Revisiting Linnaean and Wallacean Shortfalls in Mindanao Fanged Frogs: The Limnonectes magnus Complex Consists of Only Two Species

Authors: Abraham, Robin Kurian, Herr, Mark William, Sterkhova, Viktoria V., Otterholt, Rayanna, Siler, Cameron D., et al.

Source: Herpetological Monographs, 35(1) : 112-140

Published By: The Herpetologists' League

URL: https://doi.org/10.1655/HERPMONOGRAPHS-D-20-00010

Herpetological Monographs, 35, 2021, 112–140

Revisiting Linnaean and Wallacean Shortfalls in Mindanao Fanged Frogs: The *Limnonectes magnus* Complex Consists of Only Two Species

Robin Kurian Abraham[1], Mark William Herr[1], Viktoria V. Sterkhova[1], Rayanna Otterholt[1,2], Cameron D. Siler[3], Marites Bonachita Sanguila[4], and Rafe M. Brown[1,5]

[1] Biodiversity Institute and Department of Ecology and Evolutionary Biology, 1345 Jayhawk Boulevard, University of Kansas, Lawrence, KS 66045, USA
[2] Haskell Indian Nations University, 155 E Indian Avenue, Lawrence, KS 66046, USA
[3] Sam Noble Oklahoma Museum of Natural History and Department of Biology, University of Oklahoma, 2401 Chautauqua Avenue, Norman, OK 73072, USA
[4] Biodiversity Informatics and Research Center, Father Saturnino Urios University, San Francisco Street, Butuan City, 8600 Agusan del Norte, Philippines

Abstract: We revisit the question of species diversity among Mindanao Fanged Frogs of the *Limnonectes magnus* complex consisting of *L. magnus*, *L. diuatus*, *L. ferneri*, and a previously hypothesized putative new species, inferred in the first molecular phylogenetic studies of the genus almost 2 decades ago. Using a multilocus molecular deoxyribonucleic acid sequence data set and comprehensive sampling of 161 individuals from throughout the Mindanao Pleistocene aggregate island complex landmasses (a distinct faunal region of the southern Philippines) we characterize geographically structured genetic diversity, focusing on the phylogenetic placement of individuals from each species' type locality. We also present new morphometric data from large samples of freshly collected material from the type localities of each included species; together with examination of the name-bearing original type specimens, we conclude that an overestimation of species diversity has occurred and has been exacerbated by the indiscriminate acceptance of the hypothesis of the existence of widespread cryptic species in this group. We place *L. ferneri* in synonymy with *L. diuatus*, clarify the identification of the latter taxon with respect to *L. magnus*, and apply this name to the widespread, generalist, highly variable giant Fanged Frog distributed throughout the Mindanao faunal region of the southern Philippines.

Key words: Geographic radiation; Mindanao Pleistocene aggregate island complex; Stream frogs

Island archipelagos have provided numerous examples of the evolutionary processes and biogeographic patterns involved in generating biodiversity, especially the interplay of geological processes, colonization, and isolation (Paulay 1994; Brown et al. 2013; Brown 2016). Home to numerous clades of codistributed terrestrial vertebrates (Brown and Diesmos 2002), the Philippine Archipelago recently has been the focus of several integrative studies of amphibian radiations (Setiadi et al. 2011; Blackburn et al. 2013; Brown et al. 2013, 2015). A particularly interesting group are the fanged frogs of the genus *Limnonectes*, which consists of 73 named species distributed across Southeast Asia. This diverse clade includes 10 described, morphologically diagnosable, and noncontroversial (taxonomically unproblematic) endemic species in the Philippine Archipelago (Evans et al. 2003; Setiadi et al. 2011).

In a previous review, Brown et al. (2013) distinguished between the archipelago's partially or fully characterized adaptive radiations (Brown et al. 2013, 2015) and the possibly nonadaptive, geographic radiations (Setiadi et al. 2011; Brown and Siler 2014; Brown et al. 2015, 2016). The latter, loosely defined category (Brown et al. 2013) includes clades with one or more representative species on each island bank, or Pleistocene aggregate island complex (PAIC; Brown and Diesmos 2002; Brown and Guttman 2002). In these clades, or suites of taxa (in cases of nonmonophyly [Brown and Guttman 2002; Evans et al. 2003]), species have been characterized as ecologically similar, with little to no evidence of a phenotype–environment correlation or within-island, ecologically associated diversification (Brown et al. 2013; Brown and Siler 2014). Of particular interest are clades that show a mixture of diversification patterns, with single ecological generalists on some islands, and evidence of intraisland diversification, habitat and reproductive mode specialization, and multiple sympatric species on some islands (Inger et al. 1986; Alcala and Brown 1998; Brown and Iskandar 2000; Evans et al. 2003; Setiadi et al. 2011; Brown et al. 2013, 2015, 2016). One unclear case of potentially mixed, adaptively versus nonadaptively radiated frogs are the Philippine Fanged Frogs, genus *Limnonectes*, which are comprised of no fewer than three invasions of the archipelago (Inger 1954; Evans et al. 2003; Brown et al. 2013) and which have differentiated (or ecologically sorted) into composite communities with conspicuously distinct size classes (Setiadi et al. 2011).

We undertook this study to estimate the phylogeny of a Philippine endemic clade comprising *Limnonectes magnus* (Stejneger 1910) and related taxa (Inger 1954; Brown and Alcala 1977; Evans et al. 2003; Siler et al. 2009; Setiadi et al. 2011), with the goal of clarifying species boundaries (uncertainty around which has slowed the pace of taxonomic descriptions and recognition of biodiversity, constituting the so-called "Linnaean shortfall"; Raven and Wilson 1992) and characterizing the geographic distributions of these units, which has been so poorly understood (the "Wallacean shortfall"; Lomolino et al. 2010).

Limnonectes magnus, a large-bodied Mindanao faunal region Fanged Frog (male holotype snout–vent length [SVL] = 113 mm; Stejneger 1910) was described from the mid-lower-elevation slopes (≤1200 m above sea level [asl]) of Mt. Apo, the country's highest mountain (2954 m asl), located on southeast Mindanao Island (Fig. 1), at the southern extent of the archipelago. Brown and Alcala (1977) later named *Rana diuata* (= *Limnonectes diuatus*; male holotype SVL = 58.4 mm) from higher elevations of Mt. Hilong-hilong, in the Diuata Mountain Range (northeastern Mindanao) and Siler

