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A New, Morphologically Cryptic Species of Fanged Frog, Genus *Limnonectes* (Amphibia: Anura: Dicroglossidae), from Mindoro Island, Central Philippines

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We describe a new species of fanged frog (genus *Limnonectes*) from Mindoro and Semirara Islands, of the Mindoro Pleistocene Aggregate Island Complex, of the central Philippines. Although morphologically indistinguishable from its closest relative, *Limnonectes acanthi*, of the Palawan faunal region, the two species can be readily diagnosed on the basis of spectral (dominant frequency) and temporal (pulse number and structure) properties of their advertisement calls, and their allopatric insular geographic ranges on permanently separate geological platforms which have not been connected by dry land in the recent geological past—all of which we interpret as congruent and independent lines of evidence supporting our recognition of two independently evolving evolutionary lineages (species). Ribosomal RNA mitochondrial gene sequences were used to provide genetic identification of specimens and estimate phylogenetic relationships; genetic divergences between Palawan and Mindoro faunal regions exceed those estimated among other, uncontroversial, phenotypically distinct Philippine species with equivalent levels of allopatry and biogeographic isolation. The recognition of the new species further emphasizes the degree to which even well-studied Philippine landmasses still harbor unrecognized biodiversity, and suggests that other widespread Philippine fanged frogs should be scrutinized for non-traditional diagnostic character differences (mate-recognition signal divergence, ecological differences, larval characteristics, life-history trait variation), especially when their geographic ranges span the archipelago's permanent, deep-water trenches, which define its well-characterized Pleistocene Aggregate Island Complexes.

FANGED frogs of Southeast Asia are a species-rich clade of approximately 75 described species (Evans et al., 2003; McLeod, 2008; McLeod et al., 2011; Frost, 2020) that are distributed from India to China and Indochina, through the Thai–Malaysia Peninsula, and across the Sunda Shelf landmasses (Borneo, Sumatra, and Java), the Malukus, the Lesser Sunda island chain, parts of western New Guinea, and the Philippines (Taylor, 1920; Smith, 1927; Inger, 1954, 1966, 1999; Duellman, 1993; Zhao and Adler, 1993; Inger and Tan, 1996; Diesmos et al., 2015; AmphibiaWeb, 2020).

Over the last two decades, numerous proposed, but heretofore unconfirmed, "candidate" species have been identified (Evans et al., 2003; Matsui et al., 2010; McLeod et al., 2011; Setiadi et al., 2011). Additionally, many conspicuously widely-distributed species complexes have been hypothesized to harbor morphologically cryptic evolutionary lineages, presumably composed of multiple independently evolving but undescribed species, characterized by little to no phenotypic variability (McLeod, 2008; Suwannapoom et al., 2016). Discussion of these unconfirmed candidate species have been commonplace in regional summaries of species richness and underestimated biodiversity (Inger, 1999; Brown and Diesmos, 2002; Zhang et al., 2005; Stuart et al., 2006; Fei et al., 2009; Matsui et al., 2010; Brown and Stuart, 2012), and their potential impact on conservation planning (the expectation of heightened urgency; Brown et al., 2008, 2012; Ron and Brown, 2008) has been assumed as an almost inevitable outcome of advancing technology, pluralistic approaches to species delimitation (e.g., integrative taxonomy: Padial et al., 2010), and future sampling (Brown et al., 2013; AmphibiaWeb, 2020).

In the Philippines, systematic and biogeographic summaries of clade- and archipelago-wide amphibian species diversity (Inger, 1954; Brown et al., 2000, 2008, 2009, 2013, 2016; Ron and Brown, 2008; Brown, 2009; Diesmos et al., 2015) have emphasized the impact of ancient geological events on early colonization and population establishment, lineage isolation, and geographically based processes of evolutionary diversification in the archipelago's unique and highly endemic terrestrial amphibian biota (Brown and Diesmos, 2009; Brown et al., 2013). Changes in the orientation and configuration of island arcs (Oliver et al., 2018), crustal collisions, accretion events (Zamoros et al., 2008; Aurelio et al., 2013), periodically accreting and disconnecting microterranes (Hall, 1996, 1998; Yumul et al., 2003, 2009a, 2009b), and possible paleotransport of isolated biota on these well-characterized and highly mobile microcontinent block landmasses (Blackburn et al., 2010; Siler et al., 2012; Brown et al., 2013, 2016) may have all allowed for colonization of the archipelago from multiple sources (Evans et al., 2003; Brown et al., 2013). More recent

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dispersal-facilitated geographical isolation, promotion of lineage divergence, and speciation in Philippine fanged frogs (Brown et al., 2002, 2009; Evans et al., 2003; Setiadi et al., 2011) may have occurred, along with other terrestrial vertebrates, via faunal exchanges along 2–4 separate island arcs (Inger, 1954; Brown and Alcala, 1970; Diamond and Gilpin, 1983; Brown and Guttman, 2002; Evans et al., 2003; Brown et al., 2009, 2013; Esselstyn and Oliveros, 2010), followed by divergence in allopatry and climate-induced sea level vicariance (i.e., the "species-pump" action of the Pleistocene Aggregate Island Complex [PAIC] model of diversification (Evans et al., 2003; Esselstyn and Brown, 2009; Brown and Siler, 2013; Oaks et al., 2013).

The few available taxonomic studies of Philippine *Limnonectes* have all suggested explicitly, or at least implied, that additional species diversity may await discovery by biologists (Inger, 1954; Brown and Alcala, 1970), especially in widespread species that have been noted for anomalous defiance of PAIC-level distributional expectations (Brown and Alcala, 1977; Evans et al., 2003; Siler et al., 2009). However, taxonomists have been reluctant to identify and name such taxa on the basis of mitochondrial sequence divergences alone (Evans et al., 2003; Brown and Stuart, 2012). As a result, revisionary studies have understandably been held in abeyance, pending the accumulation of samples, genetic data, life history and ecological information, and/or other sources of information which may provide insight into species-level reproductive isolation or evolutionary lineage status, independent of crude, arbitrary, and genetic distance cutoffs derived from single-locus studies (Evans et al., 2003; Siler at al., 2009; see Sanguila et al., 2011, for discussion).

Eleven species of Philippine *Limnonectes* are currently recognized (Siler et al., 2009); two of these defy the biogeographical predictions of the archipelago's prevailing PAIC-based biogeographic paradigm (Heaney, 1985; review: Brown and Diesmos, 2009; Brown et al., 2013): *Limnonectes leytensis*, as presently documented (Taylor, 1920, 1923; Inger, 1954; Brown and Alcala, 1970), occupies landmasses of the Mindanao, West Visayan PAICs, as well as the Sulu Archipelago and the Romblon Island Group. Another, the subject of this paper, is *Limnonectes acanthi*, a species originally described from the Palawan PAIC and faunal region (type locality: Busuanga Island; Taylor, 1923; Inger, 1954) and which was later recorded from Mindoro Island (and, eventually, Semirara Island), to the east of the Palawan island and associated Palawan PAIC landmasses (Brown and Alcala, 1955, 1970; Alcala, 1986).

That interpretation of a closely related Mindoro population, purportedly morphologically indistinguishable from the Palawan nominal population (true *L. acanthi*), presumes the establishment of a population on Mindoro following over-seas dispersal (Evans et al., 2003) from the northern Palawan PAIC landmasses (Busuanga, Coron, or Culion Islands across Huxley's modification of Wallace's Line; Huxley, 1868; Inger, 1954; Brown and Guttman, 2002). This hypothesis has remained unchallenged and is supported by strong nodal support for a sister relationship between Palawan and Mindoro populations, despite substantial mtDNA sequence divergence between these isolated, allopatric sister lineages (Evans et al., 2003; Setiadi et al., 2011; Figs. 1, 2).

In this study, we reconsider the *L. acanthi* problem, relying on a consideration of the primary mate-recognition signal of frogs and toads (Wells, 1977), namely male advertisement calls. Together with biogeographic information, and which we interpret as evidence of independent evolutionary lineage status, we conclude that although Palawan and Mindoro PAIC landmasses' populations are morphologically indistinguishable, they each represent distinct, phenotypically "cryptic" species. We arrive at this conclusion via our failure to reject hypotheses of population differences, using robust statistical multivariate analyses of continuous mensural variation, and the complete absence of traditionally diagnostic, discrete, character-based differences of external morphology and/or color pattern.

Here, we describe the fanged frog of Mindoro and Semirara Islands and highlight an empirically confirmed case in which species recognition signals appear to have substantially diversified, unaccompanied by phenotypic divergence. Such clear, extreme cases of divergence along one axis of diversification, even in the absence of evolutionary change in another, may exemplify test-case examples of non-adaptive, geographic evolutionary radiation (Evans et al., 2003; Blackburn et al., 2010; Setiadi et al., 2011), especially if axes of differentiation in archipelago settings (Brown et al., 2013) differ from those that vary in adjacent mainland source populations (Setiadi et al., 2011; Chan and Brown, 2017; Oliver et al., 2018; Davis et al., 2020).

MATERIALS AND METHODS

Species concept.—In this study, we apply the general lineage species concept as our framework for species delimitation. Under the general lineage model (Wiley, 1978; Frost and Hillis, 1990; de Queiroz, 1998, 2005), we would consider the Mindoro and Palawan PAIC metapopulations distinct species if they represented allopatric, separately evolving lineages, characterized by cohesive ancestor-descendent series of populations, distinctive and diagnosable via some recognizable trait-based discrete character difference, and with arguably unique evolutionary histories and predictable evolutionary fates (Brown et al., 2000). We test this hypothesis with an integrative taxonomic approach (Padial et al., 2010), assessing genetic, phenotypic, biogeographic, and behavioral (mate-recognition signals) lines of evidence.

Given (1) the persistent sea-barrier between the Palawan and Mindoro PAICs (Inger, 1954; Voris, 2000; Brown and Diesmos, 2009; Yumul et al., 2009b) and (2) the relatively low overwater dispersal abilities presumed for frogs (Stebbins and Cohen, 1995; Brown and Guttman, 2002; Wells, 2007; Brown, 2016), we would consider substantive genetic divergence, accompanied by phenotypic differentiation (either fixed, traditional, diagnostic trait differences or continuous mensural and/or shape differences), acoustic mate recognition communication system attributes (male advertisement calls), or both, to constitute strong contrary evidence sufficient for rejecting the hypothesis that *L. acanthi* represents a single widespread species, with a distribution spanning throughout two faunal regions, and the numerous islands constituting the Palawan and Mindoro PAIC landmasses.

Molecular data and phylogenetic analyses.—We accessed preserved tissue samples from field-collected Philippine specimens of *Limnonectes* in the University of Kansas Biodiversity Institute cryogenic facility (fresh frozen in LN_2

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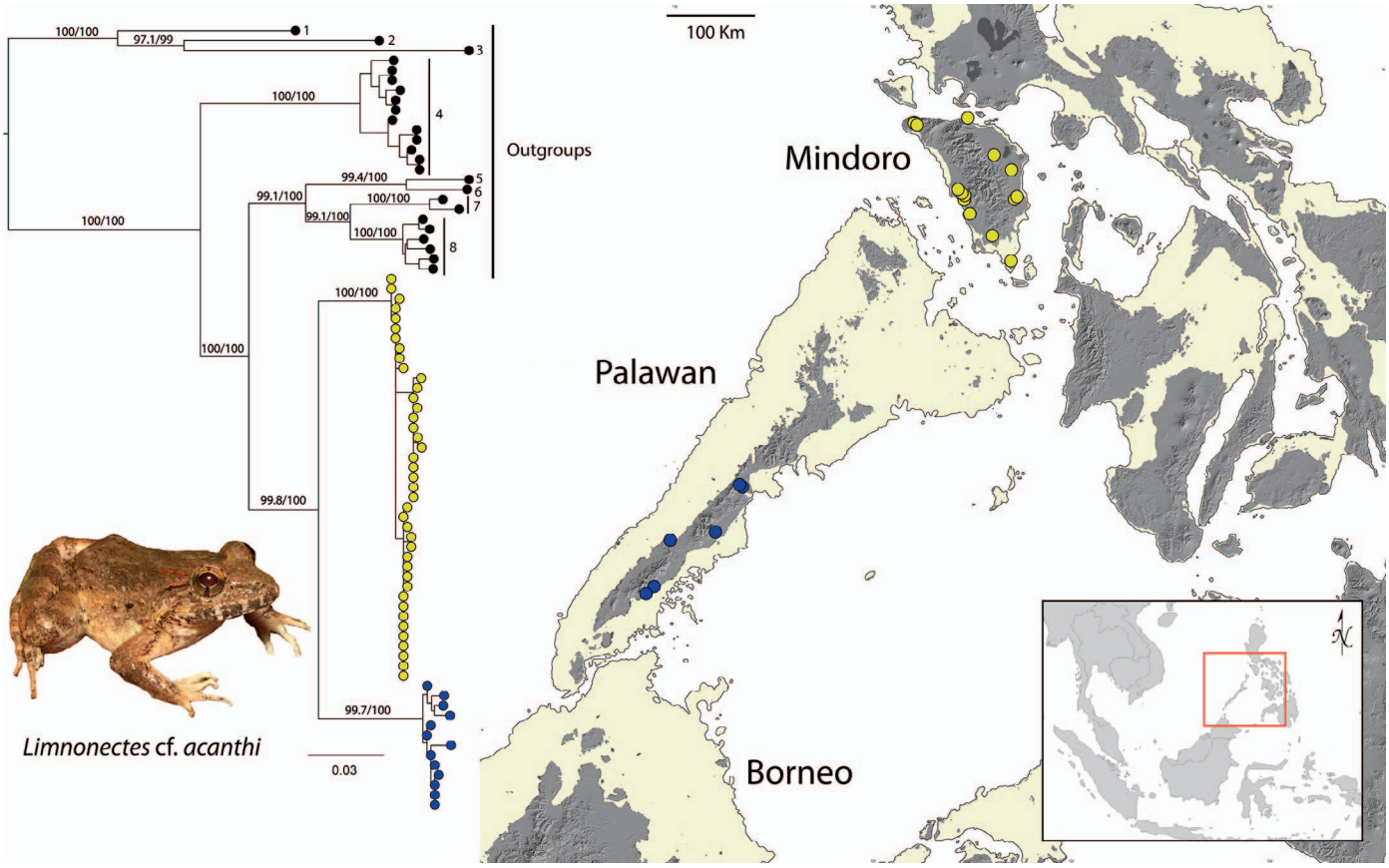

