9) longitudinal rows of dark spots around the body absent, and (10) auricular opening absent.



FIGURE 2. Illustration of head of Brachymeles ilocandia sp. nov. (PNM 9819, holotype) in dorsal, lateral, and ventral views. Taxonomically diagnostic head scales are labeled as follows: C, chin shield; F, frontal; FN, frontonasal; FP, frontoparietal; IL, infralabial; IP, interparietal; L, loreal; M, mental; N, nasal; Nu, nuchal; P, parietal; PF, prefrontal; PM, postmental; PO, preocular; PSO, presubocular; R, rostral; SC, supraciliary; SL, supralabial; SN, supranasal; and SO, supraocular. Roman numerals indicate scales in the supraocular series, with Arabic numbers indicating scales in the supraciliary series. Illustrations by MLP and CDS.


FIGURE 3. Photograph of dorsal, lateral, and ventral views of head of the preserved holotype of Brachymeles ilocandia sp. nov. (PNM 9819). Photographs taken by JLW and MLP.

Brachymeles ilocandia sp. nov. can be distinguished from congeners by the following combination of characters: (1) body size small (SVL 65.7-77.6 mm), (2) limbs digitless, (3) limb length short, (4) supralabials six, (5) infralabials five or six, (6) supraciliaries five, (7) supraoculars four, (8) midbody scale rows 22-24, (9) axillagroin scale rows 80-82, (10) paravertebral scale rows 97-100, (11) mental/first infralabial fusion present or absent, (12) prefrontal contact absent or in point contact, (13) frontoparietal contact present, (14) enlarged chin shields in three pairs, (15) nuchals enlarged, (16) auricular opening absent, (17) presacral vertebrae 50-53, and (18) uniform body color (Tables 1, 2).

TABLE 1. Summary of mensural characters among species of the Brachymeles bonitae Complex. Sample size, body length and total length among males and females, and general geographical distribution (PAIC = Pleistocene Aggregate Island Complexes, sensu Brown \& Diesmos [2002]) are included for reference (SVL, TotL, FLL, and HLL given as range over mean $\pm$ standard deviation; all body proportions given as percentage over mean $\pm$ standard deviation).

|  | bonitae $(3 \mathrm{~m}, 1 \mathrm{f})$ | ilocandia sp. nov. $(9 \mathrm{f})$ | isangdaliri $(1 \mathrm{f})$ | $\begin{aligned} & \hline \text { ligtas } \\ & (3 \mathrm{~m}, 2 \mathrm{f}) \end{aligned}$ | mapalanggaon $(3 \mathrm{~m}, 6 \mathrm{f})$ | tridactylus $(12 \mathrm{~m}, 9 \mathrm{f})$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Range | Luzon \& Polillo islands | Luzon \& Camiguin Norte islands | Luzon Island | Lubang Island | Masbate Island | West Visayan PAIC |
| SVL (f) | 69.4 | $\begin{aligned} & 65.7-77.6 \\ & (73.7 \pm 3.7) \end{aligned}$ | 59.5 | $\begin{aligned} & 60.7-69.2 \\ & (65.0 \pm 6.0) \end{aligned}$ | $\begin{aligned} & 61.7-75.8 \\ & (67.2 \pm 5.4) \end{aligned}$ | $\begin{aligned} & 59.9-82.3 \\ & (71.4 \pm 6.9) \end{aligned}$ |
| SVL (m) | $\begin{aligned} & 69.7-78.4 \\ & (72.8 \pm 4.8) \end{aligned}$ | N/A | N/A | $\begin{aligned} & 69.4-79.6 \\ & (74.5 \pm 5.1) \end{aligned}$ | $\begin{aligned} & 65.1-72.7 \\ & (68.4 \pm 3.9) \end{aligned}$ | $\begin{aligned} & 60.7-77.6 \\ & (69.0 \pm 6.0) \end{aligned}$ |
| TotL (f) | N/A | $\begin{aligned} & 122.3-146.0 \\ & (134.1 \pm 8.0) \end{aligned}$ | 106.1 | 119.4 | 120.2 | 133.6 |
| TotL (m) | 122.0 | N/A | N/A | 160.6 | $\begin{aligned} & 112.6-118.6 \\ & (115.6 \pm 4.3) \end{aligned}$ | $\begin{aligned} & 120.9-154.1 \\ & (136.0 \pm 9.8) \end{aligned}$ |
| TL/SVL | 73 | $\begin{aligned} & 81-90 \\ & (85 \pm 3) \end{aligned}$ | 78 | $\begin{aligned} & 97-102 \\ & (99 \pm 4) \end{aligned}$ | $\begin{aligned} & 67-84 \\ & (78 \pm 9) \end{aligned}$ | $\begin{aligned} & 85-112 \\ & (95 \pm 10) \end{aligned}$ |
| FLL | $\begin{aligned} & 1.0-1.7 \\ & (1.3 \pm 0.3) \end{aligned}$ | $\begin{aligned} & 1.1-1.4 \\ & (1.3 \pm 0.1) \end{aligned}$ | 1.3 | $\begin{aligned} & 1.2-1.4 \\ & (1.3 \pm 0.1) \end{aligned}$ | $\begin{aligned} & 0.8-1.0 \\ & (0.9 \pm 0.1) \end{aligned}$ | $\begin{aligned} & 1.5-2.5 \\ & (2.0 \pm 0.3) \end{aligned}$ |
| FLL/SVL | $\begin{aligned} & 1-2 \\ & (2 \pm 0) \end{aligned}$ | $\begin{aligned} & 1-2 \\ & (2 \pm 0) \end{aligned}$ | 2 | $\begin{aligned} & 2-2 \\ & (2 \pm 0) \end{aligned}$ | $\begin{aligned} & 1-2 \\ & (1 \pm 0) \end{aligned}$ | $\begin{aligned} & 2-4 \\ & (3 \pm 0) \end{aligned}$ |
| HLL | $\begin{aligned} & 1.5-2.3 \\ & (1.9 \pm 0.3) \end{aligned}$ | $\begin{aligned} & 1.6-1.9 \\ & (1.8 \pm 0.1) \end{aligned}$ | 2.2 | $\begin{aligned} & 1.6-2.0 \\ & (1.8 \pm 0.1) \end{aligned}$ | $\begin{aligned} & 1.2-1.6 \\ & (1.4 \pm 0.1) \end{aligned}$ | $\begin{aligned} & 2.6-3.6 \\ & (3.1 \pm 0.3) \end{aligned}$ |
| HLL/SVL | $\begin{aligned} & 2-3 \\ & (3 \pm 0) \end{aligned}$ | $\begin{aligned} & 2-3 \\ & (2 \pm 0) \end{aligned}$ | 4 | $\begin{aligned} & 2-3 \\ & (3 \pm 0) \end{aligned}$ | $\begin{aligned} & 2-2 \\ & (2 \pm 0) \end{aligned}$ | $\begin{aligned} & 3-6 \\ & (5 \pm 1) \end{aligned}$ |