[5] Correspondence: email, rafe@ku.edu

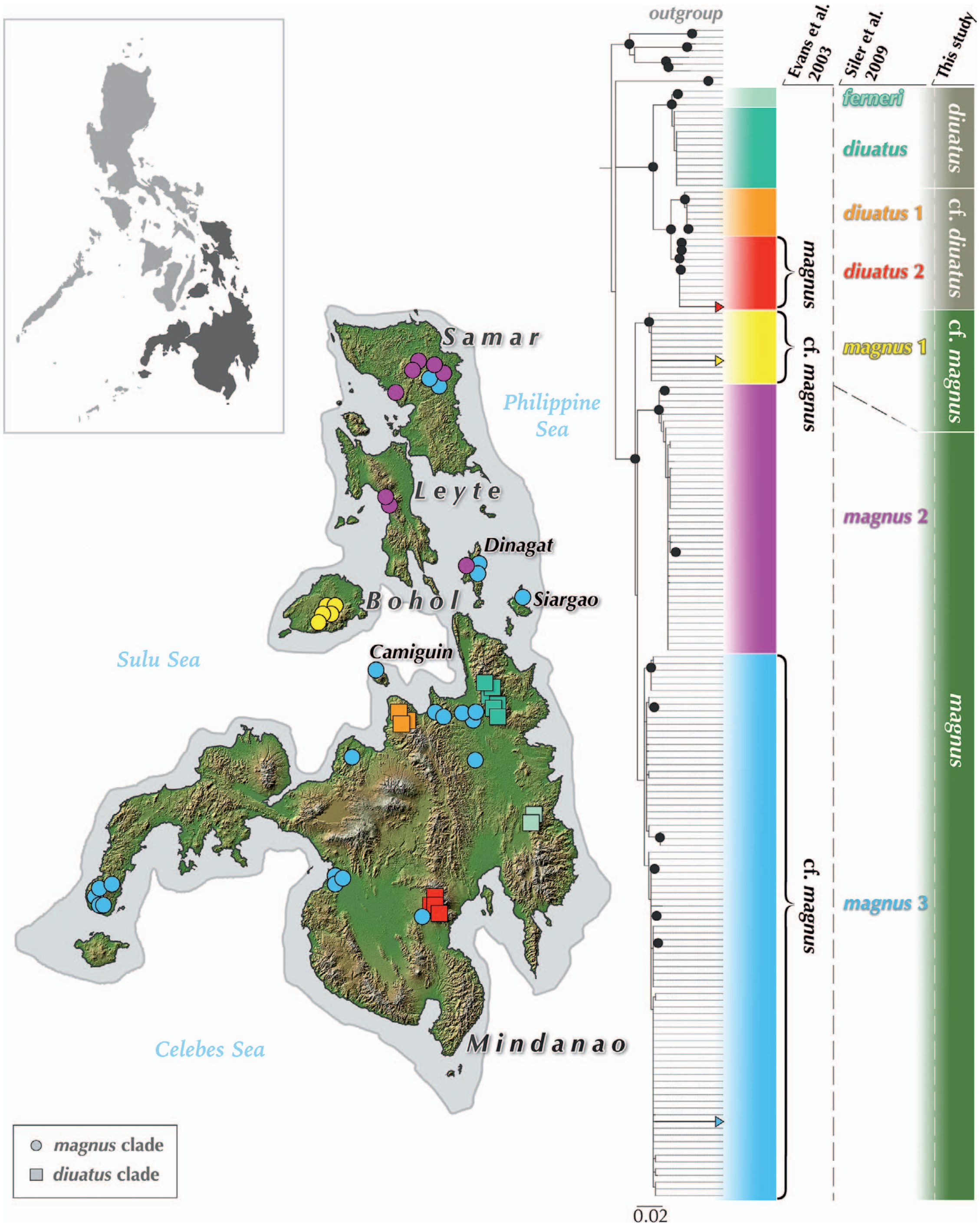

FIG. 1.—Maximum-likelihood point estimate, illustrating relationships of Mindanao Pleistocene aggregate island complex (PAIC) Fanged Frogs, inferred from analysis of 16S mitochondrial gene). Nodal support: black dots = strong support (≥70 maximum-likelihood bootstrap percentages). Sequences from Evans et al. (2003) correspond to bold branches with colored arrows. For full museum catalog voucher information, see Appendix 1 and Supplemental Fig. S2.

et al. (2009) described *Limnonectes ferneri* (male holotype SVL = 84.3 mm) from the Municipality of Monkayo, Davao del Norte Province, southeast Mindanao. Aside from Mindanao Island proper, large-bodied Fanged Frogs from other islands of Mindanao PAIC (e.g., Samar, Leyte, Bohol, Camiguin Sur) have been reported for more than half a century (Inger 1954; Brown and Alcala 1970) and consistently identified as *L. magnus* (Siler et al. 2009).

Evans et al. (2003) demonstrated that populations historically identified as *L. magnus* may not be a monophyletic assemblage, suggesting that a second (assumed then to be undescribed) species may occupy the Mindanao PAIC (Brown and Diesmos 2009), including the islands of Basilan, Bohol, Leyte, Mindanao, Samar, and many smaller islands (e.g., Biliran, Camiguin Sur, Dinagat, Siargao) associated with these major landmasses (Fig. 1). Their analyses included what Evans et al. (2003) considered to be topotypic samples of *L. magnus* (genetic samples, collected at the type locality: high elevation, Mt. Apo; Stejneger 1910). Referring to this second, widespread taxon as "*Limnonectes* cf. *magnus*," the model-based phylogenetic analyses of mitochondrial deoxyribonucleic acid (DNA) sequence data of Evans et al. (2003) revealed that populations from Mindanao were sister to those from Samar, which were, in turn, most closely related to the Bohol Island population. Specimens that Evans et al. (2003) referred to as the widespread lineage (*L.* cf. *magnus*) were genotyped from throughout the Mindanao PAIC (Fig. 1), including lower-elevation foothills of Mt. Apo itself. Other than the description of a third Mindanao PAIC species (*L. ferneri* Siler, McVay, Diesmos and Brown 2009), no further progress on this group has been made and fieldworkers have simply adopted the name *L. magnus* for the high-elevation Mt. Apo population and *L.* cf. *magnus* for the widespread low-elevation populations on all the islands of the Mindanao PAIC faunal region (Plaza and Sanguila 2015; Sanguila et al. 2016).

Here we leveraged 30 yr of genetic sampling (1990–2020) from throughout the Mindanao PAIC, including sequences from specimens reported by Evans et al. (2003) and Siler et al. (2009) as well as material from the type localities of *L. magnus* (Stejneger 1910), *L. diuatus* (Brown and Alcala 1977), and *L. ferneri* (Siler et al. 2009). We reconsider species boundaries within the *L. magnus* complex (Brown et al. 2000; Brown and Diesmos 2002) using a mitochondrial gene fragment (mtDNA: 16S) to screen genetic variation and guide reduced sampling of three nuclear gene loci for 19 population/species With our combined multilocus phylogenetic estimate and consideration of morphometric variation, we find no support for the continued recognition of *L. ferneri* and conservatively conclude that only two species of large-bodied Fanged Frogs reside in the Mindanao faunal region: (1) a single widespread low-elevation species corresponding to true *L. magnus* (Stejneger 1910) and (2) a single high-elevation species referable to *L. diuatus* (Brown and Alcala 1977; with *L. ferneri* [Siler et al. 2009] now relegated to synonymy).

Materials and Methods

Sampling, Molecular Data, Alignment, and Phylogenetic Analyses

We collected DNA sequences from 161 individuals collected from 49 localities (Appendix I). We sequenced one mitochondrial gene region corresponding to the ribosomal ribonucleic acid subunit (16S) and from a resulting preliminary mitochondrial "barcode" phylogeny we selected 19 individuals for subsequent gene sequencing of three nuclear loci: lactase (LCT), carnitine palmitoyltransferase II (CPT-2), and pro-opiomelanocortin (POMC). Primers, polymerase chain reaction methods, thermal profiles, and sequencing protocols follow Brown et al. (2013, 2015). We selected closely related outgroup species on the basis of uncontroversial higher-level phylogenetic relationships of the family Ranidae (Feng et al. 2017). All novel sequences were deposited in GenBank (Appendix 1).