Fig. 1. Maximum likelihood phylogenetic tree (left) and map of molecular sampling localities (right). Maximum likelihood tree generated in IQ-TREE (Minh et al., 2020). Support values on branches are UFBoot/SH-aLRT and outgroup terminals are *L. finchi* (1), *L. parvus* (2), *L. palavanensis* (3), *L. leytensis* (4), *L. magnus* (5), *L. diuatus* (6), *L. visayanus* (7), and *L. macrocephalus* (8). Sampling sites of *Limnonectes acanthi* on Palawan Island (blue) and samples of *L.* cf. *acanthi* from Mindoro and Semirara Islands (yellow) are plotted on islands (gray), surrounded by the 120-meter underwater bathymetric contour (pale yellow), approximating coastlines during the last glacial maximum. Branch length scale bar units = substitutions/site. See Data Accessibility for tree file.

or preserved in ≥95% ethanol and then frozen, ≤1 mo following collection); specimens were collected between 1991 and 2014. We extracted DNA from tissue samples using a Promega Maxwell® RSC extraction robot with Maxwell® RSC Tissue DNA kits. We amplified a ~900 base-pair fragment of the 16S rRNA mitochondrial gene using Polymerase Chain Reaction (PCR) under a protocol adapted from Quah et al. (2017). We summarize the PCR conditions here: 1.0 µl DNA extract, 1.0 µl (10 µM concentration) forward primer 16Sc 5′–GACCTGTGATMTGAAAAACCAYC–3′, 1.0 µl (10 µM concentration) reverse primer 16Sd 5′–GACCTGTGATMTGAAAAACCAYC–3′ (Evans et al., 2003), 2.0 µl 5x buffer (1.5 µM), 1.0 µl $MgCl_2$ 10x buffer (1.5 µM), 1.0 µl deoxynucleotide triphosphates (1.5 µM), 0.1 µl Promega Taq polymerase (5u/µl), and 7.4 µl water. We implemented the following thermal PCR protocol in a Bio-Rad gradient thermocycler: initial denaturation at 95°C for 2 min, second denaturation at 95°C for 35 s, annealing at 56°C for 35 s, followed by an extension cycle at 72°C for 95 s + 4 s per cycle for 34 cycles. We visualized PCR amplicons via electrophoresis in a 1.0% agarose gel in order to confirm the quality and molecular weight of PCR products. We sent our amplified DNA fragments to GENEWIZ® for contract sequencing (purification, cycle sequencing, clean up, and nucleotide sequence determination). GENEWIZ® produces independent sequences from the 3′ and 5′ ends of the DNA fragment. We edited and assembled the resulting forward and the reverse sequences with the software Geneious® version 11.1.5 (Kearse et al., 2012).

In addition to our newly generated sequences, we downloaded sequences from GenBank of Philippine *Limnonectes* (original data from Evans et al. [2003]). GenBank sequences consisted of an approximately 2,400 base-pair fragment of the mitochondrial gene regions $tRNA^{phe}$, 12S rRNA, $tRNA^{val}$, and 16S rRNA, which overlaps the region we sequenced here. We present a list of all sequences included in this study along with their GenBank numbers and associated information in Supplemental Table 1 (see Data Accessibility; GenBank accession numbers for new sequences from this study: MW020111–MW020160).

We employed MAFFT v7.0 (Katoh et al., 2019) to generate a 2,437 base-pair alignment utilizing the q-ins-I strategy because it accounts for the secondary structure of RNA. The 12S and 16S rRNA gene regions of the mitochondrion contain hypervariable regions that are difficult to align with confidence. Therefore, we used the program GBLOCKS v0.91b (Castresana, 2000) to excise any ambiguously aligned regions, resulting in a final alignment of 2,399 base pairs. We analyzed this alignment as a single locus in two Maximum likelihood (ML) and one Bayesian Inference (BI) phylogenetic analyses.

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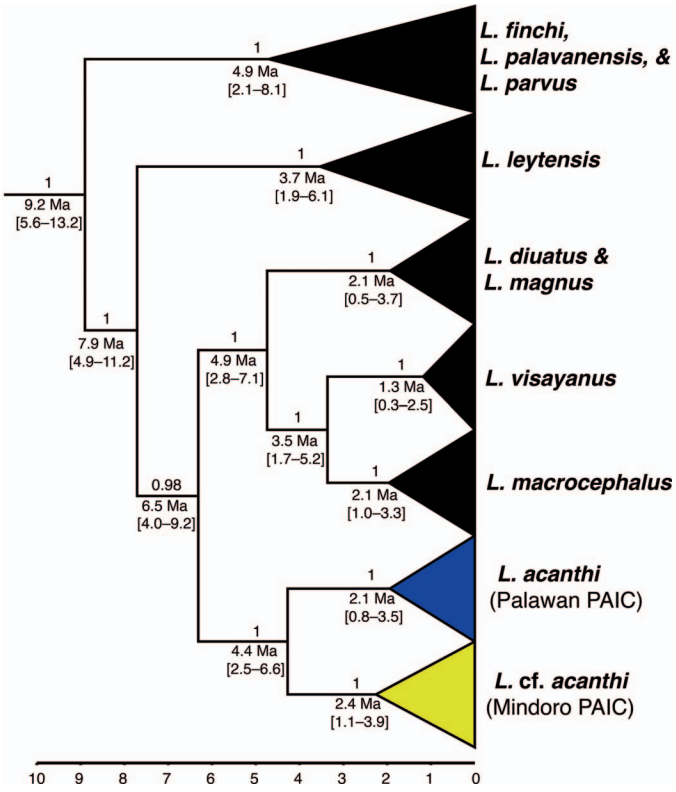

Fig. 2. Time-calibrated Bayesian phylogeny depicting divergence times between species of Philippine *Limnonectes*. Numbers above nodes show Bayesian posterior probabilities. Values below nodes represent mean node ages in millions of years (Ma) with 95% confidence intervals in brackets below node ages. See Data Accessibility for tree file.

We performed the first ML analysis in IQ-TREE on the web server (Trifinopoulos et al., 2016; Minh et al., 2020). The Bayesian Information Criterion employed in model selection within IQ-TREE selected TIM2+F+I+Γ4 as the model of evolution. We summarized nodal support in IQ-TREE with 1,000 bootstrap pseudoreplicates via the integral ultrafast bootstrap (UFBS) approximation algorithm (Hoang et al., 2018) and the Shimodaira-Hasegawa-like approximate likelihood ratio test (SH-LR). We considered nodes with UFBS values of 95 and above and SH-LR support values of 0.8 and above to be well supported (Hoang et al., 2018). We performed the second ML analysis using RAxML-HPC BlackBox 8.2.1 (Stamatakis, 2014) on the CIPRES Science Gateway (Miller et al., 2010) and employed the default GTR+Cat model with RAxML rapid bootstrapping set to halt automatically. We considered nodes with rapid bootstrap support values of 70 and above to be well supported (Hillis and Bull, 1993; Wilcox et al., 2002).

We employed BI phylogenetic analysis in BEAST 2.5 (Bouckaert et al., 2019) to estimate a time-calibrated ultrametric phylogeny, and we designated the guardian frogs (*L. finchi*, *L. palavanensis*, and *L. parvus*) as outgroups based on prior studies of the evolutionary relationships of *Limnonectes* (Evans et al., 2003; Setiadi et al., 2011). We employed a Yule tree prior and a relaxed log normal clock with rate of mitochondrial evolution set to 0.0065 to estimate a time-calibrated phylogeny. This rate corresponds to a rate of 1.3% sequence divergence per million years and has been used to estimate divergence times in *Limnonectes* (Reilly et al., 2019). We employed the reversible jump (RJ) model to select the most appropriate substitution model while simultaneously estimating model parameters and estimating tree topology; the General Time Reversible (GTR) was selected and implemented in subsequent analysis. We implemented two independent runs, each for 100 million generations and sampled every 10,000 generations. We evaluated convergence by visualizing the log file in Tracer v1.5 (Rambaut et al., 2014) to ensure that all parameter effective samples sizes reached stationarity (accepted ESS values $\geq$ 200). We combined the two runs after discarding the first 10% of each run as burn-in and used TreeAnnotator v1.8.0 to generate a maximum clade credibility tree using median heights. We considered nodes with Bayesian posterior probability (PP) support values of 0.95 and above to be well supported (Wilcox et al., 2002; Bouckaert et al., 2019). Finally, we calculated uncorrected pairwise sequence divergences among clades using MEGA v7.0 (Kumar et al., 2016).

Analyses of morphological data.—We performed all analyses of external phenotypic data in R v3.4.1 (R Core Team, 2019). To test the null hypothesis of a single species (*L. acanthi*) on both the Mindoro PAIC and Palawan PAIC landmasses, we recorded morphometric data from formalin-fixed, alcohol-preserved specimens of *L. acanthi* from the islands of Palawan, Busuanga, Mindoro, and Semirara (Material Examined). Morphometric data were collected by a single observer (RO, working with guidance from RMB, to ensure compatibility with past studies) to avoid inter-observer bias and/or extraneous error quantification of body dimensions (Lee, 1982; Hayek et al., 2001). We determined sex by inspecting gonads and/or secondary sexual characters and measured specimens with digital calipers to the nearest 0.1 mm, examined type series material (holotype, paratypes) of all Philippine species, and compared name-bearing type specimens to each species' published descriptions (Stejneger, 1910; Taylor, 1920, 1923; Inger, 1954; Brown and Alcala, 1977; Siler et al., 2009). We incorporated Köhler's (2012) color standardization scheme into our descriptions and interpretation of older (pre-2006) RMB and CDS color field notes, using digitized color images of specimens in life (deposited in KU Digital Archive; see KU Specify database: https://collections.biodiversity.ku.edu/KUHerps/).

We measured the following 15 continuous morphometric characters: snout–vent length (SVL), head length (HL), snout length (SL), tympanum diameter (TYM), head width (HW), forearm length (FLL), thigh length (THL), tibia length (TL), tarsus length (TAR), foot length (FL), hand length (HAL), eye–nostril distance (EN), internarial distance (IND), fang length (FANGL), and fang height (FANGH). All character definitions and acronyms follow Watters et al. (2016) except for fang length and height. Definitions of odontoid process/fang dimensions (fang "length" and "height") follow McLeod (2008) and Emerson (2001) and are defined here for clarity. We measured the length of recurved, posterodorsally projecting fangs as the distance from the dorsal surface of the mandible, immediately anterior to the base of the odontoid, diagonally, to the tip of the posteriorly projecting dorsal tip of the fang. Alternately, we measured the height of the tip of the fang, as the perpendicular distance from the tip of the fang to the ventral surface of the mandible just below the base of the odontoid.

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Before proceeding with statistical procedures, we transformed data to account for differences in body size by performing separate linear regressions between SVL and each of the remaining 14 variables. We then substituted residuals of these regressions for the raw data for those 14 characters in all further univariate and multivariate analyses. We did not transform the SVL data themselves but did include this measure of body size in subsequent univariate analyses. We then ensured that data conformed to assumptions of normality by performing separate Shapiro-Wilk tests on each variable (results not shown; P values ≤ 0.05). We tested whether Palawan and Mindoro PAIC populations display mean differences in single morphometric characters with two-way analyses of variance (ANOVAs), using populations from separate PAICs (Palawan vs. Mindoro) and sex (males, females) as factors, and an alpha level of $0.05/15 = 0.0033$ to adjust for multiple comparisons (Rice, 1989).

We followed these univariate comparisons with an exploration of continuous phenotypic data, surveying morphological data for recognizable group structure in multivariate space. Prior to multivariate analyses, we excluded SVL and scaled all characters (residuals) to their standard deviation to avoid overleveraging. We then performed principal component analysis (PCA) and discriminant analysis of principal components (DAPC) using the ADEGENET package in R (Jombart et al., 2010).

We employed PCA, which produces the optimal low-dimensional representation of morphological variation in the sample, to visualize variation initially, and assess whether geography (Palawan vs. Mindoro) or sex (adult male vs. female specimens) forms the basis of discernable group structure in continuous morphological data. In accordance with Kaiser's Criterion (Kaiser, 1960), we retained components with eigenvalues above 1.0 for subsequent DAPC analysis, which utilizes PCA-transformed data to identify the linear combinations of variables with the smallest within-group and largest between-group variance. Unlike PCA, group membership is designated, *a priori*, in DAPC; our prior, PCA-transformation ensured that variables were uncorrelated and reduced in numbers relative to the total number of observations (specimens). We used this procedure to determine whether proposed groups (Palawan vs. Mindoro populations, and specimens of both sexes) could be distinguished in morphospace, as visualized via bivariate ordination of PC axes.

Bioacoustic analysis of male vocalizations.—Calls were archived at Macaulay Library of Animal Sounds, at the Cornell University Laboratory of Ornithology. Calls were recorded holding the microphone at a distance ranging from 1.0 to 3.5 m, and ambient temperatures were recorded immediately after recording; cloacal temperatures and snout–vent lengths were measured immediately after recording when capture and collection of specimens was possible. Advertisement calls of adult males from Palawan ($n = 4$) were recorded in the field using a Sony™ WM DC6 Professional Walkman with a Sennheiser ME80 condenser microphone equipped with K3U power module (44.1 kHz sample rate, 16-bit resolution). Two of the recordings were obtained in January 2001 by RMB and are archived at Cornell's Macaulay Library (ML) under accession nos. ML 224149 (specimen not collected), ML 224150 (KU 326335); three others were obtained in August 2018 (by JGV and CGM; specimens not collected) and are archived as ML 273939–41. Calls from Mindoro Island ($n = 3$) were recorded by RMB and CDS in March 2005: ML 224427 (not collected), 224429 (not collected), 224431 (KU 302089).

We did not correct for differences in ambient temperature due to the narrow range of temperature variation (less than 3.0°C). Calls were analyzed using Raven Pro v.1.5 for Mac OS X (Bioacoustics Research Program, 2017). We analyzed oscillograms (waveforms) and spectrograms for the following temporal and spectral variables: (1) dominant frequency (Hz) measured along the entire call, (2) call duration (s), (3) number of notes (k) in the call, and (4) note repetition rate ([number of notes – 1]/call duration). Spectrograms were generated using a 1,024-point fast Fourier transformation (FFT) with a frequency grid resolution of 43.1 Hz. We analyzed several calls per individual (Mindoro: ML 224427 = 10, ML 224429 = 1, ML 224431 = 4; Palawan: ML 224149 = 14, ML 224150 = 7, ML 273939 = 3, ML 273940 = 3, ML 273941 = 2), calculated average values per individual for each variable measured, and used these values to calculate average values for Mindoro vs. Palawan populations. We report the mean ± one standard deviation for each acoustic variable measured. In addition, we tested for a relationship between body size (SVL) and dominant frequency, and also SVL vs. note repetition rate, using Pearson's correlation coefficients. All statistical acoustic analyses were conducted using R v3.4.1 (R Core Team, 2019).