Comparisons. Brachymeles ilocandia sp. nov. can be distinguished from B. bonitae by having fewer axillagroin scale rows ( $80-82$ versus $83-90$ ) and fewer paravertebral scale rows ( $97-100$ versus 103-110); from B. ligtas by having a greater number axilla-groin scale rows ( $80-82$ versus $74-76$ ), paravertebral scale rows ( $97-100$ versus 91-93), and fewer presacral vertebrae (47 versus 50); from B. isangdaliri by having fewer supraciliaries ( 5 versus 6), the presence (versus absence) of a third chin shield pair, and a longer snout-vent length ( $65.7-77.6 \mathrm{~mm}$ versus 59.5); from B. mapalanggaon by having a longer fore-limb length ( $1.1-1.4 \mathrm{~mm}$ versus $0.8-1.0$ ); from B. tridactylus by having a shorter fore-limb length (1.1-1.4 mm versus $1.5-2.5$ ); from $B$. isangdaliri and $B$. mapalanggaon by
having a longer total length (122.3-146.0 mm versus 106.1 [B. isangdaliri] or 120.2 [B. mapalanggaon]); from B. isangdaliri and B. tridactylus by having digitless limbs (versus unidactyl [B. isangdaliri] or tridactyl [B. tridactylus]), a greater number of presacral vertebrae (50-53 versus 47 [B. isangdaliri, B. tridactylus]), greater number of axilla-groin scale rows (80-82 versus 73 [B. isangdaliri] or 72-79 [B. tridactylus]), and a shorter hindlimb length ( $1.6-1.9 \mathrm{~mm}$ versus 2.2 [B. isangdaliri] or 2.6-3.6 [B. tridactylus]).

Brachymeles ilocandia sp. nov. can be distinguished from all limbless species of Brachymeles by having limbs, and from all pentadactyl species of Brachymeles by having digitless limbs.

Description of holotype. Details of the head scalation are shown in Figures 2 and 3. Adult, female, body small, slender, SVL 74.2 mm ; head weakly differentiated from neck, nearly as wide as body, HW $5.9 \%$ SVL, $86.4 \% \mathrm{HL}$; HL 38.4\% SnFa; $\mathrm{SnFa} 17.8 \% \mathrm{SVL}$; snout broadly rounded in dorsal and lateral profile, SNL $60.0 \%$ HL; ear completely hidden by scales; eyes small, ED $15.9 \% \mathrm{HL}, 42.0 \%$ END, pupil subcircular; body slightly depressed, nearly uniform in thickness, MBW $129.1 \% \mathrm{MBH}$; scales smooth, glossy, imbricate; longitudinal scale rows at midbody 23 ; paravertebral scale rows 97 ; axilla-groin scale rows 80 ; limbs short, diminutive, bluntly rounded; digits absent; finger and toe lamellae absent; FLL 2.0\% AGD, 1.5\% SVL; HLL 3.0\% AGD, 2.3\% SVL; tail not as wide as body, gradually tapered towards end, TW 87.2\% MBW, TL 83.3\% SVL.