The 16S data set (706 base pairs [bp]), including our sequences and outgroups from GenBank, was aligned using the default parameters of the MAFFT algorithm (Katoh and Standley 2013). The combined nuclear data set (LCT, CPT-2, POMC) for 19 individuals had a length of 2156 bp. To assess gene congruence, we estimated gene trees with maximum likelihood using the program RAxML-HPC v8.0.0 (Stamatakis 2014) and scrutinized trees inferred from these partitions for the presence of strongly supported topological conflict. Not finding strongly supported and conflicting topologies, we felt justified in concatenating our data (16S + three nuclear genes; aligned in MAFFT) for subsequent analyses.

We conducted maximum-likelihood analyses of our multilocus (16S + three nuclear genes) data set using the same partitions but with the GTR+Γ model for each of 200 independent best-tree searches and the rapid-bootstrapping algorithm. One hundred replicate tree search inferences were performed, each initiated with a random starting tree. Nodal support was assessed with 1000 bootstrap pseudoreplicates (Stamatakis 2014). We considered nodes to be strongly supported when bootstrap values were ≥70% (Hillis and Bull 1993). For our multilocus data set we performed additional likelihood analyses using IQ-TREE (Trifinopoulos et al. 2016), which used 1000 bootstrap pseudoreplicates via the ultrafast bootstrap approximation algorithm. Ultrafast bootstrap support values ≥0.95 indicate well-supported nodes in IQ-TREE analyses (Minh et al. 2013).

Partitioned Bayesian analyses for the concatenated (16S + three nuclear genes) data set were conducted in BEAST 2 (Bouckaert et al. 2014) on the CIPRES gateway server (Miller et al. 2010). We partitioned the nuclear DNA by locus, with gene-specific protein-coding regions partitioned by codon position. The corrected Akaike information criterion model to find selection parameters and the "greedy" search algorithm for finding the best models for Bayesian analysis (Darriba et al. 2012) were used to select the best model of nucleotide substitution for each partition. We ran four analyses, each with four Metropolis-coupled chains, an incremental heating of 0.02, and an exponential distribution with 25 as the rate parameter prior on branch lengths. All analyses were run for 10×10^6 generations (sampling every 1000 generations). We set the burn-in to the default value of 25%, hence discarding the initial 5×10^6 generations. To assess stationarity, we used trace plots and effective sample size values (>200) on Tracer v1.7 (Rambaut et al. 2018). We constructed a 50% majority consensus tree with posterior probabilities estimates of nodal support using the remaining sampled trees. We considered nodal support with Bayesian posterior probabilities values ≥0.95 as significant (Huelsenbeck and Rannala 2004).

Analysis of Adult Phenotype

We measured the following 15 standard continuous morphological characters following methods and definitions of Brown and Guttman (2002) and Emerson (1994): SVL, head length, snout length, tympanum diameter, head width, forearm length, femur length, tibia length, tarsus length, foot length, hand length, eye–narial distance, internarial distance, fang length, and fang height. To eliminate bias caused by ontogenetic variation, each character (except SVL) was scaled to the same size by adjusting shape according to allometry (Thorpe 1983; Lleonart et al. 2000). Measurements from 98 male and 62 female adult individuals of Fanged Frogs (from a set of 161, including subadults; Fig. 1) from throughout the Mindanao PAIC were adjusted for allometric growth using the following equation: $X_{adj} = \log(X) - \beta(\log SVL - \log SVL_{mean})$, where X_{adj} = adjusted value; X = measured value; β = unstandardized regression coefficient for each population found by regressing each mensural character on SVL; SVL = measured SVL; SVL_{mean} = overall average SVL of all samples. All downstream analyses were performed on the adjusted values.

Before attempting statistical procedures, we performed an *F*-test to test for heteroscedasticity for each character across populations (separately for each sex) and, in cases where characters violated the assumption of homogeneity of variance, we performed Kruskal–Wallis rank sum tests to evaluate whether samples originate from the same distribution.

We also 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 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. After ensuring that data conformed to assumptions of normality by performing separate Shapiro–Wilk tests on each variable in the data set (results not shown; $P \leq 0.05$), we tested if the different populations display mean differences in single morphometric characters with two-way analyses of variance (ANOVAs) using sex (males, females) as factors. We followed this up with a Tukey honestly significant difference test to determine specifically which population pair of character means differed after adjusting for multiple comparisons. All morphological analyses were performed and visualized in R v3.6.1 (R Core Team 2019). Specimens and genetic material are deposited at the University of Kansas, the Field Museum of Natural History, the Texas Natural History Collection of the University of Texas at Austin, the Cincinnati Museum of Natural History, and the National Museum of the Philippines (institutional abbreviations follow Sabaj 2019).

We used principal components analysis (PCA) to find the best low-dimensional representation of variation in the data to determine whether morphological variation could form the basis of detectable group structure. Eigenvalues > 1 were retained according to Kaiser's criterion (Kaiser 1960) and the R package hypervolume (Blonder et al. 2014) was used to construct hypervolumes using gaussian kernel density estimation to estimate the probability density function of the retained principal components (PCs). To characterize clustering and distance in morphospace, and to determine whether either past taxonomy or preliminary results from 16S mitochondrial gene phylogeography could be used to distinguish putative species, a discriminant analysis of PCs was performed to find the linear combinations of morphological variables that have the largest between-group variance and the smallest within-group variance. This approach relies on data transformation using PCs analysis as a preliminary step before a subsequent discriminant analysis, ensuring that variables included in the latter step are uncorrelated and number fewer than the sample size (Jombart et al. 2010).

Analysis of Acoustic Data

Calls were recorded by using a Nagra VI digital recorder at a sampling rate of 44.1 kHz. We inspected vocalizations as oscillograms and spectrograms that were generated using the R package seewave (Sueur et al. 2008). We measured call parameters including mean dominant frequency (maximum frequency using the analytical programs selection spectrum function over the duration of the entire call), mean call duration (time between onset of first pulse and offset of last pulse in a call), and call rise (time between onset of first pulse and onset of pulse of maximum amplitude) and fall times (time between onset of pulse of maximum amplitude and offset of last pulse) using Raven Pro v1.5 (Center for Conservation Bioacoustics 2014), with the Hanning window type and a discrete Fourier transform window size of 256 points and 50% overlap with 44.1-Hz sampling rate. We present ranges followed by mean ± 1 SD in parentheses.

Allocation of Mindanao Giant Fanged Frog Names

Given past differences in assignment of species' taxonomic epithets to giant Fanged Frogs of the Mindanao faunal region (Inger 1954; Brown and Alcala 1970, 1977; Evans et al. 2003; Siler et al. 2009), we endeavored to definitively assign existing names to genetically and phenotypically characterized units by incorporating both classes of data deliberately collected from specimens from the type locality of each species. We also examined and incorporated data from the type specimens of each species, as a final specifying measure, to independently confirm/refute our assignment of available names to groups demonstrably representing distinct evolutionary lineages (species).

RESULTS

Phylogenetic Analyses

Our RAxML maximum-likelihood analysis of 16S mtDNA data generated a single point estimate topology of a log likelihood of –logL 12,343.50 (Fig. 1). The preferred topology suggests that *L. magnus* (sensu lato) is nonmonophyletic (Fig. 1); that is, the high-elevation Mt. Apo population—considered by Evans et al. (2003) to likely represent true *L. magnus*—is in fact more closely related to *L. diuatus* than it is to the widespread *L.* cf. *magnus* from low-elevation Mindanao and the remaining Mindanao faunal region islands.