RESULTS

Phylogenetic analyses.—Both of our ML analyses, IQ-TREE and RAxML, generated phylogenetic trees with identical, well-resolved, and strongly supported topologies (Fig. 1; RAxML results not shown); therefore, hereafter we interpret results of our IQ-TREE analysis only. The outgroup topology of the ML tree is well supported and consistent with previous phylogenetic studies of Philippine species of *Limnonectes* (Fig. 1; Evans et al., 2003; Setiadi et al., 2011). *Limnonectes acanthi* is strongly supported as monophyletic and sister to *L.* cf. *acanthi* from Mindoro and Semirara Islands; together these lineages are most closely related to a lineage containing *L. diuatus*, *L. visayanus*, *L. macrocephalus*, and *L. magnus* (lineages C/E *sensu* Evans et al. [2003]; Setiadi et al. [2011]). Additionally, we estimated mean uncorrected pairwise sequence divergence between the Mindoro and Palawan clades of 5.0%, 3.4%, and 5.1% between the comparison of *L. diuatus–L. magnus* and *L. visayanus–L. macrocephalus* species pairs, respectively (Table 1).

Our time-calibrated Bayesian analysis recovered a tree with identical interspecific topology as that recovered in our ML analyses (Fig. 2), with two reciprocally monophyletic sister lineages (a Palawan clade and a Mindoro clade). The BI chronogram estimated that the Palawan and Mindoro clades diverged from one another approximately 4.4 million years ago (Ma; 95% HPD 2.5–6.6 Ma). This wide time interval suggests caution in use of temporal estimates—but as a broad comparison, we note that mean estimated divergence of the Palawan and Mindoro clades of *L. acanthi* is comparable or older than that of two other, readily diagnosable, and uncontroversial distinct sister-species pairs (*L. diuatus–L. magnus* and *L. visayanus–L. macrocephalus*; Fig. 2).

Analysis of morphological data.—We obtained measurements for a total of 100 specimens of *L. acanthi* from Palawan, and

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Table 1. Uncorrected p-distances (%) generated in MEGA v7.0.26 (Kumar et al., 2016). Bold values indicate within-species mean pairwise distances.

	L. leytensis	*L. magnus*	*L. diuatus*	*L. visayanus*	*L. macrocephalus*	*L. acanthi* (Palawan PAIC)	*L.* cf. *acanthi* (Mindoro PAIC)
L. leytensis	**2.5**						
L. magnus	8.4	—					
L. diuatus	8.7	3.4	—				
L. visayanus	8.3	6.6	7.3	**1.6**			
L. macrocephalus	8.3	5.9	6.4	5.1	**1.8**		
L. acanthi (Palawan PAIC)	7.6	8.0	7.6	7.7	7.2	**0.5**	
L. cf. *acanthi* (Mindoro PAIC)	6.9	7.7	7.3	6.3	7.0	5.0	**0.4**

Table 2. Univariate summaries of continuously varying mensural characters for *Limnonectes acanthi* from Palawan and *L.* cf. *acanthi* from Mindoro. Entries include mean ± SD, followed by range in parentheses.

	Palawan PAIC		Mindoro PAIC	
Characters (mm)	Males ($n = 12$)	Females ($n = 13$)	Males ($n = 35$)	Females ($n = 40$)
Snout–vent length	65.1±7.9 (55.6–83.8)	67.6±7.1 (55.8–81.9)	69.2±8.3 (54.2–83.1)	68.4±6.6 (55.1–79.8)
Head length	24.6±2.8 (20.8–30.1)	24.4±1.9 (21.7–27.4)	26.6±3.6 (19.4–34.2)	25±2.4 (20.5–29.5)
Snout length	11.3±1.3 (9.6–13.9)	11.7±1 (9.9–13.4)	12.5±1.6 (9.5–15.3)	12.1±1.2 (9.2–13.9)
Tympanum diameter	4.8±0.5 (4–5.5)	4.7±0.5 (4.1–5.6)	4.6±0.6 (3.8–6)	4.6±0.4 (3.9–6)
Head width	25.4±3 (21.7–31.1)	25.1±1.8 (22–27.5)	27.5±4.2 (20.1–34)	26.5±2.5 (21–30.8)
Forearm length	14.3±1.9 (11.8–18.7)	14.4±0.9 (12.3–15.8)	14.9±1.7 (11.7–17.9)	14.6±1.4 (11.6–16.9)
Femur length	35.9±3.5 (30.8–42.3)	36.5±2.8 (32.5–42.5)	37.3±4.6 (27.8–45.3)	36.9±2.9 (30.5–42.9)
Tibia length	36.6±4.2 (31.8–46.6)	36.6±3.2 (31.3–42.3)	37.6±4.3 (29.7–43.7)	37.5±2.8 (31.5–43.9)
Tarsus length	17.1±1.8 (14.5–20.4)	17.3±1.5 (15.4–19.9)	17.1±1.9 (13.1–19.9)	17.2±1.4 (14.1–20.4)
Foot length	34.4±3 (30.6–40.8)	34.1±3 (29.7–40.4)	35.1±3.9 (27.4–41.9)	35.1±2.6 (29.4–40.5)
Hand length	16.4±1.6 (14.5–20.3)	16.3±1.6 (13.6–19.5)	17.1±2 (13.6–21.3)	17.2±1.4 (14.4–19.6)
Eye–nostril distance	5.8±0.7 (4.9–7.3)	6±0.7 (5.1–7.3)	6.7±0.9 (5–8.1)	6.6±0.6 (5.6–8.1)
Internarial distance	4.9±0.5 (3.9–6)	5±0.6 (3.9–6.2)	5.5±0.6 (4.2–6.6)	5.3±0.6 (4.2–6.4)
Odontoid length	3.2±0.6 (2.4–4.2)	2.2±0.3 (1.6–2.7)	3.7±0.7 (2.6–5.6)	2.3±0.4 (1.5–3.1)
Odontoid height	3.3±0.5 (2.5–4)	2.3±0.3 (1.9–2.6)	3.6±0.7 (2.5–5.1)	2.1±0.4 (1.5–2.9)

Table 3. Loadings of 14 morphometric characters (each regressed against snout–vent length) for the principal components retained in accordance with Kaiser's Criterion (PC Eigenvalue > 1).

Character	PC1	PC2	PC3	PC4
Head length	0.268	–0.359	0.047	–0.282
Snout length	0.255	–0.201	–0.168	–0.392
Tympanum diameter	0.071	0.053	0.415	–0.563
Head width	0.291	–0.326	–0.108	–0.141
Forearm length	0.307	0.039	0.003	0.025
Femur length	0.364	0.176	–0.042	0.130
Tibia length	0.353	0.290	0.046	–0.045
Tarsus length	0.276	0.344	0.174	–0.103
Foot length	0.284	0.341	–0.088	0.158
Hand length	0.302	0.286	–0.162	0.109
Eye–nostril distance	0.205	–0.191	–0.440	–0.173
Internarial distance	0.106	–0.230	–0.454	0.289
Odontoid length	0.252	–0.314	0.359	0.379
Odontoid height	0.239	–0.318	0.435	0.326
Standard deviation	2.081	1.639	1.229	1.148
Proportion of variance	0.309	0.192	0.108	0.094
Cumulative proportion	0.309	0.501	0.609	0.703
Eigenvalues	4.330	2.685	1.511	1.318

L. cf. *acanthi* from Mindoro PAIC landmasses (Table 2). Following transformation (except SVL which was not transformed), our Shapiro-Wilk tests confirmed that all variables conformed to assumptions of normality (individual *P*-values not shown).

Two-way ANOVAs found that the Palawan and Mindoro clades differed from one another in mean values for SL, TYM, HW, TAR, HAL, END, and IND (P values ≤ 0.043). However, these comparisons were non-significant when adjusting our alpha level for multiple comparisons (P values ≥ 0.0033) and box plots revealed substantial overlap among ranges for these seven characters (Fig. S1; see Data Accessibility). Males and females did differ significantly in mean values for HL and HW, FANGL and FANGH (P values ≤ 0.00071). Additional visualization of all characters with bean plots (Fig. S2; see Data Accessibility) reveals the full overlapping distribution of values for each character by population (both sexes).

The first four principal components (PCs) had eigenvalues > 1.0 and were retained; together these components accounted for 70.3% of the total variation (Table 3). The factor loadings for the first PC were all positive, with the heaviest loadings on THL and TL. The loadings of the second PC were weighted heavily positive for TAR and FL, and negatively for HL and HW. Our PCA showed no group-based structure in the data, and our DAPC with *a priori* group designations was unable to maximize group dispersion or

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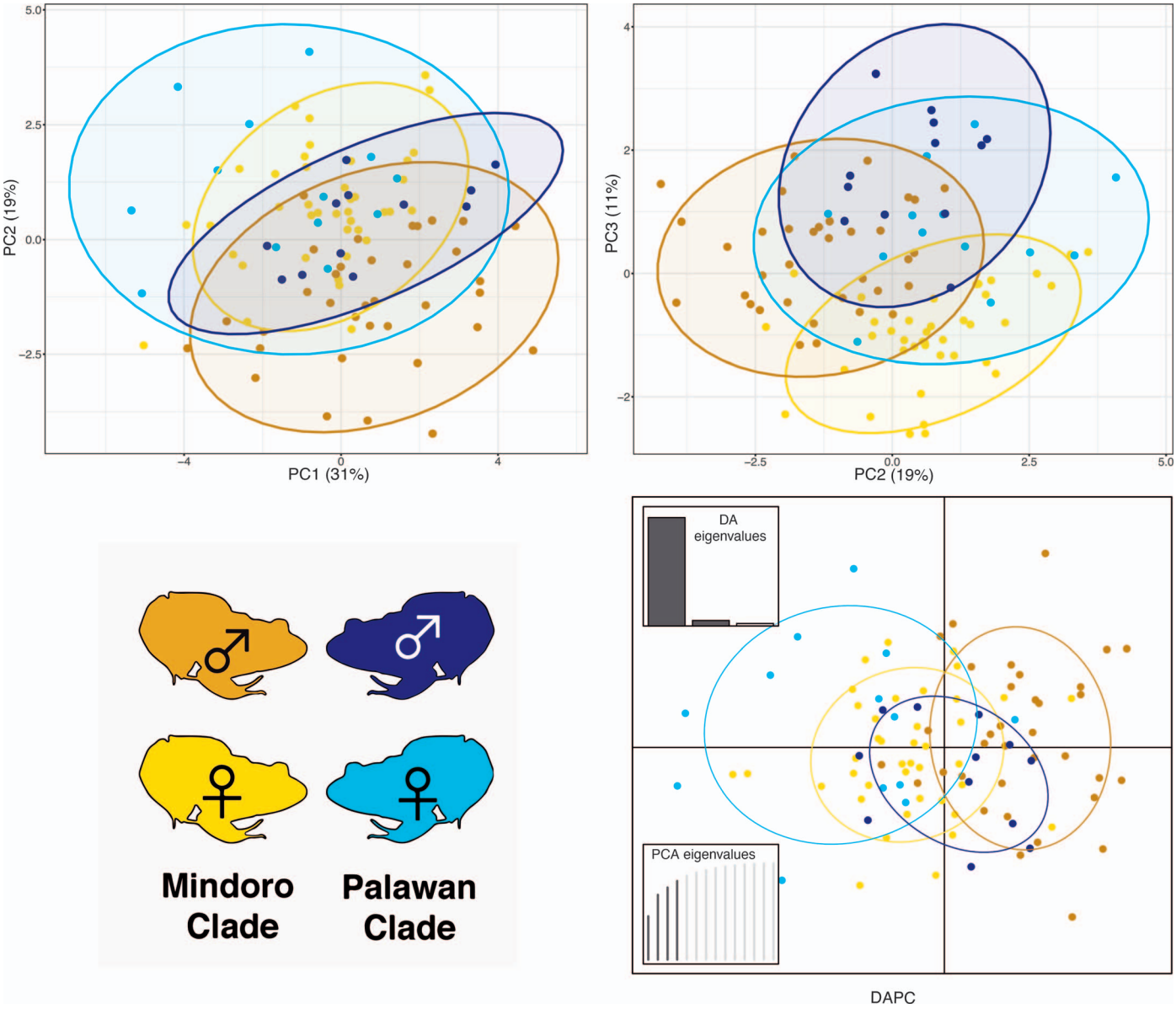

Fig. 3. Ordination of the first and second (top left) and second and third (top right) principal components for *L. acanthi* (Palawan) and *L.* cf. *acanthi* (Mindoro), with scatterplot of DAPC results (bottom right) with inertia ellipses for emphasis. Yellow shades represent Mindoro clade individuals and blue shades represent Palawan clade individuals, while light tones represent females and dark tones represent males.

discretely distinguish sexes or species clusters (Palawan vs. Mindoro populations) in morphospace (Fig. 3).

Analysis of acoustic data.—The advertisement call of *Limnonectes* cf. *acanthi* from Mindoro Island (Fig. 4A–C) is a loud, low-frequency trill (call with multiple sequential notes), which differs from that of *L. acanthi* (Fig. 4D–F) from Palawan Island in the number of notes per second (note repetition rate; Fig. 4A vs. D; Fig. 5C), number of pulses per note (Fig. 4B vs. E), and dominant frequency (Fig. 4C vs. F; Fig. 5D). The Mindoro population's calls consist of an average of 18±4 (range: 11–22) notes, with a mean duration of 1.3±0.3 (range: 0.8–1.7) s. The average note rate 12.4±0.3 (range: 11.5–12.8) notes/s, and the mean dominant frequency of the whole call is 2,331.7±182.6 (range: 2,067.2–2,799.3) Hz. The Palawan population's advertisement call is a trill, with unmistakably distinct, 2-pulse notes (Fig. 4E). Its average number of notes is 22±3 (range: 17.0–29.0), with a note rate of 15.0±0.4 (range: 14.2–15.4) notes/s. The mean call duration is 1.4±0.2 (range: 1.0–1.9) s, with an average dominant frequency of 1,467.4±99.2 (range: 1,335.1–1,679.6) Hz. Acoustic parameters for each locality are summarized in Table 4 (see Fig. 5 for each individual recorded). In addition to the differences in call structure (single note vs. 2-pulse notes; Fig. 4), Mindoro and Palawan calls can be confidently distinguished on the basis of their note repetition rates (Fig. 5C) and dominant frequency (Figs. 4C, F, 5D) with no overlap in ranges recorded for these acoustic variables. Compared to Mindoro, Palawan advertisement calls have higher note repetition rates (Fig. 5C) and lower dominant frequencies (Fig. 5D). We did not find significant relationships between SVL and dominant frequency or SVL and calling rate (all P values ≥ 0.05).