Rostral projecting onto dorsal snout to level in line with midline nasal, roughly equal in width and height, in contact with frontonasal; frontonasal wider than long; nostril ovoid, in posterodorsal corner of single trapezoidal nasal, longer axis directed posterodorsally and anteroventrally; supranasals present; postnasals absent; prefrontals narrowly separated; frontal roughly diamond-shaped, its anterior margin in moderate contact with frontonasal, in contact with first two anterior supraoculars, $4 \times$ wider than anterior supraocular; supraoculars four; frontoparietals moderate, moderately separated, each frontoparietal in contact with supraoculars two and three; interparietal large, its length roughly equal to $2 \times$ midline length of frontoparietal, longer than wide, diamond-shaped, wider anteriorly, pineal eyespot visible in center; parietals broader than frontoparietals, in broad contact behind interparietal; enlarged nuchals present; loreals two, anterior loreal slightly longer and higher than posterior loreal; preocular one; presubocular one; supraciliaries five, the anteriormost contacting prefrontal and separating posterior loreal from first supraocular, posteriormost extending to midline of fourth supraocular; subocular scale row single, incomplete, in contact with supralabials; lower eyelid with one row of scales; supralabials six, first nearly twice the width of others, third, fourth and fifth subocular; infralabials five (Fig. 2).

Mental wider than long, fused with first infralabials; postmental single, enlarged, its width narrower than width of mental; followed by three pairs of enlarged chin shields, first pair narrowly separated, second pair largest, narrowly separated, third pair smallest, broadly separated by three medial scales (Fig. 2). Scales on limbs smaller than body scales.

Variation. Differences in scalation patterns were observed among the type series. Observed scale row counts variation included: midbody scale rows of 22 (FMNH 259449, KU 308030), 23 (CAS 61377, KU 307967, 308004, 308019, 308027), and 24 (KU 304567, 308020); axilla-groin scale rows of 80 (CAS 61377, FMNH 259449, KU 308004, 308030), 81 (KU 307967, 308019, 308020), and 82 (KU 304567, 308027); paravertebral scale rows of 97 (KU 308004), 98 (FMNH 259449, KU 307967, 308019, 308020, 308030), 99 (CAS 61377), and 100 (KU 304567, 308027); and five (KU 308004, 308027, 308030) or six (CAS 61377, FMNH 259449, KU 304567, 307967, 308019, 308020) infralabials. Additionally, a low level of variation was observed in the presence of a fused mental and first infralabial scale (both sides of head in KU 308004 and 308030, right side of head only in KU 308027). This character was absent in all other specimens examined.

Coloration of holotype in life. Coloration in life is unrecorded; however, because Brachymeles specimens do not change significantly during preservation (CDS, RMB personal observations), we suspect that the preserved coloration and patterns are much like those in life.

Coloration of holotype in preservative. The dorsal, lateral and ventral regions of the trunk and tail are a solid Prout's Brown (Color 47; Köhler 2012). The head has the same background color, with dense speckling on the dorsal and lateral surfaces, causing the head to appear more Hair Brown (Color 277; Köhler 2012) in color. In the vicinity of each orbit there is a Fuscous (Color 283; Köhler 2012) splotch. The ventral region of the head is the same solid Prout's Brown (Color 47; Köhler 2012) as the trunk.
TABLE 2. Summary of meristic and qualitative diagnostic characters (present, absent) among species of the Brachymeles bonitae Complex. The pairs of enlarged scales posterior to the postmental scale are abbreviated as chin shield pairs with reference to the $1^{\text {st }}, 2^{\text {nd }}$, and $3^{\text {rd }}$ pairs (when present). In cases of scale
count variation within species, numbers of individuals showing specific counts are given in parentheses. Numbers in parentheses after each species indicate
male ( m ) and female (f) individuals examined.

| Diagnostic character | bonitae $(3 \mathrm{~m}, 1 \mathrm{f})$ | ilocandia sp. nov. $(9 \mathrm{f})$ | isangdaliri $(1 \mathrm{f})$ | $\begin{aligned} & \hline \text { ligtas } \\ & (3 \mathrm{~m}, 2 \mathrm{f}) \end{aligned}$ | mapalanggaon (3 m, 6 f) | tridactylus $(12 \mathrm{~m}, 9 \mathrm{f})$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Number of digits (fingers/toes) | $\begin{aligned} & \hline 0 / 0^{1} \\ & 2 / 1^{1} \end{aligned}$ | 0/0 | 1/1 | 2/0 | 0/0 | 3/3 |
| PSV | 53 | 50-53 | 47 | 50 | 51 | 47 |
| MBSR | 21-24 | 22-24 | 22 | 22 | 22, 23 | 22-24 |
| AGSR | 83-90 | 80-82 | 73 | 74-76 | 80-84 | 72-79 |
| PVSR | 103-110 | 97-100 | 97 | 91-93 | 99-102 | 90-98 |
| SL | 6 | 6 | 6 | 6 | 6 | $\begin{aligned} & 6(13) \\ & 7(8) \end{aligned}$ |
| IFL | 5 | $\begin{aligned} & 5(3) \\ & 6(6) \end{aligned}$ | 6 | 6 | $\begin{aligned} & 5(8) \\ & 6(1) \end{aligned}$ | $\begin{aligned} & 6(13) \\ & 7(8) \end{aligned}$ |
| SC | 5 | 5 | 6 | 5 | 5 | 5 |
| SO | 4 | 4 | 4 | 4 | 4 | 4 |
| Prefrontal contact | Absent | Absent or Point contact | Absent | Absent | Absent | Absent |
| Frontoparietal contact | Absent | Absent | Absent | Present | Point contact or Absent | Absent |
| $1{ }^{\text {st }}$ chin shield pair contact | Absent | Absent | Absent | Present or Absent | Absent | Present or Absent |
| $3{ }^{\text {rd }}$ chin shield pair | Present | Present | Absent | Present | Present or Absent | Present |
| Mental/1 $1^{\text {st }}$ IFL fusion | Present | Present or Absent | Absent | Absent | Present or Absent | Absent |
| Enlarged nuchals | Present | Present | Present | Present | Present | Present |
| Longitudinal rows of dark spots | Absent | Absent | Absent | Absent | Absent | Absent |