The 16S mtDNA maximum-likelihood tree containing populations sampled from throughout the Mindanao PAIC infers the presence of two subclades with strong bootstrap support, with moderate levels of genetic divergence between these two clades, and low levels of divergence within each clade (Supplemental Figs. S1, S2, available online). One strongly supported subclade corresponds to the Mindanao-endemic high-elevation clade containing the type locality of *L. diuatus* (green clade: high elevations [≥1000 m] from Mt. Hilong-hilong, NE Mindanao; Fig. 1), along with closely related haplotype clades from Mt. Lumot (*L. diuatus* 1, orange clade: Municipality of Gingoog, Misamis Oriental, northern Mindanao), and Mt. Apo (*L. diuatus* 2, red clade: Municipality of Toril, Davao City Province, SE Mindanao), and *L. ferneri* (green clade: Municipality of

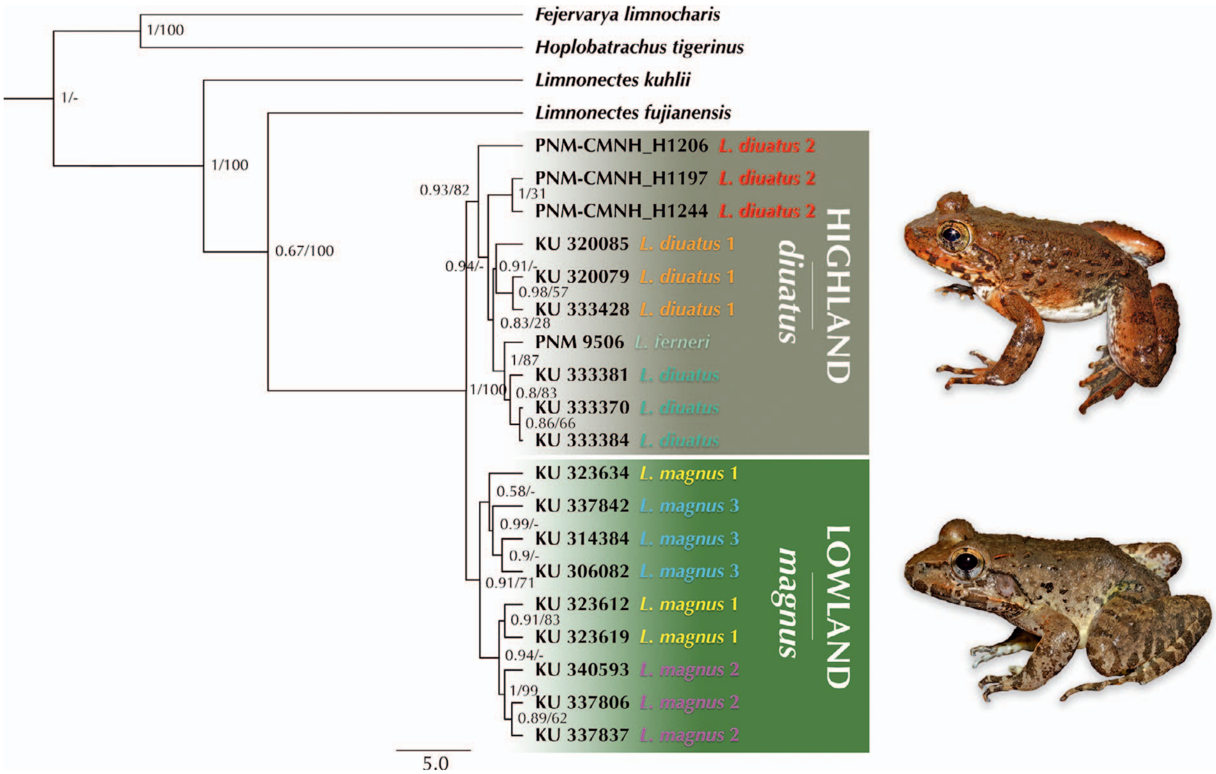

Fig. 2.—Bayesian maximum clade credibility tree, illustrating relationships among Mindanao Pleistocene aggregate island complex (PAIC) Fanged Frogs, inferred from analysis of four concatenated loci (16S ribosomal ribonucleic acid [rRNA], carnitine palmitoyltransferase II [CPT-2], lactase [LCT], pro-opiomelanocortin [POMC]). Nodal support: Bayesian posterior probabilities and bootstrap percentages from a separate maximum-likelihood analysis, which inferred the same topology (see text for details). Clades color-coded as in Fig. 1.

Monkayo, Davao del Norte Province, south-central Mindanao).

The second, moderately supported subclade included three weakly supported groups from across low elevations of the Mindanao PAIC. One contained haplotype clade (*L. magnus* 1, yellow clade) is limited to Bohol, whereas another (*L. magnus* 2, purple clade) is distributed among the islands of Samar, Leyte, and Dinagat. A third haplotype clade (*L. magnus* 3, blue clade) is widely distributed throughout Mindanao, Samar, Dinagat, Siargao, and Camiguin Sur. Pairwise divergence for 16S within the lowland *L. magnus* clade was as high as 3.4% (Supplemental Fig. S1), whereas that within the high-elevation *L. diuatus* clade was 4% at maximum. Divergence between these two clades ranged 5–7.5% (Supplemental Fig. S1).

Bayesian and maximum-likelihood IQ-TREE analyses of our complete multilocus concatenated data set (16S + three nuclear genes) both estimated two primary clades (Fig. 2). Populations sampled from high-elevation sites ($\geq$1000 m) on Mindanao Island formed a clade, as did remaining samples from lower-elevation sites throughout the Mindanao PAIC (Fig. 2). The high-elevation clade (united by only moderate support) contains type locality *L. diuatus* 1 (orange clade) and *L. diuatus* 2 (red clade) and includes two moderately supported clades of *L. diuatus* and *L. ferneri*. The Mindanao PAIC widespread clade of mostly low-elevation *L. magnus* contains two poorly supported subclades: Bohol, Samar, Dinagat, Siargao, Camiguin Sur, and Mindanao and another from Bohol, Samar, Leyte, and Dinagat.

Morphometric Characterization of Phenotype

After transformation (except SVL, which was not transformed), we rejected the null hypothesis of equal variances (homoscedasticity) for internarial distance (F = 0.471, P = 0.043), and subsequently we implemented a Kruskal–Wallis test, which identified marked interpopulational variation ($\chi^2 = 11.54$, df = 4, $P > 0.05$). For all other variables we implemented an ANOVA. Our Shapiro–Wilk tests confirmed that our mensural characters satisfied the assumption of normality ($P > 0.05$; individual P-values not shown). Our ANOVAs showed that there were differences among populations for every character except femur length ($P = 0.928$) and internarial distance ($P = 0.07$) in males, and for fang length ($P = 0.98$) and fang height ($P = 0.71$) in females. Our nonparametric tests were consistent with the ANOVA results, except for internarial distance in males ($P = 0.48$), but this does not affect our conclusions. The Tukey test further revealed differences between males of true *L. diuatus* (green) and *L. diuatus* 1 (orange) for numerous characters (all except SVL, femur length, eye–narial distance, and internarial distance), whereas comparisons between the *L. magnus* (purple) and *L. magnus* (yellow) populations yielded the few statistical differences (only foot length differed; Table 1).