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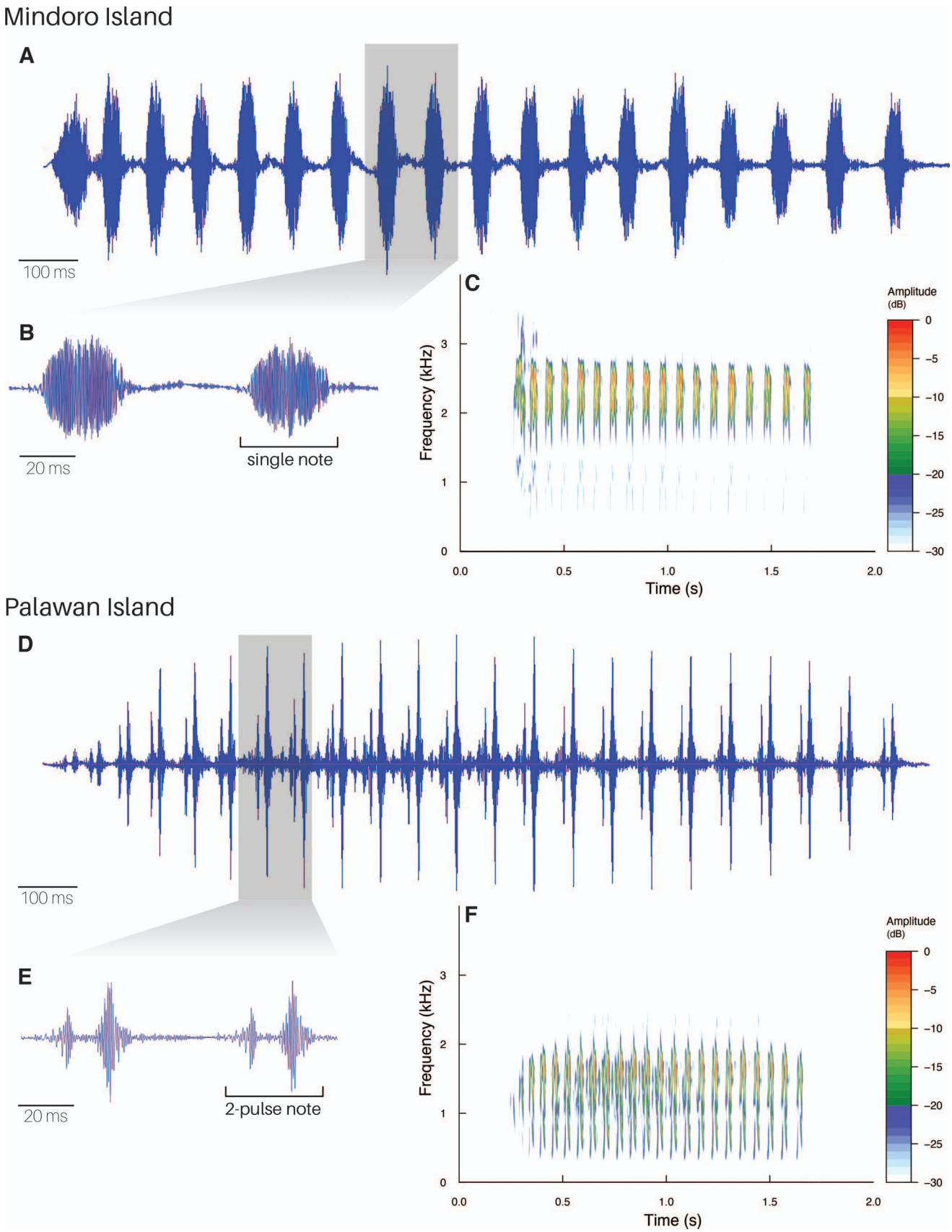

Fig. 4. Oscillograms and spectrograms of advertisement calls of *Limnonectes* cf. *acanthi* from Mindoro (A–C) and *L. acanthi* from Palawan (D–F). (A) Oscillogram of the entire advertisement call of *L.* cf. *acanthi* from Mindoro; (B) a close-up showing two consecutive notes. (C) A spectrogram showing the dominant frequency of the entire call. (D) Oscillogram of the advertisement call of *L. acanthi* from Palawan; (E) a close-up of two consecutive notes showing the two-pulse nature of each note. (F) Spectrogram showing the dominant frequency of the Palawan advertisement call.

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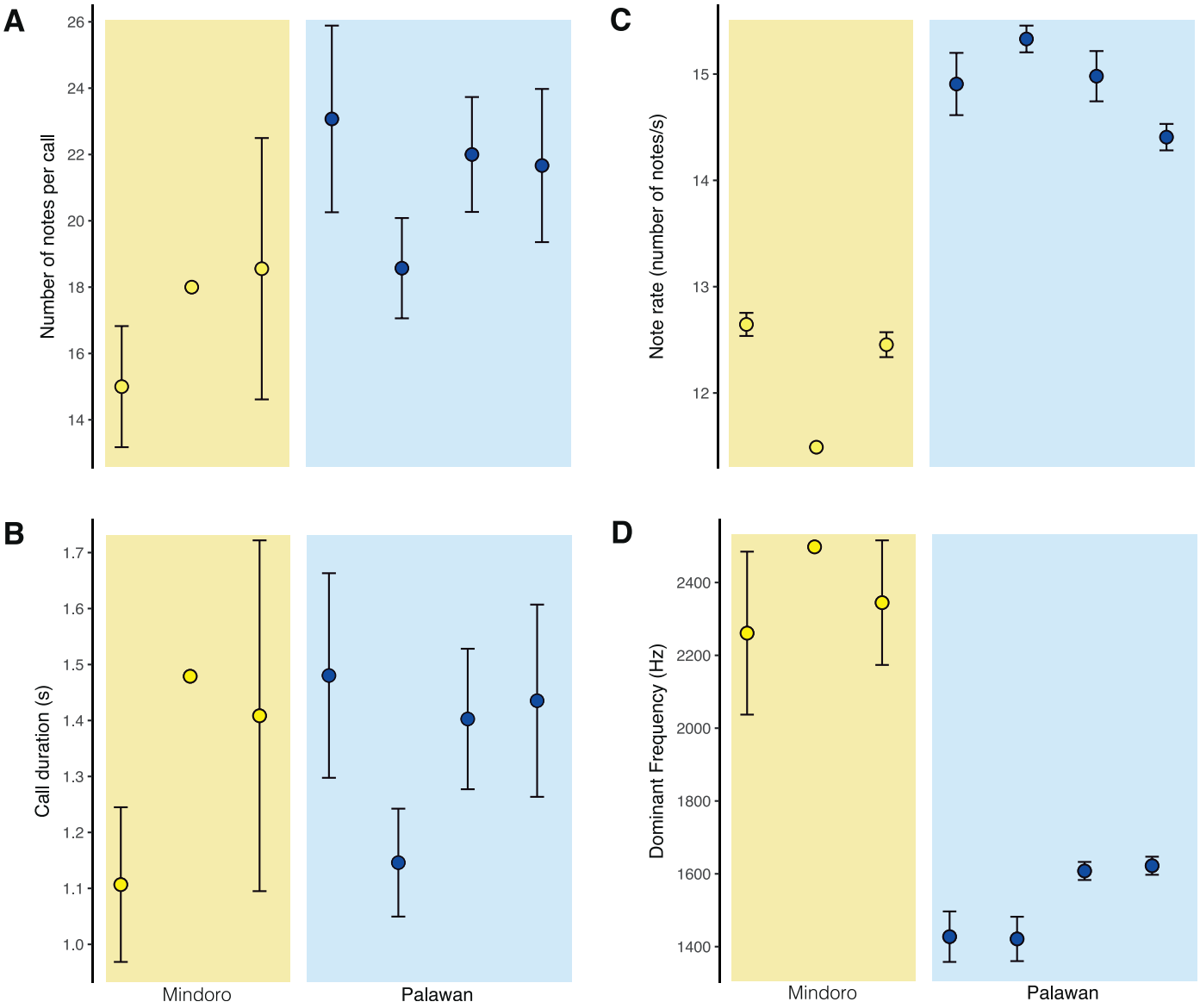

Fig. 5. Variation between *Limnonectes* cf. *acanthi* from Mindoro Island ($n = 3$ males) and *L. acanthi* from Palawan Island ($n = 4$ males) in the four acoustic variables measured. (A) Number of notes per call, (B) call duration, (C) note rate, and (D) dominant frequency. Left side of each panel, *L.* cf. *acanthi* Mindoro; right side of each panel, *L. acanthi* Palawan.

Conclusion and justification for the recognition of a new cryptic species.—We find that the totality of evidence requires us to reject the hypothesis of conspecificity for *L. acanthi* from Palawan and Mindoro PAICs. Thus, given that the Palawan PAIC population corresponds to the nominal species, (i.e., true *L. acanthi* [Taylor, 1923]), then the population from the Mindoro PAIC represents an undescribed, morphologically cryptic species. Analyses of DNA sequences do not contradict this view. Although we do not use genetic distances to diagnose the new species, all three phylogenetic analyses identified two reciprocally monophyletic lineages corresponding to Mindoro and Semirara versus Palawan populations. Additionally, the divergence between these two clades is comparable to or larger than observed differences between

Table 4. Summary of temporal and spectral acoustic variables measured for male advertisement calls of *L.* cf. *acanthi* Mindoro PAIC, and *L. acanthi* Palawan PAIC.

	Mindoro ($n = 3$)		Palawan ($n = 4$)	
Parameters	Mean ± SD	Min–Max	Mean ± SD	Min–Max
Number of notes (k)	18±4	11–22	22±3	17.0–29.0
Note rate ([k–1]/s)	12.4±0.3	11.5–12.8	15.0±0.4	14.2–15.4
Call duration (s)	1.3±0.3	0.8–1.7	1.4±0.2	1.0–1.9
Dominant frequency (Hz)	2,331.7±182.6	2,067.2–2,799.3	1,467.4±99.2	1,335.1–1,679.6

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other closely related, phenotypically distinctive, uncontroversial, formally recognized species of Philippine *Limnonectes* (e.g., *L. macrocephalus–L. visayanus*, *L. magnus–L. diuatus*).

Given that the Mindoro versus Palawan PAIC populations did not differ significantly in multiple body-size related dimensions after adjusting for multiple comparisons, their lack of traditional fixed character differences (non-overlapping character state ranges, anatomical character states, color pattern difference, etc.; Inger, 1954), as well as their high degree of overlap in multivariate morphospace, renders unequivocal diagnosis impossible on the basis of external morphology alone (Figs. 3, 4). However, the Mindoro and Semirara population can be readily diagnosed from its sister species, *L. acanthi*, of the Palawan PAIC, on the basis of acoustic data. Because male advertisement call is the primary mate recognition signal in anurans (Wells, 1977, 2007), and the two lineages differ unambiguously in call spectral structure and temporal characteristics (note structure, note repetition rate, and dominant frequency), we do not hesitate to use this variation, plus biogeographical information (below), to form the basis of our diagnosis of the new species.

Our results are also entirely consistent with predictions based on geology and biogeography (see also Brown and Guttman [2002] and Brown et al. [2009] for discussion of other species pairs from Palawan and Mindoro). The Mindoro and Palawan PAICs are separated by a deep-water channel and have not been connected by land (Yumul et al., 2003, 2009a, 2009b; Brown and Diesmos, 2009). Because amphibians generally are poor long-distance overwater dispersers (Stebbins and Cohen, 1995; Wells, 2007), we interpret the permanent deep-water marine barrier represented by the Mindoro Straits to have most likely severely limited gene flow between fanged frog populations on the two PAICs. This is consistent with the reciprocal monophyly and deep divergences between clades in our phylogeny (Evans et al., 2003; Setiadi et al., 2011). In contrast, we would expect much higher rates of historical gene flow among islands within each PAIC because such islands were repeatedly connected to one another by land during Pleistocene glaciations. Consistent with that expectation, we found no evidence of genetic structure between the islands of Mindoro and Semirara, both of which are part of the Mindoro PAIC.

The results of our phylogenetic and acoustic analyses, concordant with historical biogeography, provide strong evidence that *L.* cf. *acanthi*, of Mindoro and Semirara Islands, represents a cohesive, separately evolving lineage, recognizable under any modern lineage-based species concept (review: de Queiroz, 1998, 2005), and we describe this lineage as a new species.

Limnonectes beloncioi, new species

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Mindoro Fanged Frog

Figures 1, 6, 7

Rana macrodon blythi Boulenger, 1920 (*partim*).
Rana acanthi Taylor, 1923; Taylor and Elbel, 1958.
Rana macrodon acanthi (Inger, 1954).
Rana macrodon macrocephala (Inger, 1954) (*partim*: three Mindoro specimens [USNM] provisionally referred by Inger's "tentative identification" [Inger, 1954: 129]).
Rana magna acanthi (Inger, 1958).
Limnonectes (*Limnonectes*) *acanthi* Dubois, 1987 (*partim*).
Limnonectes cf. *acanthi* Evans et al., 2003; Setiadi et al., 2010; Diesmos et al., 2015.

Holotype.—PNM 9870 (adult male; formerly KU 303343; Field collector No. RMB 4957), Philippines, Mindoro Island, Oriental Mindoro Province, Municipality of Bongabong, Barangay Carmundo, Sitio Paypay-Ama, Paypay-Ama River, 12.7354°N, 121.4141°E, 100 m above sea level, WGS 84, R. M. Brown, A. C. Diesmos, C. D. Siler, and E. L. B. Rico, 13 March 2005.

Paratypes (Paratopotypes).—KU 302084, 302087–88 (adult females), 302085–86, 302089 (adult males), 303343 (juvenile of undetermined sex), 303369–78 (10 subadults of undetermined sex), bearing the same data as the holotype.