[^0]Distribution, ecology and natural history. Brachymeles ilocandia sp. nov. is known only from northern Luzon and Camiguin Norte islands (Fig. 1A). The new species likely once occurred in low- to mid-elevation primary forest habitats; however, all recent observations of this species have occurred in secondary growth forest habitats. In contrast to the other members of the B. bonitae Complex, this species appears to be quite common in secondary growth forest fragments throughout the northern Philippines. Brachymeles ilocandia sp. nov. is found in parts of its distribution with B. bicolor, B. kadwa, and B. boulengeri. Other species of Brachymeles known to occur in the Luzon PAIC include B. bicolandia, B. bonitae, B. brevidactylus, B. cobos, B. elerae, B. isangdaliri, B. kadwa, B. lukbani, B. makusog, B. minimus, B. muntingkamay, and B. wrighti (Davis et al. 2014).

We have evaluated this species against the International Union for Conservation of Nature (IUCN) criteria for classification and find that it does not qualify for Critically Endangered, Endangered, Vulnerable, or Near Threatened status. Not only does B. ilocandia sp. nov. occur on more than one island, but also the species appears common in secondary growth and disturbed habitats throughout its recognized distribution. Therefore, we recommend that this species be classified as Least Concern, LC (IUCN 2015).

Etymology. The specific epithet is chosen in reference to the biogeographically and culturally distinct homeland, "Ilocandia", of the Ilokano people of the northern Philippines, the third largest ethnolinguistic group in the country. Including the Babuyan Island Group north of Luzon Island, Ilocandia stretches from the western coast of northern Luzon, across the Cagayan Valley, to parts of central Luzon and the boundaries of Aurora Province in the east. The region is home to many endemic vertebrates, diverse geographic landscape, unique local cuisine, and rich cultural traditions. Suggested common name: Ilokano Slender Skink.

## Discussion

With the description of Brachymeles ilocandia sp. nov. the total number of species within Brachymeles increases to 40. Only 18 species of Brachymeles were recognized prior to 2010 (for review, see Siler et al. 2010); therefore, described Brachymeles diversity has increased by more than $220 \%$ within the last decade. Cryptic, as well as phenotypically distinct, evolutionary lineages within Brachymeles have been detected recently, largely a result of comprehensive biodiversity surveys across the Philippines, careful examination of vouchered natural history collections, and the use of genetic data (Table 3). Furthermore, it is likely that continued survey efforts throughout the Philippines and thorough investigation of phenotypic and genetic variation will result in the recognition of additional species-level diversity within the genus.

TABLE 3. Uncorrected pairwise sequence divergence (\%) for mitochondrial data for focal species of the Brachymeles bonitae Complex (Brachymeles bonitae, B. ilocandia sp. nov., B. isangdaliri, B. ligtas, B. mapalanggaon, and B. tridactylus). Percentages on the diagonal represent intraspecific genetic diversity (bolded for emphasis). Data based on Siler et al. (2011a) and Davis et al. (2014).

|  | bonitae | ilocandia sp. nov. isangdaliri | ligtas | mapalanggaon | tridactylus |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| bonitae | $\mathbf{0 . 2 - 1 . 5}$ |  |  |  |  |  |
| ilocandia sp. nov. | $9.5-9.7$ | $\mathbf{0 . 0}$ |  |  |  |  |
| isangdaliri | $9.5-10.0$ | 10.5 | $\mathbf{0 . 0}$ |  |  |  |
| ligtas | $8.8-9.5$ | $6.9-7.0$ | 10.0 | $\mathbf{0 . 7}$ |  |  |
| mapalanggaon | $9.0-11.1$ | $10.5-11.2$ | $10.4-11.2$ | $10.3-11.1$ | $\mathbf{2 . 6}$ |  |
| tridactylus | $8.6-9.6$ | $10.5-11.0$ | $9.5-10.3$ | $9.8-10.2$ | $7.8-8.8$ | $\mathbf{0 . 1 - 5 . 0}$ |