Among males, the first four PCs had eigenvalues >1 and accounted for 75.2% of the total variation. Among females, the first five PCs had eigenvalues >1 and accounted for 81.2% of the total variation. These were retained for the discriminant analysis, the results of which are as follows. In males, the first PC accounted for 36.2% of the variation and

TABLE 1.—Analysis of variance (ANOVA) and Tukey honestly significant difference (HSD) tests on 15 morphometric characters of male and female adult individuals. Asterisks (*) denote characters for which we rejected the hypothesis of being drawn from a single distribution, on the basis of $\alpha = 0.05$. Characters include (1) snout–vent length, (2) head length, (3) snout length, (4) tympanum diameter, (5) head width, (6) forearm length, (7) femur length, (8) tibia length, (9) tarsus length (10), foot length, (11) hand length, (12) eye–narial distance, (13) internarial distance [Kruskal–Wallis *P*-value in brackets], (14) odontoid length, (15) odontoid height.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Males															
ANOVA	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.928	0.000*	0.000*	0.000*	0.000*	0.000*	0.070 [0.481]	0.001*	0.054*
Tukey HSD															
L. diuatus (green)–*L. diuatus* 1 (orange)	0.995	0.000*	0.000*	0.003*	0.000*	0.000*	0.915	0.000*	0.000*	0.000*	0.000*	0.991	0.558	0.014*	0.046*
L. magnus 3 (blue)–*L. diuatus* (green)	0.000*	0.111	0.000*	0.409	0.994	0.000*	0.503	0.000*	0.000*	0.000*	0.111	0.000*	0.998	0.972	0.695
L. magnus 3 (blue)–*L. diuatus* 1 (orange)	0.019*	0.000*	0.315	0.016*	0.000*	0.000*	1.000	0.999	0.417	0.691	0.000*	0.002*	0.395	0.018*	0.130
L. magnus 2 (purple)–*L. diuatus* (green)	0.849	0.051*	0.000*	0.000*	0.905	0.979	0.949	0.000*	0.000*	0.000*	0.051*	0.000*	0.665	0.824	0.999
L. magnus 2 (purple)–*L. diuatus*1 (orange)	0.871	0.001*	0.399	0.682	0.001*	0.000*	0.989	0.719	0.032*	0.368	0.001*	0.002*	0.916	0.002*	0.046*
L. magnus 1 (yellow)–*L. diuatus* (green)	0.984	0.999	0.021*	0.542	0.930	0.998	1.000	0.000*	0.007*	1.000	0.999	0.000*	0.835	0.590	0.998
L. magnus 1 (yellow)–*L. diuatus* 1 (orange)	1.000	0.001*	0.441	0.379	0.001*	0.002*	0.925	0.977	0.591	0.006*	0.001*	0.009*	0.280	0.617	0.280
L. magnus 3 (blue)–*L. magnus* 2 (purple)	0.000*	0.934	0.999	0.000*	0.953	0.000*	0.850	0.105	0.014*	0.619	0.934	0.998	0.177	0.170	0.690
L. magnus 3 (blue)–*L. magnus* 1 (yellow)	0.012*	0.859	0.994	0.943	0.822	0.047*	0.840	0.984	0.999	0.005*	0.859	0.950	0.868	0.719	0.997
L. magnus 2 (purple)–*L. magnus* 1 (yellow)	0.798	0.709	0.987	0.805	0.680	1.000	0.974	0.990	0.837	0.035*	0.709	0.978	0.366	0.226	1.000
Females															
ANOVA	0.000*	0.000*	0.000*	0.000*	0.014*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.005*	0.982	0.710
Tukey HSD															
L. diuatus (green)–*L. diuatus* 1 (orange)	0.845	0.000*	0.460	0.608	0.231	0.013*	0.000*	0.000*	0.000*	0.000*	0.000*	0.254	0.168	1.000	0.920
L. magnus 3 (blue)–*L. diuatus* (green)	0.004*	0.000*	0.000*	0.007*	0.014*	0.000*	0.016*	0.000*	0.000*	0.000*	0.000*	0.000*	0.997	1.000	0.918
L. magnus 3 (blue)–*L. diuatus* 1 (orange)	0.000*	0.998	0.122	0.000*	0.998	0.018	0.005*	0.950	0.999	0.019*	0.998	0.000*	0.116	1.000	0.999
L. magnus 2 (purple)–*L. diuatus* (green)	0.474	0.008*	0.005*	0.000*	0.808	0.040*	0.670	0.000*	0.000*	0.288	0.008*	0.000*	0.685	0.987	0.841
L. magnus 2 (purple)–*L. diuatus*1 (orange)	0.104	0.794	0.429	0.000*	0.840	0.981	0.002*	1.000	0.905	0.002*	0.794	0.008*	0.858	0.984	1.000
L. magnus 1 (yellow)–*L. diuatus* (green)	0.220	0.000*	0.001*	0.001*	0.460	0.000*	0.113	0.000*	0.000*	0.012*	0.000*	0.000*	0.792	1.000	1.000
L. magnus 1 (yellow)–*L. diuatus* 1 (orange)	0.027*	0.997	0.486	0.000*	0.875	0.230	0.002*	0.988	0.839	0.003*	0.997	0.000*	0.005*	0.999	0.926
L. magnus 3 (blue)–*L. magnus* 2 (purple)	0.584	0.350	0.998	0.008*	0.426	0.001	0.640	0.942	0.600	0.375	0.350	0.994	0.689	0.982	0.988
L. magnus 3 (blue)–*L. magnus* 1 (yellow)	0.263	0.828	0.788	0.708	0.242	0.528	0.915	0.998	0.666	0.669	0.828	0.958	0.215	1.000	0.891
L. magnus 2 (purple)–*L. magnus* 1 (yellow)	1.000	0.818	0.991	0.115	0.998	0.034*	0.940	0.987	0.186	0.913	0.818	0.921	0.083	0.995	0.832

Table 2.—Summary statistics and factor loadings for the first five components extracted in a principal components analysis of Mindanao Pleistocene aggregate island complex Fanged Frog populations, analyzed separately by sex. See text for discussion of heavily loading individual characters (bolded for emphasis).

	Males					Females				
Characters	1	2	3	4	5	1	2	3	4	5
Snout–vent length	0.1121	0.2913	0.0954	−0.489	−0.2669	0.1498	0.1660	−0.1230	−0.4170	−0.0266
Head length	0.263	−0.3611	0.1472	−0.3103	−0.0728	0.3234	0.2779	−0.0886	0.2877	0.1990
Snout length	**0.3828**	−0.0012	0.1083	0.0213	0.2602	0.3002	0.2078	−0.0434	0.0296	−0.2654
Tympanum diameter	0.1818	−0.3285	0.1634	0.1682	0.2948	0.1220	**0.3505**	−0.0152	−0.3774	−0.3612
Head width	0.1681	**−0.3848**	0.0746	−0.119	−0.4067	0.2586	0.2146	−0.0231	0.3487	0.2386
Forearm length	0.1028	**0.3893**	0.1447	−0.2911	−0.2478	0.3273	−0.1601	−0.0091	−0.2570	0.2027
Femur length	0.2715	0.1965	−0.0835	0.3061	−0.3325	0.2663	−0.3952	0.1159	0.2283	−0.0475
Tibia length	**0.3609**	0.186	0.131	0.0371	0.1584	**0.3573**	−−0.2471	0.0786	−0.1256	−0.1436
Tarsus length	**0.3554**	0.2086	−0.0751	0.1073	0.0177	**0.3464**	−0.2408	0.0399	−0.1674	−0.1445
Foot length	**0.3297**	0.1963	−0.0018	0.2538	−0.2449	0.2642	**−0.4184**	0.1445	0.1095	−0.0955
Hand length	0.263	−0.3611	0.1472	−0.3103	−0.0728	0.3234	0.2779	−0.0886	0.2877	0.1990
Eye–narial distance	0.2834	0.1651	0.2381	−0.0352	0.4691	0.3154	0.2417	−0.0586	−0.2060	−0.0418
Internarial distance	0.1357	−0.2249	0.1202	0.493	−0.3343	**−0.0328**	0.1302	0.1083	0.4146	−0.7279
Fang length	0.1949	−0.1014	−0.6397	−0.136	0.0556	0.0195	0.1686	0.6784	−0.0564	0.0104
Fang height	0.2344	−0.0584	−0.6104	−0.0828	0.0768	−0.0038	0.1619	0.6700	−0.0648	0.1911
Standard deviation	2.3307	1.7555	1.2847	1.0594	0.9235	2.3459	1.4838	1.3840	1.2338	1.0188
Eigenvalues	5.4324	3.0819	1.6504	1.1223	0.8528	5.5034	2.2016	1.9156	1.5222	1.0380
Proportion of variance	0.3622	0.2055	0.11	0.0748	0.0569	0.3669	0.1468	0.1277	0.1015	0.0692
Cumulative proportion	0.3622	0.5676	0.6776	0.7525	0.8093	0.3669	0.5137	0.6414	0.7428	0.8121