Other paratypes.—Mindoro Island, Oriental Mindoro Province, Municipality of Bongabong, Barangay Formon: KU 302090–91 (adult females), 302093, 302095, 302097, 302100 (3 adult males, 1 female), 302109–11 (3 adult males), C. D. Siler, 12 March 2005; Municipality of Victoria, Barangay Loyal: KU 302112–18 (2 adult males, 2 adult females, 3 juveniles of undetermined sex), C. D. Siler, 13 March 2005; Barangay Loyal, Sitio Panguisan, Panguisan River: KU 303470–78 (4 adult females, 5 subadults of undetermined sex), R. M. Brown, A. C. Diesmos, and C. D. Siler, 14 March 2005; Municipality of Gloria, Barangay Malamig: KU 302108 (adult female), 303344 (juvenile), J. B. Fernandez and R. M. Brown, 17 March 2006; KU 303346–54 (2 adult males, 2 females, 5 juveniles), R. M. Brown, C. D. Siler, and A. C. Diesmos, 13 March 2005; Sitio Balogbog, Cueba Simbahan: KU 303379–80 (2 subadults of undetermined sex), R. M. Brown, C. D. Siler, and E. L. B. Rico, 12 March 2005; Sitio Pastohan, Tanguisian Falls: KU 303381–402 (22 subadults of undetermined sex), A. C. Diesmos and E. L. B. Rico, 11 March 2005; Occidental Mindoro Province, Municipality of Calintaan, Barangay New Dagupan: KU 303266, 303345 (subadults), R. M. Brown, 8 March 2005; Municipality of Magsaysay, Barangay Nicolas, Sitio Banban: KU 303404–30 (1 adult female, 25 subadults and juveniles/metamorphs of undetermined sex), C. D. Siler and R. M. Brown, 9 March 2005; KU 304131–32 (adult male and subadult of undetermined sex), R. M. Brown; Municipality of Sablayan, Barangay Batong Buhay, Sitio Batulai, Mt. Siburan: KU 303430–52 (5 adult males, 6 adult females, 12 subadults of undetermined sex), E. L. B. Rico, 14 February 2006; KU 305450–51, 306637 (adult female, 2 subadult females), E. L. B. Rico, 19 February 2006; Barangay Malisbong, Sitio Aruyan: KU 335863–83 (11 females, 10 males), S. N. Travers, C. H. Oliveros, and R. M. Brown, 6 July 2013; Barangay Burgos, Sitio Posoy, Posoy River: KU 303453–69 (adult male, adult female, 15 juveniles of undetermined sex), R. M. Brown, 8 March 2005; Municipality of Paluan, Barangay Harrison, Sitio Ulasan, local name "Matingaram": KU 308307, 308309, 308313–18, 308321–23, 308327, 308360, 308362–63, 308367–68, 308370–71, 308385, 308391, 308393, 308422, 308457, 308462, 308464–65, 308469, 308472 (15 adult females, 15 adult males), E. L. B. Rico, 4 January 2007; Municipality of Puerto Galera, Barangay San Isidro, Sitio Minolo, Ponderosa Golf Resort, adult female, J. A. McGuire and V. Yngente, 15 January 1996: TNHC 54920; Municipality of San Teodoro, Barangay Villaflor, Tamaraw Falls, approximately km 15 from

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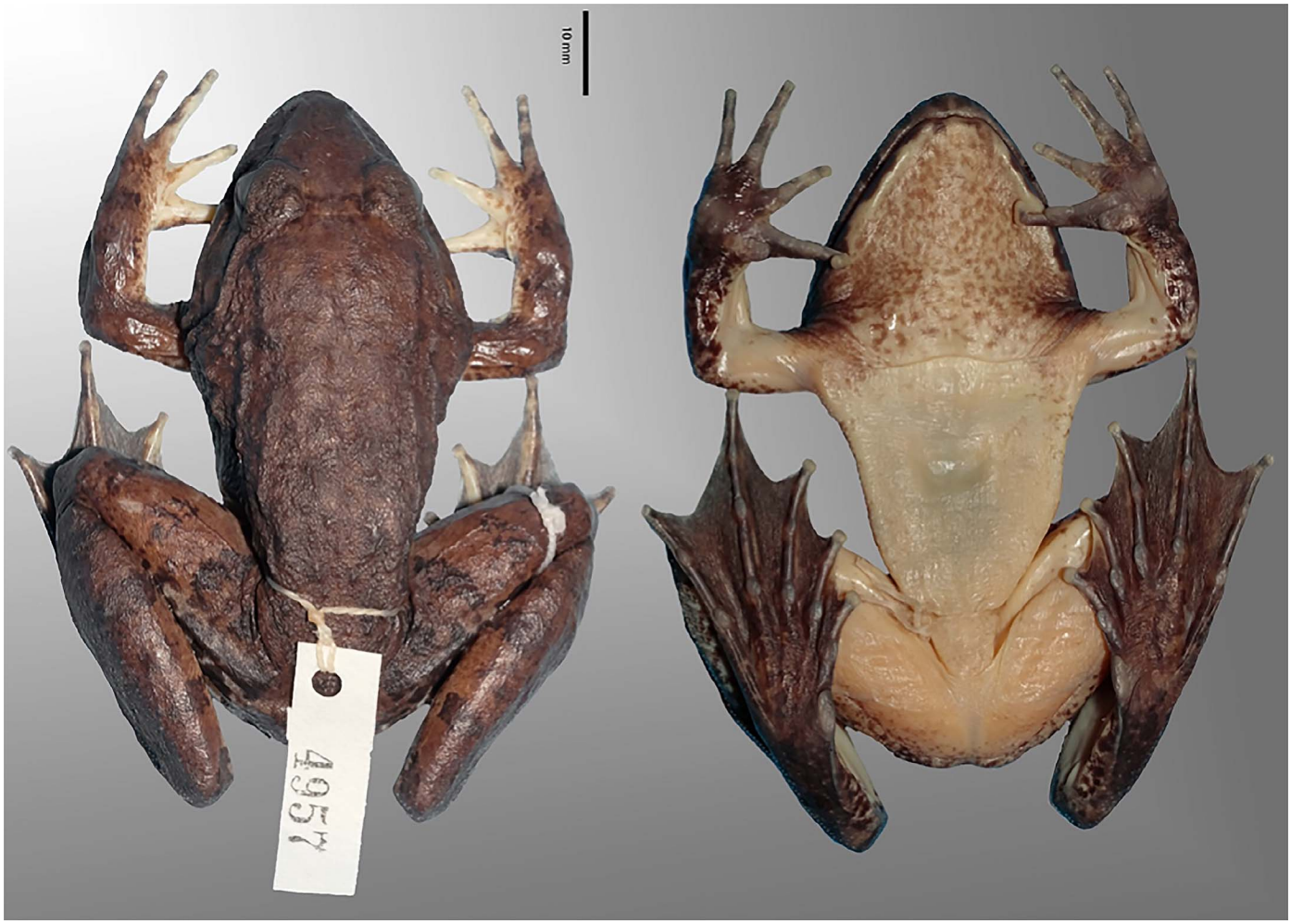

Fig. 6. Dorsal and ventral views of PNM 9870 (formerly KU 303343; Field Collector No. RMB 4957), adult male holotype of *Limnonectes beloncioi*, new species.

Puerto Galera on Calapan-to-Puerto Galera road, 8 subadult males, 1 immature female, 3 adult males, J. A. McGuire and V. Yngente, 17 January 1996: TNHC 54921–29, 55023, 55025, 55029, 55033; same locality, 10 adult males, 11 adult females, R. I. Crombie and V. Yngente, 8 March 1995: USNM 556073–94; Municipality of Baco, Barangay Lantuyan, near Cabinuangang River: 6 adult males, R. I. Crombie and V. Yngente, 2 July 1991: USNM 508558–63; 5 adult males, 3 adult females, 1 immature specimen of undetermined sex, R. I. Crombie and V. Yngente, 7 March 1995: USNM 508564–72; Municipality of Tarogin, ca. 30 km S of Calapan Town, Mt. Halcon SE slope: CAS-SU 22146 (adult female), Q. Alcala and party, 1 April 1963; CAS-SU 22145 (adult female), same data, 31 March 1962; CAS-SU 22147–49 (adult male, 2 adult females), 1 April 1963; CAS-SU 22150 (adult female), S. Magusara and C. Batal, 14 April 1963; CAS-SU 22576 (adult male), Q. Alcala and party, 13 March 1963; CAS-SU 22577, 23508 (adult male and female), 31 March 1963; CAS-SU 23499, 23501, 23525 (adult females), 23505, 23514–15, 23519–20 (adult males), CAS-SU 23485, 23487, 23496–97, 23512–13, 23522 (subadult males), 23489, 23498, 23502 (subadult females), Q. Alcala and party, 10 March 1963; Municipality of Tarogin, Mt. Halcon: CAS-SU 22240 (juvenile), Q. Alcala and party, 14 April 1963; CAS-SU 22288–22295, 23500, 23510–11, 23517–18, 23521 (juveniles), Q. Alcala and party, 1–20 April 1963; E side of Mt. Halcon, SE slope of Barawanan Peak, 830 m: CAS-SU 22151 (adult female), M. Pinero and party; Semirara Island, Oriental Mindoro Province, Municipality of Caluya, Barangay Tinogboc: KU 302105–07 (2 adult males, 1 adult female), C. D. Siler, 16 November 2000.

Referred specimens.—Mindoro Island, Oriental Mindoro Province, Municipality of Baco, Mt. Baco, Alangsa River: USNM 508534–57; Occidental Mindoro Province, Municipality of Paluan, Barangay Harrison, Sitio Ulasan, local name "Matingaram": KU 308308, 308310–12, 308319–20, 308324–26, 308361, 308364–66, 308369, 308372–76, 308386–90, 308392, 308394, 308416–21, 308423, 308430, 308451–52, 308456, 308461, 308463, 308467–68, 308470–87, 308500, 308528, 308538, 308561–69, 308586, 308589, 308590–92; Municipality of Paluan, Barangay 1, Sitio Ipol: KU 308593, 308597, 308599.

Diagnosis and comparisons.—*Limnonectes beloncioi* is a medium-sized fanged frog, assigned to the genus *Limnonectes* (family Dicroglossidae), on the basis of its prominent, sexually dimorphic odontoid processes characteristic of the genus among other osteological synapomorphies (Inger, 1954, 1966; Emerson and Berrigan, 1993). The new species

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Fig. 7. Adult female paratype of *Limnonectes beloncioi*, new species (KU 335866; Field Collector No. RMB 17,605) in life (photo copyright S. L. Travers).

can be distinguished from all other known congeners based on a combination of its single-pulse/note advertisement call (vs. dual-pulses/note in *L. acanthi* from Palawan Island faunal region and PAIC landmasses), its phylogenetic position (sister to *L. acanthi* from Palawan PAIC; Evans et al., 2003; Setiadi et al., 2011), and its geographic distribution on Mindoro and Semirara Islands (vs. Palawan PAIC); it is the only species of *Limnonectes* known to occur on Mindoro and Semirara Islands and associated small satellite islands and, therefore, has no sympatric congeners.

The new species is morphologically similar to its closest relative, *L. acanthi*; however, it may be distinguished from this allopatric congener by its male advertisement call. The note pulse substructure of *L. beloncioi* is singular (1 pulse per note vs. 2 pulses per note in *L. acanthi*), and the new species has a slower note repetition rate (11.5–12.8 notes per second vs. 14.2–15.4 notes per second), and has a higher dominant frequency (2,067.2–2,799.3 Hz vs. 1,335.1–1,679.6 Hz in *L. acanthi*).

With the exception of the morphologically indistinguishable *L. acanthi*, the new species can be distinguished from all other Philippine species of *Limnonectes* (*L. diuatus*, *L. ferneri*, *L. leytensis*, *L. macrocephalus*, *L. magnus*, *L. micrixalus*, *L. palavanensis*, *L. parvus*, *L. visayanus*, and *L. woodworthi*) by a combination of body size, fang (odontoid) length, snout shape, relative lengths of the first and second finger, dorsal skin rugosity, restriction of white-tipped dermal asperities to the sacral region (not aggregated in radial clusters), the presence of irregular, elongate, discontinuous dorsolateral ridges (absence of a continuous dorsolateral fold), complete interdigital webbing of the foot, and the absence of a dark inverted "V"-shaped mark on the dorsum. We provide morphological comparisons below, based on our data, in conjunction with or with consideration of the descriptions of Stejneger (1910), Taylor (1923), Inger (1954), Brown and Alcala (1977), and Siler et al. (2009).

Limnonectes beloncioi differs from *L. diuatus* and *L. ferneri* by its rounded snout in lateral aspect (vs. posteroventrally sloping), its Finger I > Finger II relative finger lengths (vs. approximately equivalent length), and by restriction of white-tipped dorsal asperities to dorsal sacral region, and not distributed in radial clusters (vs. asperities not posteriorly restricted in *L. diuatus*; and densely distributed across entire of dorsum, and concentrated in radial sacral clusters in *L. ferneri*); and the presence of irregular dorsolateral ridges (absent in *L. diuatus* and *L. ferneri*); from *L. leytensis*, the new species can be distinguished by its larger adult body size (SVL range 54.2–83.1 vs. 25.8.2–34.0 mm in *L. leytensis*), rounded snout (vs. snout moderately pointed in lateral aspect in *L. leytensis*), Finger I > Finger II (equivalent length in *L. leytensis*), complete webbing (webbing incomplete/reduced in *L. leytensis*), and the absence of an inverted "V"-shaped mark on the anterior dorsum (vs. present in *L. leytensis*); from a large male specimen of *L. macrocephalus* (the species

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endemic to the Luzon PAIC landmasses of Luzon, Polillo, Catanduanes, and Marinduque), the new species can be distinguished by the observation that it attains a considerably smaller maximal adult male body size (SVL range 54.2–83.1 vs. 78.9–144.6 mm in *L. macrocephalus*); the new species also possesses a fully exposed tympanum (vs. dorsal and/or posterior edge of tympanum hidden beneath overlapping supratympanic dermal ridge skin in *L. macrocephalus*) and lacks sexual size dimorphism (Table 2), whereas *L. macrocephalus* exhibits reverse sexual size dimorphism (males larger); from a large adult male specimen of *L. magnus*, the new species can similarly be distinguished by its smaller adult body size (SVL range 54.2–83.1 vs. 66.3–164.4 mm in *L. magnus*), rugose middorsal skin texture (vs. smooth to shagreened in *L. magnus*), fully exposed tympanum (vs. dorsal and/or posterior edge of tympanum hidden beneath overlapping supratympanic dermal ridge skin in *L. magnus*), rounded snout (vs. pointed in *L. magnus*), and by the absence of reverse sexual size dimorphism (present in *L. magnus*); from *L. parvus*, *L. micrixalus*, and *L. palavanensis*, the new species can be distinguished by its larger adult body size (SVL 54.2–83.1 mm; vs. 24.2–35.5 in *L. parvus*; 28.1–30.2 in *L. micrixalus*; 30.0–37.6 in *L. palavanensis*), rugose (vs. smooth) dorsal skin, Finger I > Finger II (equivalent length), the presence (vs. absence) of white-tipped sacral asperities and the presence of irregular, discontinuous dorsolateral ridges (vs. asperities absent, dorsolateral folds continuous), complete webbing (vs. reduced), and by the absence (vs. presence) of an inverted "V"-shaped middorsal marking (vs. present); the new species is additionally distinguished from these species by the absence of sexual size dimorphism (vs. females larger in *L. parvus*, *L. micrixalus*, and *L. palavanensis*); from *L. visayanus*, *L. beloncioi* is readily diagnosed by its rounded snout (vs. pointed in *L. visayanus*), a tendency towards longer adult male fangs (2.6–5.6 vs. 1.8–3.0 mm in *L. visayanus*), by the presence (vs. absence) of white-tipped sacral asperities; finally, the new species can be distinguished from *L. woodworthi* by its longer male fangs (2.6–5.6 vs. 1.3–1.6 mm in *L. woodworthi*), moderately rugose middorsal skin (vs. smooth in *L. woodworthi*), rounded snout (vs. snout moderately pointed in *L. woodworthi*), the presence (vs. absence) of white-tipped sacral asperities, and by the absence (vs. presence) of continuous dorsolateral folds.