Brachymeles ilocandia sp. nov. is a new species within the B. bonitae Complex found in areas of secondarygrowth forests on northern Luzon Island and Camiguin Norte Island. Originally thought to be a single widespread species distributed across the central and northern Philippines, $B$. bonitae is now recognized as a species complex containing multiple unique evolutionary lineages (Davis et al. 2014; Geheber et al. 2016). The new species is the sixth recognized species of the $B$. bonitae Complex, with a unique digitless body form only shared with one other species in the genus (B. mapalanggaon from Masbate Island; Davis et al. 2014). Brachymeles ilocandia sp. nov. also possesses an allopatric distribution compared with all other species in the complex (Davis et al. 2014; Geheber
et al. 2016), including: true B. bonitae sensu Davis et al. (2014) from Polillo Island and central Luzon Island, B. isangdaliri from southeastern Luzon, B. mapalanggoan from Masbate Island, B. ligtas from Lubang Island, and B. tridactylus from Boracay, Carabao, Inampulugan, Negros, and Panay islands. Lineages of the B. bonitae Complex represented in phylogenetic and systematic studies have revealed considerable genetic divergence among populations with available vouchered genetic samples (Siler et al. 2011a; Davis et al. 2014). In fact, mitochondrial sequence divergences among all recognized members of the complex range from $6.9-11.2 \%$, with an average among lineage uncorrected pairwise mitochondrial sequence divergence of $9.9 \%$ (Table 3 ). This level of divergence is considerable for any species complex, particularly when compared with divergences between previously defined species-viz., B. cebuensis, B. minimus, B. lukbani (Table 3; Siler et al. 2011a,b, 2012a; Davis et al. 2014).

Interestingly, species within the B. bonitae Complex are found on several different PAICs. Brachymeles ilocandia sp. nov., $B$. bonitae, and $B$. isangdaliri have been recorded from islands of the Luzon PAIC, $B$. mapalanggoan and B. tridactylus from the Western Visayan PAIC, B. ligtas from the Mindoro PAIC, and B. ilocandia sp. nov. from the Babuyan Island Group. Phylogenetic studies focused on the genus have rejected PAIC formation and fragmentation as an explanatory mechanism behind patterns of diversification in this group (Siler et al. 2011a); therefore, it is possible that the distribution and diversification of species within the B. bonitae Complex occurred as a result of overseas dispersal (Siler et al. 2011a). This is further supported by the distribution of $B$. ilocandia sp. nov., which inhabits islands that are part of two separate PAICs and were never connected by land (Fig. 1A).

Furthermore, the results of ecological niche modeling support the possibility that additional envelopes of suitable climate conditions exist across the northeast Luzon PAIC and Babuyan Island Group beyond those verified by vouchered populations of B. ilocandia sp. nov. observed during biodiversity surveys (Fig. 1B). Specifically, the remainder of the Babuyan Island Group, the entirety of Aurora Province, and eastern Quezon Province (General Nakar Province) on the Luzon PAIC represent regions predicted to possess suitable climatic conditions; however, no records of populations of B. ilocandia sp. nov. are known from these regions (Fig. 1B). Additional surveys of these regions are necessary to ascertain whether this species truly has a broader range than is currently recognized. These geographic regions are known to possess other species of Brachymeles, including microendemic congeners (e.g., B. elerae and B. isangdaliri; Siler 2010; Siler et al. 2011d; Davis et al. 2014), and thus represent unique faunal subregions on Luzon Island that warrant further study and conservation efforts (Siler et al. 2011d; Davis et al. 2014). Moreover, discovery of additional populations of B. ilocandia sp. nov. in these predicted regions may provide new insights into intraspecific genetic and morphological variation.

Luzon Island is the largest island within the Philippine archipelago, and, as such, contains the greatest number of species of Brachymeles. Following the recognition of B. ilocandia $\mathbf{~ s p}$. nov., 13 species are now recognized to occur on Luzon Island: B. bicolandia, B. bonitae, B. brevidactylus, B. cobos, B. elerae, B. isangdaliri, B. kadwa, B. lukbani, B. makusog, B. minimus, B. muntingkamay, B. wrighti, and B. ilocandia sp. nov. (Davis et al. 2014). Brachymeles ilocandia sp. nov. is co-distributed across parts of its range with the large pentadactyl species $B$. bicolor, B. kadwa, and B. boulengeri (Siler \& Brown 2011; Davis et al. 2014). All species of Brachymeles are known to be semi-fossorial, with sympatric species often found within the same rotting log or root network (CDS, personal observation). However, to date, little is known of the ecology or natural history of species in the genus, and future research on community structure, functional capacities, and species microhabitat requirements within Brachymeles should be conducted to improve our understanding of this unique radiation of lizards.