possessed heavy loadings for snout length, tibia length, tarsus length, and foot length, indicating that these characters explained most of the variation along the first axis; this axis did not form the basis of group separation for any a posteriori recognized groups. The second component accounted for 20.5% of the variation with heavy loadings for head width and forearm length (Table 2). In females, the first PC accounted for 36.7% of the variation with strong loadings for tibia length, tarsus length, and internarial distance, and the second PC accounted for 14.7% of the variation, with highest loadings for tympanum diameter and foot length (Table 2). These formed the basis of discrete structure, separating the high-elevation Mindanao Island Fanged Frog populations from those widely distributed throughout the Mindanao PAIC (Fig. 3).

When we applied discriminant analysis procedures to our a priori designated groups (DAPC), not surprisingly we found discrete clustering of the high-elevation populations (*L. diuatus* [green] + *L. ferneri* + *L. diuatus* 1 [orange]) versus the widespread *L. magnus*; our minimum-spanning network, on the basis of the squared distances between populations, demonstrated marked distance in morphospace between these two primary groups (Fig. 3).

In both our phylogenetic estimates (Figs. 1, 2), we found two primary clades; this dichotomy also formed the basis of group structure in our PCA and these two groups were successfully, and discretely, discriminated in morphospace by our DAPC, particularly for adult males, which are larger than females and possess the secondary sexual character of prominent fangs on the lower jaw (Fig 3). Within these groups, additional units could not be discretely identified (Fig. 3). Tendencies toward minimal group separation was observed within the high-elevation clade (with the caveat that morphometric data from this lineage were not available from Mt. Apo), but extensive overlap among the groups (haplotype clades; Fig. 1) of low-elevation *L. magnus* was evident (Fig. 3).

Allocation of Available Names

Limnonectes magnus **(Stejneger 1910) versus "*L.* cf. *magnus*" sensu Evans et al. (2003)**.—In their phylogenetic analysis of the genus *Limnonectes*, the assignment of the name *L. magnus* to the high-elevation Mt. Apo population by Evans et al. (2003) was based on Stejneger's (1910:437) report that the holotype (USNM 35231) specimen originated "between Todaya and camp, 4000 to 6000 ft elevation" (1219–1828 m asl) and the assumption that "camp" referred to Lake Venado (an endorheic lake on Mt. Apo, situated at 7200 ft [2194 m] asl), which has been featured in numerous expedition accounts (e.g., Hoogstral 1951; Inger 1954) and where E.A. Mearns was known to have made collections. Thus, the assumption that the holotype of *L. magnus* originated between 1219 and 2194 m on Mt. Apo, combined with the fact that the several immature specimens sequenced by Evans et al. (2003) were collected (by RMB in 1991, deposited at Cincinnati Museum of Natural History) between 1200 and 1550 m on Mt. Apo, lent support to what seemed at the time to be a reasonable assumption.

However, three newly available lines of evidence argue against the assignment of Evans et al. (2003). First, the high-elevation genotype (then assumed to be *L. magnus*, but reassigned herein to *L. diuatus*, see below) was also collected and genetically confirmed at lower elevations, in the vicinity of Barangay Baracatan (Municipality of Toril; Davao City Province) at 900 m. Second, the larger-bodied, widespread, low-elevation form was also collected and genotyped by Evans et al. (2003) from as high as 1275 m (Barangay Baracatan). The fact that both forms were collected sympatrically indicates a wider elevational range for the high-elevation taxon than previously appreciated and introduces the possibility that the assumption of Evans et al. (2003) could be questioned. Third, and more important, examination of the holotype (USNM 35231; male, 110 mm SVL; no paratypes were designated by Stejneger 1910) makes it clear that the name *L. magnus* applies to the larger-bodied, widespread, low-elevation species, which Inger