Description of holotype.—A mature male, specimen in excellent condition; small portion of liver preserved separately for genetic material; habitus robust; head broader than body, its length 98.3% of its width, 39.0% of SVL; snout tip rounded in dorsal and lateral aspect (Fig. 6); supralabial region markedly swollen, increasingly protuberant towards angle of jaw; interorbital region and dorsal rostrum nearly flat; eye diameter 62.0% snout length, 97.5% eye–nares distance, 1.4× eye–tympanum distance; pupil horizontally sub-elliptical with discontinuous posterior margin; canthus rostralis distinct, slightly medially bowed in dorsal aspect; loreal region concave; nostrils oriented dorsolaterally, narial openings visible in dorsal view; internarial region slightly convex; tympanum exposed, annulus slightly distinct, diameter 55.7% of eye diameter; supratympanic fold thick, strongly protuberant, moderately rugose, extending from posterior corner of eye, extending horizontally over (concealing) dorsoposterior corner and posterior margin of tympanic annulus, turning ventrally at nearly right angle, to end in supra-axillary region, where it is discontinuous with postrictal tubercular swelling at angle of jaw. Tongue elongate, tapered anteriorly, with narrow anterior attachment and laterally expanded, free, bilobed posterior margin at rest (anterior edge when tongue projected); choanae situated at anterolateral edge of palate, subcircular, their anterolateral edge partially concealed by palatal shelf of maxilla in ventral view; choanae widely separated by distance five or six times greater than diameter of single choana, each located just anterolaterally to (in contact with) lateral tip of dentigerous process of vomer; dentigerous process of vomer distinct, with four or five conical teeth on each side; dentigerous process angled anterolaterally (rostrally), approximately at 45° inclination, with closest (posterior) points separated by distance approximately equal to one choana, their most distant (anterior) ends separated by distance equal to three choanae; enlarged odontoid "fangs" large, recurved, unsheathed by oral mucosa for > distal half their length, situated on either side of mandibular symphysis/medial bulge, their tips sharply pointed, total length 4.6 mm (perpendicular distance from ventral edge of mandible), inclined dorsoposteriorly, tips 2.9 mm perpendicular from dorsal mandible surface; maxillary fang "sockets" anteromedial to choanae, large, round, similar in size to one choana; vocal apertures large, elongate, surrounded by extensive mucosal invaginations, situated at posteroventral margin of buccal floor, just medial to angle of jaw.

Hand length 46.8% foot length; foot 93.4% tibia length; tibia length 58.3% SVL; fingers laterally, irregularly ovoid in cross section, due to presence of slight lateral dermal flange, extending from base of each digit, on either side, to proximal margins of terminal finger discs; terminal discs not expanded beyond widths of penultimate phalanges (Fig. 6), their relative descending lengths: III > I > II = IV; subarticular tubercles prominent, their ventral surfaces convex and velvety in texture; one subarticular tubercle below Fingers I and II, two tubercles under Fingers III and IV; terminal discs and subarticular tubercles with gray, velvety, thickened surfaces; distal margins of tubercle more distinct than their proximal margins, and supernumerary tubercles absent, but articular surfaces of fingers between subarticular tubercles of digits, and at base of all digits covered medially with thickened tubercular surface; palmar surface with large, elongate, thenar tubercle (ventromedial surface of Finger I), enlarged, flattened, squarish medial "inner" (base of Finger III) metacarpal tubercle, and small, ovoid, convex outer (base of Finger IV) metacarpal tubercle; surface of these palmar structures, intervening, and surrounding surfaces all covered with similar, thickened, velvety (matte) tubercular dermis layer; nuptial excrescences or pads, asperities, and webbing absent; forearm musculature not hypertrophied.

Tarsus folds and flaps absent; terminal discs of toes slightly expanded, with distinct circummarginal grooves; plantar surfaces of foot with well-developed, prominently protruding (ventrally), rounded subarticular tubercles (Fig. 6); plantar surfaces of foot smooth, with velvety-textured subarticular tubercles; relative lengths of toes: I < II < V < III < IV; toes fully webbed (interdigital webbing extending to proximal edges of terminal discs of all toes); postaxial flap of skin running along entire outer edge of Toe V; inner metatarsal tubercle prominent, elongate, with raised ventral edge; outer metatarsal tubercle absent.

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Skin of dorsal surfaces of trunk and head smooth to slight shagreened texture, bearing low but clearly evident fleshy dermal tubercle clusters in supra- and post-tympanic regions, and tuberculate dorsolateral ridges, immediately following supratympanic region, and continuing posteriorly to the scapular region approximately to the points of forearm insertion (Fig. 6); similar dorsolateral tubercular ridges extend from this point, along more lateral (flanks) and slightly medial (dorsal) surfaces, and extend back to the sacral region; on posterior half of trunk and sacral region, dermal tubercles present mid-dorsally, consisting of single, raised tubercles or short, raised tubercular ridges; in sacral region, some tubercles capped with round, weakly keratinized dermal asperities; not arranged in clusters, or rows, but lightly dispersed in sacral region and upper one-third of dorsal surface of thigh and supra-cloacal region; ventral surfaces of head smooth; lateral and ventral surfaces of limbs smooth; remaining dorsal surfaces of limbs smooth to lightly shagreened, with occasional low tubercles; tarsus smooth on dorsolateral surface; cloacal region rugose (wrinkled), with smooth laterally and ventrally surrounding skin.

Coloration of holotype in preservative.—Dominant dorsal color on head, body, and forelimbs uniform Dark Grayish-Brown (Köhler, 2012; color 284) Dark Grayish-Olive (275) with irregular, diffuse, Dusky Brown markings (285) concentrated on occiput and sacral regions; lateral head surfaces Drab (19) with diffuse Warm Sepia (40) markings, canthal bar, pigmentation associated with supratympanic ridge; four Medium Neutral Gray (298) labial bars alternate with lighter, Pale Buff (2) labial region coloration; Sepia bar (286) spans the interorbital region; tympanum Dark Gray (299) with Pale Neutral Gray (296) central spot; dorsal surfaces of hindlimbs Brussels Brown (33) to Brick Red (36), with darker, Sepia (286) diffuse transverse crossbars; dorsal surface of outer (Finger IV) hand and (Toes III–V) Drab Gray (256); inner dorsal surfaces of hand (Fingers I–III) and Toes (I–II) Bright White Buff (a) to Cream White (52); ventral body and proximal limb segment surfaces Cream White (52) to Chamois (84), nearly Cream Yellow (82) on upper ventral thigh surfaces and infracloacal region; sternal region and throat with dense aggregation of distinct Orange-Rufous (56) blotches; infralabial region Grayish Horn (268), mandibular region Cream White (52); ventral surfaces of hand and foot Vandyke Brown (181) to Glaucous (291) with Jet Black (300) ventral palmar surfaces, post-brachial surfaces of forearms, and ventral surfaces of tarsal (shank) surfaces; central surfaces of subarticular tubercles of hand and foot Light Neutral Gray (297) and terminal discs of fingers and toes Pale Neutral Gray (296).

Coloration of holotype in life.—Based on field notes and color images by RMB. Dorsal surfaces light brown (Sayal to Mikado browns, colors 41–42) with Burnt Umber Brown (48) and Grayish Horn (268) diffuse, irregular, scattered darker markings and Jet Black pigmentation associated with dorsolateral and lateral flank tubercles, the supratympanic ridge, postrictal coloration, and labial bars; dorsal surfaces of limbs Sayal Brown (41), Prout's Brown (41), to Natal (49) dark brown blotches and thick transverse limb bars; lateral head with Dark Neutral Gray (299) canthal, snout, and post-ocular pigment; tympanum Medium Neutral Gray (298) with Buff White (1) spot; flanks fade dorsal-to-ventral from Drab Gray (256) to Cinnamon Drab (50), to Light Buff (2) yellowish-white; ventral surfaces Bright White to Pale Buff (1); throat with Cinnamon- or Orange-Rufous (50, 56) brown blotches; posterolateral throat (skin overlying vocal sacs) Very Dark Brown Umber (23); posterior ventrum and inguinal region transitions to Straw Yellow (53) and Orange Yellow (8) below the cloaca; ventral surfaces of distal segments of fore- and hindlimbs Pinkish Buff (3) to Buff Yellow (5); forearm, tibia, and tarsus ventral surfaces with denser aggregation of Cinnamon- to Orange-Rufous (50, 56) brown blotches medially and Jet Black (300) laterally; ventral (palmar) surfaces of hand and (plantar) surface of foot Dusky Brown (285) with Dark Pearl Gray (290) subarticular tubercles and lighter, Pale Neutral Gray (296) to Light Pearl Gray (262) terminal discs of digits.

Measurements of holotype (mm).—SVL 74.9; HL 29.2; SL 13.0; TYM 4.4; HW 29.7; FLL 16.1; THL 40.2; TL 43.7; TAR 18.9; FL 40.8; HAL 19.1; EN 7.2; IND 5.7; FANGL 4.6; FANGH 4.1.

Variation.—Summaries of univariate morphological variation in the type series are presented in Table 2. We observed no apparent sexually dimorphic color variation in our large series of paratypes; similarly, although comparisons among older specimens from particular localities (CAS, FMNH, and USNM paratypes, collected over the past century) and more recent material from some of the same, but also novel localities on Mindoro (KU, and more recent USNM specimens) revealed some variation suggestive of geographically variable color variation, these initial observations could conceivably reflect circumstances of preservation and color shifts with time. As a result, we emphasize color variation across all specimens available to us (from throughout Mindoro Island): three general ground-pattern dorsal coloration types are immediately apparent, including (1) specimens with very dark brown to black dorsal surfaces, and transverse hindlimb bars, forearm blotches, and interorbital bar indistinct or barely evident (Sepia 286, Jet Black 300; e.g., KU 302095, 303432, 308303, 335866), (2) specimens with medium brown to gray dorsal surfaces (Glaucous 291 to Brownish Olive 292 or Dark Neutral Gray 299) and darker transverse hindlimb bars, forearm blotches, interorbital bar, and labial bars all evident (the holotype [PNM 9870; Fig. 6] and paratypes [KU 302084–88, 302100, 302105–07, 303451, 303353], plus nearly all older CAS, FMNH, and USNM paratypes and referred specimens, collected 40–100 y ago), and (3) specimens with light gray (Pale Neutral Gray 296 to Pratt's Gray 293) dorsal body surfaces, with a dense network or reticulum of dark gray (Plumbeous 295 to Dark Neutral Gray 299; e.g., KU paratypes 302084, 302085) throughout the body, and densely congregated into hindlimb bars, forearm blotches, a darkly pigmented interorbital bar, and labial bars. Ventral body surfaces are generally white (Buff White l to Cream White 52) and transitioning posteriorly to more yellowish white (Pale Horn 11 to Light Yellow Ocher 13) in inguinal region and posterior surfaces of the thighs. Darker pattern elements situated around posterolateral surfaces of head (chin and throat lateral edges), and lateral margins of ventral limb surfaces (lateral edges of ventral forelimbs and hindlimbs) correspond to the same general dorsal coloration patterns (above), which wrap laterally onto ventral surface and sharply fade to white. Thus, the specimens with dark dorsal coloration are also the specimens with the darkest ventral pattern elements (infralabial blotch-

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Fig. 8. Typical appearance of forested habitat of *Limnonectes beloncioi*, new species, near Sablayan Prison and Penal Farm, Mindoro, Philippines (photo copyright S. L. Travers).

es, lateral forearm ventral coloration, ventral shank color, and anteroventral thigh pattern), and the specimens with the medium brown to gray dorsal surfaces (including most paratypes and the holotype) have corresponding medium pigmentation in these same characters contributing to the ventral pattern (Fig. 6). Ventral surfaces of hands and feet are surprisingly invariant and do not differ from those described in the holotype (Fig. 6), and no ontogenetic color variation was evident in our series. The one ventral color pattern character that seemed to depart from the above was the concentration of pigment contributing to throat and pectoral region. Throats ranged from homogeneously medium gray (offset and darker from ventral body surface; males KU 302104, 303432, females KU 302105, 303451) to darkly spotted brown (males KU 302095, 302106, 308313, PNM 9870 [holotype], females KU 302100, 302118, 335866), to pale cream (not differing from remainder of ventral body coloration; males KU 302085, 302086, 302089, 303353, 304132, females KU 302084, 302387, 302088). In life, some specimens have more yellowish hues in lateral head surfaces, the flanks, inguinal region, ventral hindlimb and cloacal color (Fig. 7); these are lost and fade to shades of cream to light gray in preservative; iris gold above and silver below pupil.

Distribution.—*Limnonectes beloncioi* is known only from Mindoro and Semirara Islands, central Philippines (Fig. 1). Minor land-bridge and deep-water islands to the east and southwest of Mindoro have not yet been surveyed for herpetofauna; as such, the identity of any populations of *Limnonectes* that might eventually be discovered on Ilin, Sibay, Ambulong, Caluya, Maestre de Campo, and/or the Cuyo Islands group cannot yet be confirmed. The genetic identification of populations of *Limnonectes* on Busuanga, Coron, and Culion (currently considered *L. acanthi* [Taylor, 1923, 1928; Inger, 1954; Brown and Alcala, 1970; Diesmos et al., 2015]; thus, we anticipate these populations will be more closely related to Palawan Island *L. acanthi* than to *L. beloncioi*) would be of particular interest to herpetologists, biogeographers, and speciation geneticists (Esselstyn et al., 2010; Brown et al., 2013).

Etymology.—We derive the specific epithet, a patronym, to honor the Philippine army scout and freedom fighter Esteban Beloncio, who contributed substantially to the armed resistance against the Japanese WWII occupation of Mindoro Island, 1942–1945. Suggested common name = Mindoro Fanged Frog.

Ecology and natural history.—The new species is commonly encountered in riparian habitats, and in the vicinity of moving water in galley forests; it has been collected from rocks, sandy shingles, and muddy river banks of streams and rivers of Mindoro Island and its land-bridge associated island, Semirara; the species also is anticipated to be present on Ilin and Ambulong Islands, which are separated from Mindoro by shallow channels. On Mindoro, the new species has been collected from just above sea level in coastal lowland habitats associated with river mouths (the type locality: Barangay Carmundo, Sitio Paypay-Ama, at the mouth of the Paypay-Ama River; the Municipality of Victoria, Barangay Loyal, Sitio Panguisan, Panguisan River), and in coastal habitats in the northern Mindoro Municipalities of Puerto Galera, Naujan, Calapan, and San Teodoro, southern Municipalities of San Jose, Bulalacao, and Roxas, and western coast Municipalities of Bongabong, Gloria, and Pinamalayan; Mindoro's interior regions, in which the new species has been recorded, collected, or observed include the relatively undisturbed low to mid-elevation forests of the Municipalities of Sablayan (Fig. 8), San Teodoro, Calapan, and Baco (Brown and Guttman, 2002; Brown et al., 2009).