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## References

Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S.P., Peterson, A.T., Soberón, J. \& Villalobos, F. (2011) The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecological Modeling, 222, 1810-1819.
http://dx.doi.org/10.1016/j.ecolmodel.2011.02.011
Brown, J.L. (2014) SDMtoolbox: a python?based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. Methods in Ecology and Evolution, 5, 694-700. http://dx.doi.org/10.1111/2041-210X. 12200
Brown, R.M. \& Diesmos, A.C. (2002) Application of lineage-based species concepts to oceanic island frog populations: the effects of differing taxonomic philosophies on the estimation of Philippine biodiversity. Silliman Journal, 42, 133-162.
Brown, R.M. \& Diesmos, A.C. (2009) Philippines, Biology. In: Gillespie, R., Clague, D. (Eds.), Encyclopedia of Islands. University of California Press, Berkeley, California, pp. 723-732.
Brown, R.M. \& Guttman, S.I. (2002) Phylogenetic systematics of the Rana signata complex of Philippine and Bornean stream frogs: reconsideration of Huxley's modification of Wallace's Line at the Oriental-Australian faunal zone interface. Biological Journal of the Linnean Society, 76, 393-461. http://dx.doi.org/10.1111/j.1095-8312.2002.tb01704.x
Brown, R.M. \& Siler, C.D. (2013) Spotted stream frog diversification at the Australasian faunal zone interface, mainland versus island comparisons, and a test of the Philippine dual umbilici hypothesis. Journal of Biogeography, 41, 182-195. http://dx.doi.org/10.1111/jbi. 12192
Brown, R.M., Diesmos, A.C. \& Alcala, A.C. (2002) The state of Philippine herpetology and the challenges for the next decade. Silliman Journal, 42, 18-87
Brown, R.M., Siler, C.D., Diesmos, A.C. \& Alcala, A.C. (2009) The Philippine frogs of the genus Leptobrachium (Anura; Megophryidae): phylogeny-based species delimitation, taxonomic revision, and descriptions of three new species. Herpetological Monograph, 23, 1-44. http://dx.doi.org/10.1655/09-037.1
Brown, R.M., Siler, C.D., Oliveros, C.H., Esselstyn, J.A., Diesmos, A.C., Hosner, P.A., Linkem, C.W., Barley, A.J., Oaks, J.R., Sanguila, M.B., Welton, L.J., Blackburn, D.S., Moyle, R.G., Peterson, A.T. \& Alcala, A.C. (2013) Evolutionary processes of diversification in a model island archipelago. Annual Review of Ecology, Evolution, and Systematics, 44, 411-435. http://dx.doi.org/10.1146/annurev-ecolsys-110411-160323
Brown, W.C. (1956) A revision of the genus Brachymeles (Scincidae), with descriptions of new species and subspecies. Breviora, 54, 1-19.
Brown, W.C. \& Alcala, A.C. (1970) The zoogeography of the Philippine Islands, a fringing archipelago. Proceedings of the California Academy of Sciences, 38, 105-130.
Brown, W.C. \& Alcala, A.C. (1980) Philippine Lizards of the Family Scincidae. Philippine University Press, Dumaguete City, 264 pp.
Brown, W.C. \& Rabor, D.S. (1967) Review of the genus Brachymeles (Scincidae), with descriptions of new species and subspecies. Proceedings of the California Academy of Sciences, 15, 525-548.
Davis D.R., Feller, K.D., Brown, R.F. \& Siler, C.S. (2014) Evaluating the diversity of Philippine Slender Skinks of the Brachymeles bonitae Complex (Reptilia: Squamata: Scincidae): redescription of B. tridactylus and descriptions of two new species. Journal of Herpetology, 48, 480-494. http://dx.doi.org/10.1670/13-173
de Queiroz, K. (1998) The general lineage concept of species, species criteria, and the process of speciation: a conceptual unification and terminological recommendations. In: Howard, D.J. \& Berlocher, S.H. (Eds.), Endless Forms: Species and Speciation. Oxford University Press, New York, pp. 57-75.
de Queiroz, K. (1999) The general lineage concept of species and the defining properties of the species category. In: Wilson, R.A. (Ed.), Species: New Interdisciplinary Essays. Massachusetts Institute of Technology Press, Cambridge,