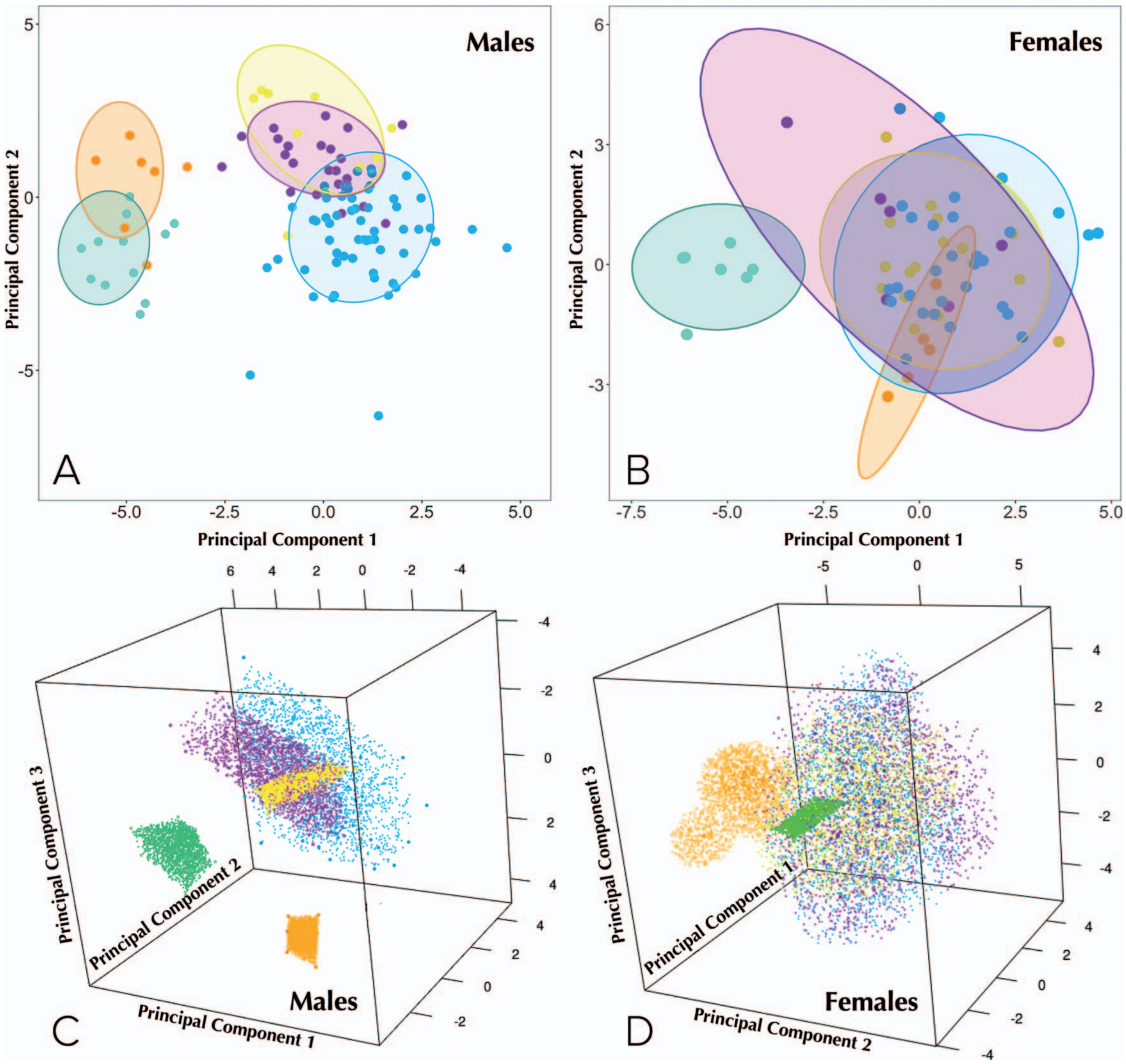

FIG. 3.—Discriminant and principal components analyses for (A) males and (B) females; dots = individuals; ellipses = groups identified by discriminant analysis of principal components. Three-dimensional plots in (C) males and (D) females depict first three principal components (larger circles = specimens; minute kernels = gaps or clusters identified by the hypervolume multivariate kernel density estimation). Color-coding as in Fig. 1.

(1954:287) characterized as "frequently in excess of 100 mm, and occasionally over 120 mm snout to vent." We note that this body size is far larger than the high-elevation form (*L. diuatus*, see below) in which adult male body size varies 58.4–84.3 (Brown and Alcala 1977; Siler et al. 2009). The holotype specimen (Fig. 4) is an adult male (sex confirmed by gonadal inspection) with evident secondary sexual characteristics typical of full-sized adult male *L. magnus* (hypertrophied jaw adductor musculature, greatly enlarged head, with jaw [in ventral aspect] laterally expanded). The holotype's boldly contrasting transverse tibial bars, pale subarticular tubercles, pale ventral surfaces of finger discs, and smooth dorsal skin are all in agreement with the widespread, low-elevation species (Fig. 5) and stand in contrast to the diffuse tibial markings, dark gray/black subarticular tubercles, dark ventral surfaces of finger discs, bright white ventrum (Figs. 2, 6), and irregularly shagreened dorsal skin texture of the high-elevation species (Figs. 5, 6). Stejneger (1910:437) and Inger (1954:277) both commented on the widespread Mindanao population's uniquely distinctive color pattern, with posterior abdomen and ventral surfaces of rear limbs densely spotted with dark brown pigment. This conspicuous color pattern has been observed by the authors at numerous localities on Mindanao, Bohol, Samar, and Leyte; it is evident in the holotype as well (Fig. 4), although unpigmented ventral surfaces in *L. magnus* have been documented (Fig. 5).

In summary, with newly acquired evidence from additional genetic data, plus definitive examination of the holotype of *L. magnus* (USNM 35231), all available data point to the same conclusion and we have no hesitation in reversing the assignment of Evans et al. (2003) of the name *L. magnus* (Stejneger 1910) to the low-elevation, widespread species of Mindanao PAIC Fanged Frog (Fig. 1; Table 3).

***Limnonectes diuatus* (Brown and Alcala 1977)**.—In their description of *R. diuata*, Brown and Alcala (1977) recognized the high-elevation population from Mt. Hilong-hilong (approximate altitude 1000+ m, of the Diuata Mountain Range, Municipality of Cabadbaran, Agusan del Norte Province) as a new species. They diagnosed it from *L. magnus* (numerous specimens of which were available at that time; represented by large sample sizes from various islands

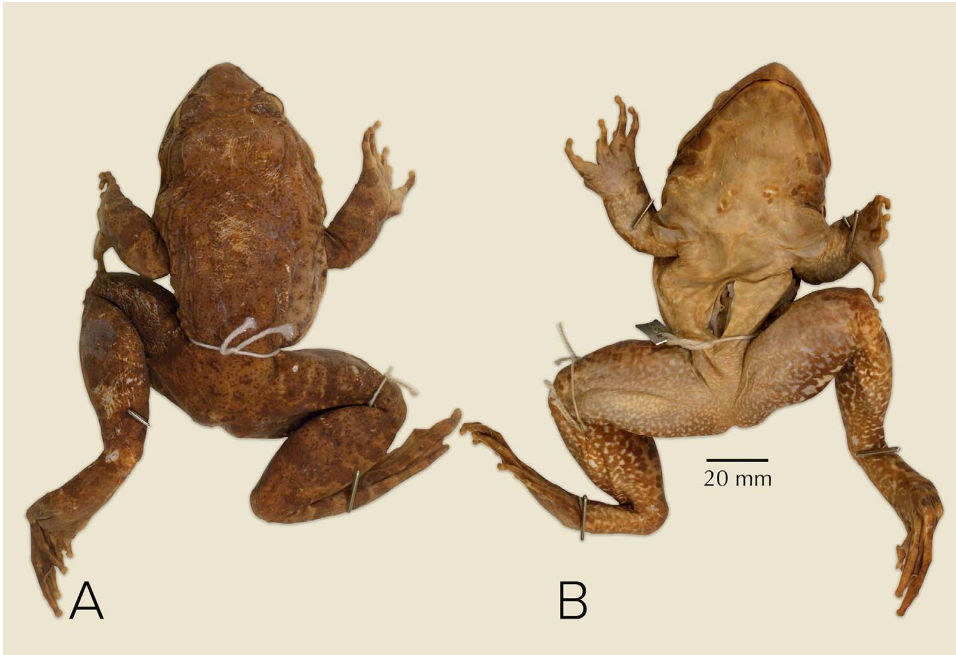

FIG. 4.—Adult male holotype (USNM 35231) of *Limnonectes magnus* from Mt. Apo (collected between Todaya and Camp), Mindanao Island. A color version of this figure is available online.