Other native species of amphibians encountered on Mindoro Island (Diesmos et al., 2015) include *Platymantis corrugatus* (Ceratobatrachidae), *Fejervarya moodiei*, *F. vittigera*, *Occidozyga laevis* (Dicroglossidae), *Kaloula conjuncta*, *K. picta* (Microhylidae), *Leptobrachium mangyanorum* (Megophryidae), *Pulchrana mangyanum* (Ranidae), *Polypedates leucomystax*, *Philautus schmackeri*, and *Rhacophorus pardalis* (Rhacophoridae). Invasive species of frogs introduced to Mindoro include *Rhinella marina* (Bufonidae), *Kaloula pulchra* (Microhylidae), *Hylarana erythraea* (Ranidae), and *Hoplobatrachus rugulosus* (Dicroglossidae). The last of these is a voracious predator, which we have observed on numerous occasions, feeding on juveniles and metamorphs of *Limnonectes*.

With very little original vegetation present at lower elevations on Mindoro Island, and with the rising human population, the loss of original forest, development, and agriculture throughout most the island's lower elevations, the loss of forest cover must be viewed as a primary threat to all native forest-associated amphibians, including *L. beloncioi*. Estimates of forest loss or severe alteration between 2003 and 2010, for example, range from 8–9% annually, of 53–61% cumulatively for over this 7-yr period (ELBR, pers. comm. with Center for Conservation Innovations [unpubl. data, 2020]). Despite the resilience of the new species in heavily disturbed and highly degraded riparian habitats (Brown and Guttman, 2002; Brown et al., 2009; ELBR and RMB, pers. obs.), its ubiquitous persistence in Mindoro's chronically degraded lowland watersheds (Lizuka et al., 2009) suggests that poor water quality may be less of a threat to larval development in *L. beloncioi* than might otherwise be expected of amphibians with aquatic larval development (Wells, 2007).

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An important source of protein in the diets of many indigenous communities (including the eight ethnolinguistic Mangyan tribal groups of Mindoro; Lopez, 1976; Kikuchi, 1984), species of fanged frogs are widely hunted and consumed in alarming numbers throughout their ranges in the Philippines (RMB, CDS, and ELBR, pers. obs.). Although the new species is one of the most common species of frogs on Mindoro Island (as evinced by numbers of specimens available for this study in collections), it is heavily hunted and widely consumed by humans on Mindoro (Schult, 1991), including the migrant Tagalog (Luzon-derived) majority in the lowlands (Scheffers et al., 2012) and interior highlands indigenous peoples (Mangyans) who target river frogs ("Palakang Ilog") during the rainy season (ELBR, pers. obs.). We have evaluated this species against the IUCN conservation status classification rubric (IUCN, 2020), and find that it does not qualify for Critically Endangered (CR), Endangered (EN), Vulnerable (VU), or Near Threatened (NT) status. *Limnonectes beloncioi* has a geographic distribution that spans multiple islands, including the large landmass of Mindoro, and is quite abundant at all sampled localities. We therefore classify this species as Least Concern (IUCN, 2020), but acknowledge that some other, currently undefined, threatened status may be conceivable, following consideration of unrelated, or secondary sources of information which do not bear directly on the biology of the new species (Gonzalez et al., 2018).

DISCUSSION

Although we did not diagnose the new species on Mindoro from its closest relative (*L. acanthi* from Palawan) via genetic distance thresholds, we note that the mean pairwise mitochondrial sequence divergence from its sister species is $\geq$5.0%, which is commensurate with, or exceeds, divergences between uncontroversial and phenotypically distinct sister-species pairs (Table 1), such as *L. macrocephalus* (Luzon PAIC) versus *L. visayanus* (West Visayan PAIC), and *L. magnus* versus *L. diuatus* (both of the Mindanao PAIC). *Limnonectes beloncioi* (Mindoro PAIC) and *L. acanthi* (Palawan PAIC) occupy allopatric insular distributions on separate Philippine geological platforms (PAICs; Brown and Diesmos, 2009) as do most other species-pairs comparisons used for reference here, and it does not surprise us that genetic divergence between the new species and its sister taxon is equivalent to or exceeds divergences observed among other Philippine sister-species pairs.

With the description of *Limnonectes beloncioi*, and the recognition of a distinct evolutionary lineage of fanged frog from the Mindoro PAIC, the number of species of Philippine *Limnonectes* climbs to 12. We consider the formal description of a new, endemic Mindoro PAIC fanged frog to represent a long-overdue step, which ameliorates a persistent taxonomic shortfall allowed to lie unresolved for more than half a century (Inger, 1954; Brown and Alcala, 1970; Evans et al., 2003). The numbers of native amphibian species, previously thought of as distributed on both Palawan and Mindoro PAICs, has steadily declined through time; this trend has been a consequence of successive taxonomic revisions involving one or both populations (Taylor, 1920, 1923; Inger, 1954; Brown and Alcala, 1970; Brown and Diesmos, 2002; Brown and Stuart, 2012; Diesmos et al., 2014, 2015). Moreover, as the geographic ranges of Philippine amphibians have become properly characterized (Brown and Alcala, 1970; Diesmos et al., 2015), cases of true, widely distributed, single species exhibiting geographic ranges that span PAIC boundaries has become increasingly uncommon (Brown et al., 2013; Diesmos et al., 2015). With one exception, all other Philippine *Limnonectes* are restricted to the landmasses encompassed by single Pleistocene Aggregate Islands (as defined by Brown and Diesmos, 2009; Brown et al., 2013); the single exception is the remarkably widespread *Limnonectes leytensis*, which occupies four PAICs (the Sulu, Mindanao, West Visayan, and Romblon faunal regions). The hypothesis of conspecificity of all these populations of *L. leytensis*, however, remains untested (Evans et al., 2003; Siler et al., 2009; Brown et al., 2013).

It is interesting that, although Taylor (1923) and Inger (1954) both recognized the Palawan faunal region lineage (*L. acanthi*) as a clearly distinct species, the close affinities of the Mindoro population escaped their attention. However, as pointed out by Brown and Alcala (1955, 1970), large sample sizes of herpetological specimens from Mindoro did not come available until much later; thus, it is not surprising that Inger (1954) tentatively identified three Mindoro specimens available at the time of his review as *L. macrocephalus*. As explained by Brown and Guttman (2002), the prevailing view of Mindoro's land vertebrate biogeography for much of the late 20th century was that its fauna was assembled primarily by colonization of lineages from Luzon (Taylor, 1928; Inger, 1954; Leviton, 1963; Brown and Alcala, 1970; Heaney, 1985), which has proven to be an oversimplification (Inger, 1999; Brown and Guttman, 2002; Brown and Diesmos, 2009; Brown et al., 2009, 2013; Esselstyn et al., 2010; Blackburn et al., 2013).

Although traditional, character-based, taxonomic approaches were unable to convincingly identify fixed diagnostic differences between Palawan and Mindoro populations, even under a polytypic species concept (Inger, 1954; Brown and Alcala, 1970; Brown et al., 2000), the identification of other amphibian lineages that have been capable of dispersing across Huxley's modification of Wallace's Line have been associated with the eventual recognition of species of amphibians now considered endemic to Mindoro Island (Brown and Guttman, 2002; Brown et al., 2009; Esselstyn et al., 2010). However, like *Limnonectes beloncioi*, these Mindoro endemics were only recognized after a considerable delay (80–100 yrs after their populations were first surveyed by herpetologists; Taylor, 1920, 1923; Inger, 1954), due almost certainly to their phenotypic similarity with other species from neighboring landmasses adjacent to Mindoro (e.g., *Pulchrana mangyanum* [Brown and Guttman, 2002]; *Leptobrachium mangyanorum* [Brown et al., 2009]). It is unclear why some Mindoro amphibian populations historically were recognized early (Inger, 1954; Brown, 2007) and their taxonomic status never questioned (e.g., *Philautus schmackeri* [Boettger, 1882]; Brown and Alcala, 1970, 1994), whereas others have gone historically confused and never had their status clarified—despite suggestions of apparent phenotypic and/or genetic distinctiveness on this island (e.g., Mindoro Island *Platymantis corrugatus* and *Kaloula conjuncta*; Inger, 1954; Blackburn et al., 2013; Brown et al., 2015). Suffice it to say, Mindoro's amphibian populations have been historically understudied, most likely due to a combination of logistical challenges and untested, indiscriminately applied taxonomic expectations ascribed to

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its land vertebrates by the last two generations of biogeographers who assumed Mindoro's fauna to be derived from, and closely related to, that of Luzon (Inger, 1954; Leviton, 1963; Brown and Alcala, 1970; Heaney, 1985). Evans et al. (2003) first identified a deep, ~5.0% divergence in mitochondrial gene sequences (12S–16S) and hypothesized that the Mindoro population might constitute a distinct evolutionary lineage, or unrecognized species. Although this level of genetic divergence certainly is commensurate with those empirically estimated between other, uncontroversial, recognized Philippine fanged frogs separated on isolated PAICs (e.g., Luzon PAIC *L. macrocephalus*, West Visayan PAIC *L. visayanus*, and Mindanao PAIC *L. magnus*; Table 2), the use of unreliable single-locus genetic distances, combined with arbitrarily assigned cut-offs, or divergence thresholds, has been criticized on multiple grounds, which need not be repeated here. As such, to reconsider Evans et al.'s (2003) finding, we required data from other sources (character data, mensural data, advertisement calls, biogeographic information) before taxonomic recognition of the Mindoro population might be justified by our rejection of the single-species hypothesis. Unfortunately, legal restrictions preventing faunal surveys and voucher specimen collection and other logistical obstacles to fieldwork on Mindoro have historically hampered the amassing of the necessary specimen-associated data. We are encouraged that the factors preventing the realization of this long-anticipated eventuality (the recognition of a species of fanged frog, endemic to Mindoro; Evans et al., 2003; Siler et al., 2009; Diesmos et al., 2015) have been alleviated by the dedicated efforts of field biologists with a shared commitment to international collaboration and conservation of Mindoro's unique and imperiled amphibian biodiversity (Alcala and Brown, 1998; Stuart et al., 2008; Diesmos and Brown, 2011; Alcala et al., 2012).

MATERIAL EXAMINED

Institutional abbreviations follow Sabaj (2020).

Limnonectes acanthi: Palawan Island: Palawan Province: Puerto Princesa City: Barangay Irawan, Irawan Watershed: KU 308975, 308979, 308989–92, 309049, 309051, 309056–57, 309065, 309083–85, 309139–45, PNM 7604; Municipality of Brooke's Point: Barangay Mainit: KU 309146–54, 309437–38, 326332–35, 326353, 327464, PNM 7605; Municipality of Quezon: Barangay Poblacion: KU 309155–63; Municipality of Nara, Barangay Estrella Falls: PNM 6694, 7607, TNHC 59903; Palawan Island, Palawan Province: FMNH 51185–96, 51199–217, 51219–20, 51222–40; Palawan Island, Palawan Province: FMNH 51185–95; Municipality of Puerto Princesa, Mt. Bloomfield: PNM 6280, 6295, 6301; Barangay Lamod, sitios Kayasan & Tagabinet: PNM 6375–77, 6390–94, 6409–10, 6431–33, 6440–43; Municipality of Iwahig, WNW of Iwahig Town, Malatgaw River: CAS-SU 21432–34, 21437, 21439–41, 21444–49, 21465; Tugbuni Creek, ca. 10 km S Iwahig: CAS-SU 21496–501; ca. 8 km S. of Iwahig: CAS-SU 21525–26; Malatgaw River tributary, ca. 5 km W. of Iwahig: CAS-SU 21502–08; 9 km SW of Iwahig: CAS-SU 21520–24; ca. 9 km SSW of Iwahig: CAS-SUA 21509–17, 21519, 21527–41; Malatgaw River tributary, ca. 1.5 km SSW of Iwahig: CAS-SU 21453–60; Malabosog Creek, 95.5 km NE of Puerto Princesa: CAS 157215–16, 158100–04; Malabosog Creek, 95.5 km NE of Puerto Princesa: CAS 158131–33; W of coast road, 96.5 km NE of Puerto Princesa: CAS 158136–40; Pelotan Creek, 94 km NE of Puerto Princesa: CAS 158144–48; Langogan River tributary, 1.5 km upstream from mouth, 85 km NE Puerto Princesa: CAS 158151–53; Puerto Princesa District, Municipality of Iwahig, Iwahig Penal Colony, Sitio Balsahan: USNM 229492–93; Municipality of Narra, Taritien Barrio, Estrella Falls: USNM 287281–83, 287342–45; Municipality of Quezon, National Museum compound: USNM 287370–73; Municipality of Brooke's Point, Barangay Macagua: USNM 158204, 158205–09; Boundary of Barangay Samarinana and Saulog: Mt. Mantalingahan Range: Area "Pitang": KU 309155; Palawan Island: MCZ A-14268–69, 23171–73; Sugod Island, Palawan Province: Municipality of Puerto Princesa, Barangay Cabayugan: PNM 6306, 6319–21, 6345, 6356, 6365; Balabac Island, Palawan Province: FMNH 51196–204; Minagas Point, Dalawan Bay: USNM 158285–94; Busuanga Island, Palawan Province: FMNH 51205–17, 51219–20, 51222–40, KU 79043, 79045, 79059, 79060, CAS 62577 (holotype); Siñgai: CAS-SU 5986–99, 6000–03, 6026–29, 6038–40, 14710–13, MCZ A-14067–69 (paratypes); Coron Island, Palawan Province: CAS 158154–77, CAS-SU 5943–45, 5954, 13965–67; Wayan Creek, 1–3 km N of San Nicolas: CAS 62133–35, 62562 (paratypes); 6 km NE San Nicolas: KU 79041–60; Culion Island, Palawan Province: CAS-SU 3284, FMNH 51241–79; 6.5 km SW Culion Town: KU 79061–68.

Limnonectes beloncioi: See holotype, paratypes, and referred specimens sections.

Limnonectes diuatus: Philippines: Mindanao Island, Agusan del Norte Province: Municipality of Cabadbaran, Tagibo River: south side of Mt. Hilong-hilong: CAS 133430–32, 133434, 139389–93, FMNH 197934, MCZ A-88036 (paratypes), 133500 (holotype); Municipality of Remedios T. Romualdez, Mt. Hilong-hilong, Barangay San Antonio, 1130 m, local area name "May Impit": KU 333325, 333369–75, 333381–89, 333392–93; Dinagat Island, Dinagat Islands Province: Municipality of Loreto, Barangay Santiago, Sitio Cambinlia (Sudlon): KU 309992–310000.

Limnonectes ferneri: Philippines: Mindanao Island, Davao Del Norte Province: Municipality of Monkayo, Simulaw River Drainage, Mt. Pasian: CMNH 5572, 5573 (paratypes), PNM 9506 (holotype).