Massachusetts, pp. 49-89.
Diesmos, A.C., Watters, J.L., Huron, N.A., Davis, D.R., Alcala, A.C., Crombie, R.I., Afuang, L.E., Gee-Das, G., Sison, R.V., Sanguila, M.B., Penrod, M.L., Labonte, M.J., Davey, C.S., Leone, E.A., Diesmos, M.L., Sy, E.Y., Welton, L.J., Brown, R.M. \& Siler, C.D. (2015) Amphibians of the Philippines, part I: checklist of the species. Proceedings of the California Academy of Sciences, Fourth Series, 62, 457-539.
Duméril, A.M.C. \& Bibron, G. (1839) Erpétologie Général ou, Histoire Naturelle Compléte des Reptiles. Librairie Encylopédique de Roret, Paris, France, 488 pp.
ESRI (2013) ArcGIS Desktop: Release 10.2. Environmental Systems Research Institute, Redlands, CA.
Frost, D.R. \& Hillis, D.M. (1990) Species in concept and practice: herpetological applications. Herpetologica, 46, 87-104. http://www.jstor.org/stable/3892607
Geheber, A.D., Davis, D.R., Watters, J.W., Penrod, M.L., Feller, K.D., Davey, C.S., Ellsworth, E.D., Flanagan, R.L., Heitz, B.D., Moore, T., Nguyen, M.D.C., Roberts, A., Sutton, J., Sanguila, M.B., Linkem, C.W., Brown, R.M. \& Siler, C.D. (2016) Additions to the Philippine slender skinks of the Brachymeles bonitae Complex (Reptilia: Squamata: Scincidae: Brachymeles) I: a new species from Lubang Island. Zootaxa, 4132 (1), 1-14. http://dx.doi.org/10.11646/zootaxa.4132.1.1
Heyer, W.R. (1972) A new limbless skink (Reptilia: Scincidae) from Thailand with comments on the generic status of the limbless skinks of Southeast Asia. Fieldiana: Zoology, 58, 109-129.
http://dx.doi.org/10.5962/bhl.title. 3184
Hijmans, R.J. (2012) Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null model. Ecology, 93, 679-688.
Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. \& Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology, 25, 1965-1978. http://dx.doi.org/10.1002/joc. 1276
Hikida, T. (1982) A new limbless Brachymeles (Sauria: Scincidae) from Mt. Kinabalu, North Borneo. Copeia, 1982, 840-844. http://dx.doi.org/10.2307/1444095
International Union for Conservation of Natura (IUCN) (2015) IUCN Red List of Threatened Species. Version 2015.4. Available from: http://www.iucnredlist.org (accessed 15 July 2015)
Köhler, G. (2012) Color Catalog for Field Biologists. Herpeton, Offenbach, Germany, 49 pp.
Linkem, C.W., Hesed, K.M., Diesmos, A.C. \& Brown, R.M. (2010) Species boundaries and cryptic lineage diversity in a Philippine forest skink complex (Reptilia; Squamata; Scincidae: Lygosominae). Molecular Phylogenetics and Evolution, 56, 572-85. http://dx.doi.org/10.1016/j.ympev.2010.03.043
Linkem, C.W., Diesmos, A.C. \& Brown, R.M. (2011) Molecular systematics of the Philippine forest skinks (Reptilia: Scincidae: Sphenomorphus): testing morphological and biogeographic hypotheses of interspecific relationships. Zoological Journal of the Linnaean Society, 163, 1217-1243. http://dx.doi.org/10.1111/j.1096-3642.2011.00747.x
Pearson, R.G., Raxworthy, C., Nakamura, M. \& Peterson, A.T. (2007) Predicting species' distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. Journal of Biogeography, 34, 102-117. http://dx.doi.org/10.1111/j.1365-2699.2006.01594.x
Phillips, S.J., Anderson, R.P. \& Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. Ecological Modelling, 190, 231-259.
http://dx.doi.org/10.1016/j.ecolmodel.2005.03.026
Phillips, S.J. \& Dudík, M. (2008) Modeling of species distributions with MaxEnt: new extensions and a comprehensive evaluation. Ecography, 31, 161-175. http://dx.doi.org/10.1111/j.0906-7590.2008.5203.x
Sabaj Pérez, M.H. (Ed.) (2014) Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an online reference. Version 5.0. American Society of Ichthyologists and Herpetologists, Washington, D.C. Available from: http://www.asih.org/ (accessed 1 June 2015)
Siler, C.D. (2010) Squamata, Scincidae, Brachymeles elerae (Taylor, 1917): Rediscovery in Old Balbalan, Cordillera Mountain Range, Luzon Island, Philippines, and natural history. Check List, 6, 616-618. http://www.checklist.org.br
Siler, C.D. \& Brown, R.M. (2010) Phylogeny-based species delimitation in Philippine slender skinks (Reptilia: Squamata: Scincidae: Brachymeles): taxonomic revision of pentadactyl species groups and description of three new species. Herpetological Monographs, 24, 1-54. http://dx.doi.org/10.1655/HERPMONOGRAPHS-D-10-00003.1
Siler, C.D. \& Brown, R.M. (2011) Evidence for repeated acquisition and loss of complex body-form characters in an insular clade of Southeast Asian semi-fossorial skinks. Evolution, 65, 2641-2663.
http://dx.doi.org/10.1111/j.1558-5646.2011.01315.x
Siler, C.D., Rico, E.L., Duya, M.R. \& Brown, R.M. (2009) A new limb-reduced, loam-swimming skink (Squamata: Scincidae: Brachymeles) from central Luzon Island, Philippines. Herpetologica, 65, 449-459. http://dx.doi.org/10.1655/08-076.1