Limnonectes leytensis: Philippines: Mindanao Island, "Mindanao": FMNH 14868 (batch of 16 specimens). MCZ A-14137–41 (+11 duplicates); "Zamboanga Province": FMNH 63200; "Zamboanga": MCZ A-10480; Zamboanga Del Norte Province: Katipunan: CAS-SU 13960; 1 km S of Gumay, 7 km SE Buena Suerte, Dapitan River: CAS 147303; "Cotobato Province": FMNH 50060–131; "Takayan, near Saub, Cotobato Coast" (=S. Cotobato and/or Sulturan Kudarat Provinces): MCZ A-23198–99, 14134–36; Davao City Province: Municipality of Kalinan, Barangay Malagos, Malagos Eagle Station: TNHC 61940–41; Lanao Del Norte Province: Municipality of Kolambugan, Marata Bogan: CAS-SU 6060; Lanao del Sur Province: Municipality of Marawi, "Viscar Landing, Lake Lanao": MCZ A-25755; Misamis Occidental Province: Municipality of Misamis: CAS-SU 13956; Misamis Oriental Province: Municipality of Cartegena Bo, Plaridel: CAS-SU 16910–12; Leyte Island, Leyte Province: FMNH 42855–84, 54121–22, 60789–91; Leyte City: CAS-SU 15483; Calabian:

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MCZ A-14099; Camiguin SUR Island, Camiguin Province: Mambajao: CAS-SU 23088–91; Negros Island, Negros Oriental Province: Dumaguete City: KU 306006, 306008–09, 306011–12, 306014, 306016–18; "Philippines": FMNH 99212–24; "Negros Island," FMNH 61524–29; Municipality of Dumaguete City, Barangay Valinad: MCZ A-45654, 45660–61; Samar Island: FMNH 61453–64, 96180, 96206, 96208, 96228–32, 96241, 96248, 172611–21; Northern Samar Province: Municipality of San Isidro, Matuquinao: CAS-SU 18161; Basilan Island: FMNH 174034, 174049–51; Basilan Province: MCZ A-14125–33; Basilan Province, Port Holland: CAS 60377–78, MCZ A-14103–10; Mt. Abung-abung, "NE of Maluso": MCZ A-22741–42; Jolo Island, FMNH 40538–39; Jolo Isl., Sulu Archipelago: MCZ A-10481; Bohol Island, Bohol Province: Municipality of Sierra Bullones, ca. 13 km SE Sierra Bullones Town, Cantaub: CAS-SU 23243, 23246–47, 23252, 23258, 23274, 23280, 23283, 23293, 23330–01; Municipality of Sierra Bullones, 10 km SE of Sierra Bullones Town, Dusita: CAS 131950–51, CAS-SU 23140–42, 23144, 23251, 23272, 23284, 23287, 23291, 23299, 23307, 23317, 23326–30, 23331–35, 23241, 23265; Dinagat Island, Dinagat Province: MCZ A-14100–02, 14270; Tawi-tawi Island, Sulu Archipelago: MCZ A-10479, 14111–19, 14271–72.

Limnonectes macrocephalus: Philippines: Luzon Island, "Northern Luzon": FMNH 161676–78, 161680, 161694–96, 161698; Kalinga Province: Municipality of Lubuanga: KU 306049, 306053, 306056, 306058, 306059; Ifugao Province: FMNH 174591–93, 175262, 175264–67, 175269, 175278; Mountain Province: Mt. Data MCZ A-28294 (paratype); Benguet Subprovince: Baguio City: CAS 62546, MCZ A-14491 (paratype), MCZ A-14155–75 (+ 4 duplicates); Laguna Province: CAS-SU 14706, 14748–49; Municipality of Siniloan: CAS-SU 14733–35; Municipality of Los Baños, University of the Philippines Campus, Mt. Makiling: TNHC 54952; Camarines Sur Province: Municipality of Naga City, Barangay Panicuason, Mt. Isarog National Park, Mt. Isarog: TNHC 61913, 62744–45; Albay Province: Municipality of Tiwi, Barangay Banhaw, Sitio Purok 7, Mt. Malinao: TNHC 61914, 62746; Municipality of Malinao, Barangay Tagoytoy, Sitio Kumangingking, Mt. Malinao: TNHC 61917, 62747; Barangay Labnig, Sitio Palali: CAS-SU 140046; Quezon Province: Municipality of Tayabas, Sampaloc: CAS-SU 14731–32; Cavite Province: CAS 15714–15; Polillo Island, Quezon Province: Municipality of Polillo: KU 303480, 303481, 307505; Catanduanes Island, Catanduanes Province: FMNH 248015, 259811–12.

Limnonectes magnus: Philippines: Camiguin Sur Island: Camiguin Province: Municipality of Mambajao: KU 302139–40; 5.5 km NE Catarman Town, Mt. Mambajao, Sangsangan: CAS-SU 24119–20, 24122–24, 24056–57, 24059, 24078; Nasawa Crater, Mt. Hibok-hibok: CAS-SU 22862; 4.5 km S of Mambajao Town, Catibawasan Falls: CAS-SU 22856; Barrio Naasag, Sitio Vulcan: CAS-SU 23095–96; Dinagat Island: Suriago del Norte Province: Municipality of Loreto: KU 306003, 306062–63, 306068–70; Samar Island: Eastern Samar Province: Municipality of Taft: KU 306028–30, 306033, 306036, 306041–42, 306077, 306082–84, 309272–74; Western Samar Province: Municipality of Paranat, Barangay San Isidro, Sitio Nasarang: TNHC 54947–50; Municipality of Tarabucan, Matuquinao: CAS-SU 18174–79, 18182–83, 18188–90, 18192, 18194–95, 18198; Sequinan: CAS 11235; Mindanao Island: Bukidnon Province: Mt. Kitanglad: FMNH 258974; Municipality of Malaybalay, Kalasungay: CAS-SU 16799–800; Davao City Province: Mt. Apo: MCZ A-2597 (paratype); Municipality of Gumay, W side of Dapitan Peak, 6 km SE of Buena Suerte: CAS 19981; Municipality of Calinan, Barangay Malagos, Baguio District, Eagle Foundation Malagos Eagle camp: TNHC 59904–05, 59941; Davao Del Sur Province: Municipality of Toril, Barangay Baracatan ("Upper Baracatan"), Sitio San Roque: TNHC 59906, 59942; Misamis Occidental Province: Mt. Malindang: CAS-SU 13968; Zamboanga City Province: Municipality of Zamboanga City, Barangay Pasonanca: CAS 61870–71; Agusan Del Norte Province: W side of Mt. Hilong-hilong: CAS 133792, 133554, CAS-SU 133673–74; Municipality of Cabadbaran, S side of Mt. Hilong-hilong Peak, crossing of Tagibo and Dalaydayan rivers: CAS-SU 186128; Zamboanga Del Norte Province: Municipality of Katipunan, Labao: CAS-SU 16804; Bohol Island: Bohol Province: Municipality of Carmen, Chocolate Hills Complex, Barangay Buena Vista: TNHC 56397–402; Municipality of Sierra Bullones, 11 mi SE Sierra Bullones Town: CAS 23415, 23417, 23420; Sandayong Barrio: CAS 17170–211; Cantub Barrio: CAS 17135–37; Cantub, 15 km SE Sierra Bullones Town: CAS-SU 23429–30; 11 mi SE Sierra Bullones, Dusita: MCZ A-23167–70, "Bohol Island": CAS 23416, 23418–19, 23424; Leyte Island, Leyte Province: Municipality of Calabian: MCZ A-14152 (paratype of *Rana magna visayanus* Inger, 1954); Basilan Island, Basilan Province: Basilan Isl.: MCZ A-14152–54, 14267.

Limnonectes micrixalus: Basilan Island, Basilan Province: Mt. Abung-Abung: CAS 20144, 60143 (holotype and paratype of *Rana micrixalus* Taylor, 1923), MCZ A-14187; Mindanao Island, Zamboanga City Province: Municipality of Zamboanga City: CAS 61874 (paratype of *Rana micrixalus* Taylor, 1923).

Limnonectes palavanensis: Philippines: Palawan Island: Palawan Province: Municipality of Brooke's Point: Barangay Mainit: KU 309133–35, 309136, 309138; S slope of Thumb Peak, 330–660 m, WNW of Iwahig: CAS 14744, 20432–34, 20438, 20445–47, 20449, 20451, CAS-SU 20421–26, 20448; 7–8 km SW of Santiago: CAS 20466–71; Municipality of Iwahig, Thumb Peak, Iwahig Penal Colony: MCZ A-14214–16.

Limnonectes parvus: Philippines: Mindanao Island: Zamboanga del Norte Province: Mt. Malindang: Dapitan River: CAS 139445–46; Misamis Occidental Province: Dapitan Peak: CAS 145767–68; between Sitio Masawan and Sitio Gandawan: CAS 17511; Misamis Occidental Province: W side of Dapitang Peak, 1 km E of Masawan: CAS 20399; Municipality of Gumay, New Piñan, 5–6 km S Buena Suerte, headwaters of the Dapitan River, 7–8 km SE of Masawan: CAS 145760–61; W. side Dapitan Peak, 1500 m, 5 km E of Masawan: CAS-SU 20396; New Piñan, Municipality of Gumay, W. side Dapitan Peak, 6 km SE of Buena Suerte: CAS-SU 20403; Dapitan River, 833 m, New Piñan, ca. 2 km SE Municipality of Gumay, 8 km SE Buena Suerte: CAS-SU 20411.

Limnonectes visayanus: Philippines: Masbate Island: Masbate Province: Municipality of Mobo: CAS-SU 144253–59, KU

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302171; Mt. Mobo, Tugbo watershed: CAS 144345, CAS-SU 144260–61, 144327, 14482–84; Panay Island: Antique Province: Municipality of Culasi: KU 302157–59, 302161, 302165; Municipality of Pandan: KU 302176, 302180–84; Municipality of San Remigio: KU 306816; Municipality of Valderrama, Barangay Lublub, base of Mt. Baloy: TNHC 56337; Aklan Province: Municipality of Makato, Castillo Barrio: CAS 139164–66; Municipality of Makato, Castillo Barrio: CAS-SU 137590; Calagna-an Island, Iloilo Province: Barangkalan: CAS 124121, 124293–97; Siquijor Island, Siquijor Province: CAS-SU 23126, FMNH 61439–43; Municipality of Lazi, Po-o: CAS-SU 16796–97; 1.5 km N of Maria Town: CAS-SU 23908; Municipality of San Jua, Tagibo Barrio, 2 km from coast: CAS-SU 16777, 16779, 16780, 16783–85, 16787–88, 16790, 16792, 16794; Sicogon Island, Iloilo Province: Buaya area: CAS 12442–44, 124950–58; Poro Island, Cebu Province: 0.4 km N of Poro Town: CAS 124515; Negros Island: Negros Occidental Province: Municipality of Cauayan: KU 302145; Negros Oriental Province: Municipality of Sibulan, Barangay Janya-janay, Sitio Balinsasayo, Cuenos, Lake Balinsasyo: TNHC 61911, 61921, 62879; Municipality of Valencia, Barangay Bongbong, Camp Lookout, Mt. Talinis, in Cuernos de Negros range: KU 302189–90, 302192, 302196, 302203–04, TNHC 62880–82; Tahiro River, 120 m above sea level: MCZ A-110944–48; Municipality of Bayanan, Malyong: CAS 17078–81; "Negros Island": FMNH 57204–33, 57234–41, 57244, 57246–47, 61403–09, 61444–48, 61504–23, 77721–22; Municipality of Sibulan Lake Balinsasaayo, 1000 m above sea level, Cuernos de Negros Range: MCZ A-110949; Municipality of Luzuriaga, Barangay Palinpino: MCZ A-28295 (paratype); Municipality of Dumaguete, Dumaguete City: MCZ A- 26809; 15 km from Dumaguete City, Camp Lookout: CAS 14723; ca. 35 km W of Bais Town, along Mamagyan River, sitio Panyabunan: CAS 17091; Municipality of Siaton: CAS 156051–56; Hacienda Louisiana: CAS-SU 14725–30; ca. 23 km W of Bais Town, 0.5 km W of Mayaposi Hill, upper Mabaja Creek: CAS 16671, 16776, CAS-SU 16672–83; W. of Mariposi Hill, 20 km W of Bais Town, Mabaja River: CAS 17074–76; ca. 20 km W of Bais, Pagyabunan: CAS 16749–51; ca. 3 km W of Palimpinon, Ocoy River: CAS 16685–736; Pulopaantao, SE slope of Makawili Peak, Mt. Canlaon: CAS 16650–70; Cebu Island, Cebu Province: 3 km NW of Cebu City: CAS-SU 23857, 23861, 23913; Minglanilla area: CAS-SU 131911–13; Municipality of Carmen, Matinao-an: CAS 131903; Guimaras Island, Guimaras Subprovince: near Buenavista: CAS 125305–07; Jordan area: CAS 125308–09.

Limnonectes woodworthi: Philippines: Catanduanes Island: Catanduanes Province: Municipality of San Miguel: KU 302231, 302234; Polillo Island: Quezon Province: Municipality of Polillo: CAS 61001 (paratype), KU 302224, 302227–28, 303483–85, 307528, 307531–34; Luzon Island: Laguna Province: Municipality of Los Baños, Mt. Makiling: CAS 61184–89, 61191–93, 61824–29, 62565–73 (paratypes), MCZ A-10555 (paratype); "Los Baños creek, between College and Camp Eldridge": MCZ A-14239–40; Municipality of Los Baños, University of the Philippines Campus, Mt. Makiling: TNHC 54953–55; Quezon Province: Municipality of Atimonan, Barangay Malinao Ilaya: TNHC 61942; Zambales Province: Municipality of Olongapo, SBMA Naval Base, "Nav-mag" area, Ilanin Forest (Triboa Bay): TNHC 62947–55; Camarines Sur Province: Municipality of Naga City, Barangay Panicuason, Mt. Isarog: TNHC 61912, 62956; Albay Province: Municipality of Tiwi, Barangay Banhaw, Sitio Purok 7, Mt. Malinao: TNHC 61915, 62957; Municipality of Tobaco, Barangay Bongabong: TNHC 61916, 62959–60; Municipality of Malinao, Barangay Tagoytoy, Sitio Kumangingking, Mt. Malinao: TNHC 61918, 62958; Sorsogon Province: Municipality of Irosin, Barangay San Rogue, Mt. Bulusan, Bulusan Lake: TNHC 61919–20, 62961–64; Polillo Island, Quezon Province: MCZ A-14241–49 (paratypes + 24 untagged duplicates); Municipality of Polillo, Barangay Sibucan, Sitio Tambangin: TNHC 54989.

DATA ACCESSIBILITY

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