Siler, C.D., Diesmos, A.C. \& Brown, R.M. (2010a) A new loam-swimming skink, genus Brachymeles (Reptilia: Squamata: Scincidae) from Luzon and Catanduanes Islands, Philippines. Journal of Herpetology, 44, 49-60. http://www.jstor.org/stable/40665006
Siler, C.D., Balete, D.S., Diesmos, A.C. \& Brown, R.M. (2010b) A new legless loam-swimming lizard (Reptilia: Squamata: Scincidae: genus Brachymeles) from the Bicol Peninsula, Luzon Island, Philippines. Copeia, 2010, 114-122. http://dx.doi.org/10.1643/CH-08-231
Siler, C.D., Oaks, J.R., Esselstyn, J.A., Diesmos, A.C. \& Brown, R.M. (2010c) Phylogeny and biogeography of Philippine bent-toed geckos (Gekkonidae: Cyrtodactylus) contradict a prevailing model of Pleistocene diversification. Molecular Phylogenetics and Evolution, 55, 699-710. http://dx.doi.org/10.1016/j.ympev.2010.01.027
Siler, C.D., Diesmos, A.C., Alcala, A.C. \& Brown, R.M. (2011a) Phylogeny of Philippine slender skinks (Scincidae: Brachymeles) reveals underestimated species diversity, complex biogeographical relationships, and cryptic patterns of lineage diversification. Molecular Phylogenetics and Evolution, 59, 53-65. http://dx.doi.org/10.1016/j.ympev.2010.12.019
Siler, C.D., Fuiten, A.M., Jones, R.M., Alcala, A.C. \& Brown, R.M. (2011b) Phylogeny-based species delimitation in Philippines slender skinks (Reptilia: Squamata: Scincidae) II: taxonomic revision of Brachymeles samarensis and description of five new species. Herpetological Monographs, 25, 76-112.
http://dx.doi.org/10.1655/herpmonographs-d-10-00013.1
Siler, C.D., Crombie, R.I., Diesmos, A.C. \& Brown, R.M. (2011c) Redescription of two poorly known slender skinks, Brachymeles bicolor and Brachymeles pathfinderi (Reptilia: Squamata: Scincidae), from the Philippines. Journal of Herpetology, 45, 355-369. http://dx.doi.org/10.1670/10-103.1
Siler, C.D., Jones, R.M., Welton, L.J. \& Brown, R.M. (2011d) Redescription of tetradactyl, Philippine slender skinks (genus Brachymeles). Herpetologica, 67, 300-317. http://dx.doi.org/10.1655/herpetologica-d-10-00071.1
Siler, C.D., Jones, R.M., Diesmos, A.C., Diesmos, M.L. \& Brown, R.M. (2012a) Phylogeny-based species delimitation in Philippine slender skinks (Reptilia: Squamata: Scincidae) III: taxonomic revision of the Brachymeles gracilis complex and descriptions of three new species. Herpetological Monographs, 26, 135-172. http://dx.doi.org/10.1655/herpmonographs-d-11-00006.1
Siler, C.D., Oaks, J.R., Welton, L.J., Linkem, C.W., Swab, J.C., Diesmos, A.C. \& Brown, R.M. (2012b) Did geckos ride the Palawan raft to the Philippines? Journal of Biogeography, 39, 1217-1234. http://dx.doi.org/10.1111/j.1365-2699.2011.02680.x
Siler, C.D., Oaks, J.R., Cobb, K., Ota, H. \& Brown, R.M. (2014) Critically endangered island endemic or peripheral population of a widespread species? Conservation genetics of Kikuchi's gecko and the global challenge of protecting peripheral oceanic island endemic vertebrates. Diversity and Distributions, 20, 756-772. http://dx.doi.org/10.1111/ddi. 12169
Simpson, G.G. (1961) Principles of Animal Taxonomy. Columbia University Press, New York, New York, 247 pp.
Taylor, E.H. (1917) Brachymeles, a genus of Philippine lizards. The Philippine Journal of Science, 12, 267-279.
Watters, J.L. \& Siler, C.D. (2016) Involving Undergraduates in Research - Herpetology, Spring 2015. Available from: http:// cameronsiler.com/biol4083-docs-2015 (accessed 3 May 2016).
Welton, L.J., Siler, C.D., Oaks, J.R., Diesmos, A.C. \& Brown, R.M. (2013) Multilocus phylogeny and Bayesian estimates of species boundaries reveal hidden evolutionary relationships and cryptic diversity in Southeast Asian monitor lizards. Molecular Ecology, 22, 3495-3510. http://dx.doi.org/10.1111/mec. 12324
Welton, L.J., Wood, P.L. Jr., Oaks, J.R., Siler, C.D. \& Brown, R.M. (2014) Fossil-calibrated phylogeny and historical biogeography of Southeast Asian water monitors (Varanus salvator Complex). Molecular Phylogenetics and Evolution, 74, 29-37. http://dx.doi.org/10.1016/j.ympev.2014.01.016
Wiley, E.O. (1978) The evolutionary species concept reconsidered. Systematic Zoology, 21, 17-26. http://dx.doi.org/10.2307/2412809

## Author contributions

CDS conceived the idea; CDS, ADG, and JLW carried out assignment instruction and mentoring; ACD, MLD, CHO, RMB, and CDS participated in fieldwork; MLP created scientific illustrations; NAH created the map; MP assisted in creating the map; AA, AA, DC, TH, AM, NP, and LP compiled and analyzed the dataset; AA, AA, DC, TH, AM, NP, and LP led the writing; CDS, DRD, ESF, NAH, ADG, and JLW assisted in finalizing the manuscript for publication; DRD, ESF, NAH, ADG, JLW, MLP, AA, AA, DC, TH, AM, NP, LP, CHO, RMB, and CDS edited drafts of the manuscript.

APPENDIX I. Additional specimens examined.

Specimens examined in addition to those in Geheber et al. (2016). Number in parentheses indicates the number of specimens examined. Several sample sizes are greater than those observed in the description due to the examination of sub-adult specimens which were excluded from morphometric analyses.

Brachymeles ilocandia sp. nov. (9). CAMIGUIN NORTE ISLAND: CAGAYAN Province: Municipality of Calayan: Holotype (PNM 9819), Paratopotypes (KU 307967, 308019, 308020, 308027, 308030), Paratype (KU 304567); LUZON ISLAND: KALINGA Province: Paratype (FMNH 259449); LUZON ISLAND: Mountain Province: Paratype (CAS 61377).


[^0]:    ${ }^{1}$ Observed for two individuals.