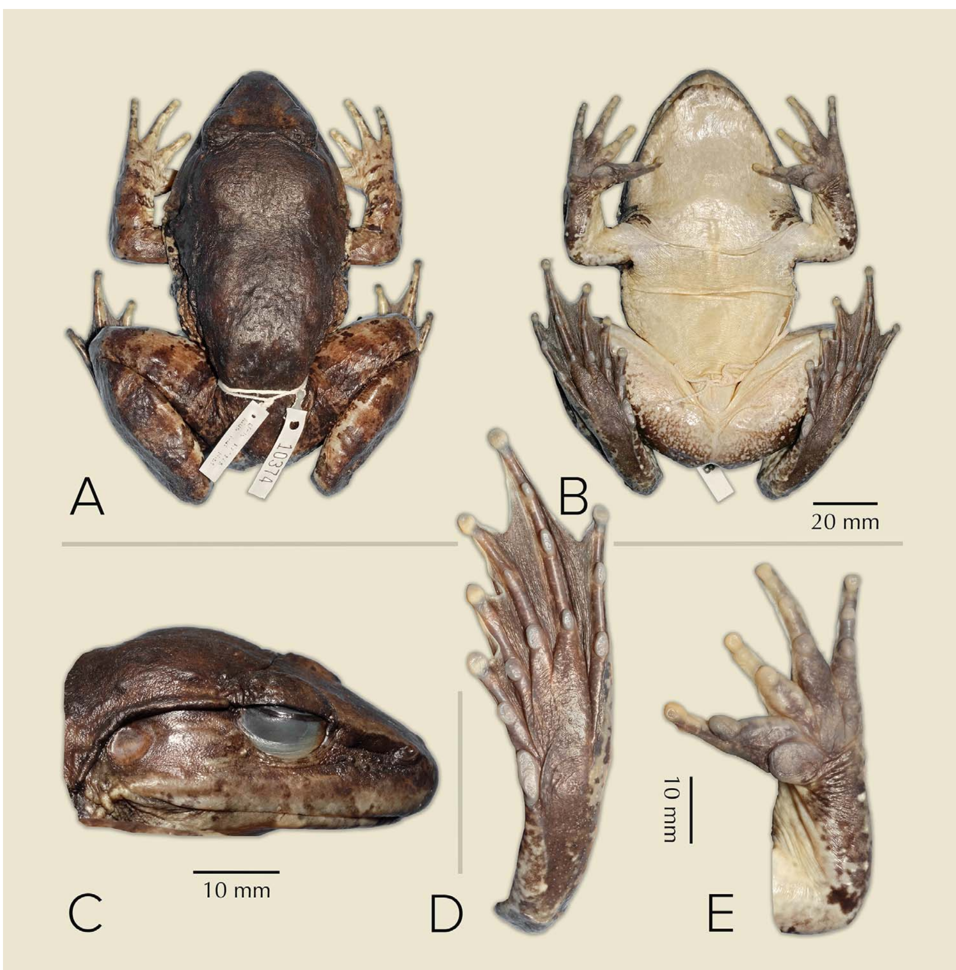

FIG. 5.—Adult male specimen of *Limnonectes magnus* (KU 314438) in (A) dorsal, (B) ventral, and (C) right lateral head views; (D) plantar surface (ventral aspect of left foot); (E) palmar surface (ventral aspect of left hand). A color version of this figure is available online.

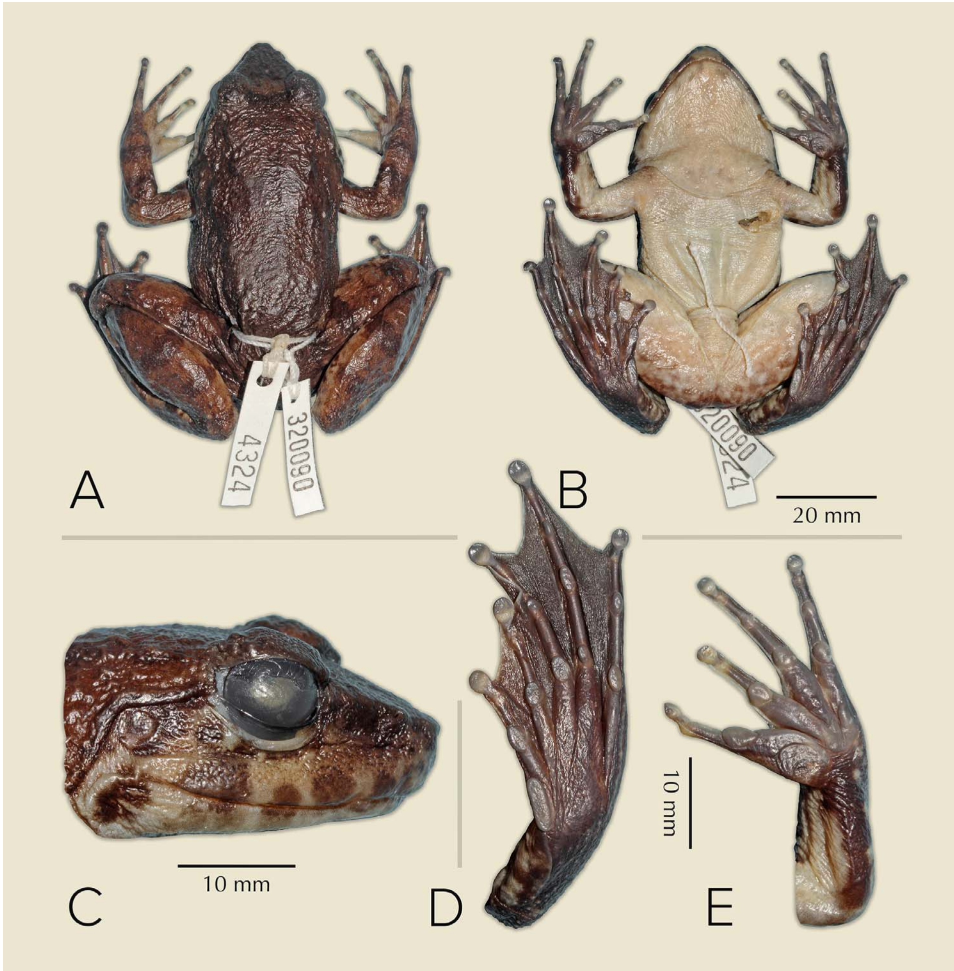

Fig. 6.—Adult male specimen of *Limnonectes diuatus* (KU 320090) in (A) dorsal, (B) ventral, and (C) right lateral head views; (D) plantar surface (ventral aspect of left foot); (E) palmar surface (ventral aspect of left hand). A color version of this figure is available online.

of the Mindanao PAIC; Brown and Alcala 1977) by its smaller body size (male SVL = 37.4–57.7 mm; *n* = 3; female = 62.5–63.1; *n* = 2 [*L. magnus*, in contrast, was reported 90.6–108.5 mm SVL in males and 80.3–93.6 in females]), darker, more uniform overall dorsal and lateral coloration, dark brown throat and sternal region pigmentation (absent in *L. magnus*), its more rugose skin texture, shorter first finger (relative to second), its somewhat more dilated toe discs, and shorter relative tibia length. With the advantage provided by the current-day availability of extensive collections from the Mindanao PAIC (Brown et al. 2013; Sanguila et al. 2016), plus genetic data presented here, it is encouraging that the majority of these qualitative characterizations is generally confirmed (Figs. 2, 4, 7)—albeit possibly nondiagnostic in the sense that they do not represent nonoverlapping ranges of discrete variation. Still, genetic data presented here indicate that all high-elevation Mindanao populations collected on Mt. Hilong-hilong, Mt. Magdiwata, Mt. Balatukan, Mt. Lumot, and Mt. Apo are closely related (Figs. 1, 2) and correspond to the smaller-bodied, range-limited, high-elevation form that exhibits geographically structured genetic variation (mountain-specific haplotype

Table 3.—Four data streams, assessed for the presence/absence of support for each haplotype clade (color-coded to match Fig. 1) summarized among Mindanao Pleistocene aggregate island complex Fanged Frog populations of the *Limnonectes magnus* complex (=*L. magnus*, *L. diuatus*, and *L. ferneri*). "Y" = yes; "N" = no (see Diagnosis sections for character states).

	Clade in mitochondrial tree	Clade in nuclear tree	Supported by morphometrics	Diagnosed with traditional character states
Highland clade: *L. diuatus*				
L. diuatus 1 (orange)	Y	N	N	N
L. diuatus 2 (red)	Y	Y	Y	Y
L. diuatus (green)	Y	Y	Y	Y
L. ferneri (green)	N	N	N	Y
Lowland clade: *L. magnus*				
L. magnus 1 (yellow)	Y	N	N	N
L. magnus 2 (purple)	Y	Y	N	N
L. magnus 3 (blue)	Y	Y	N	N

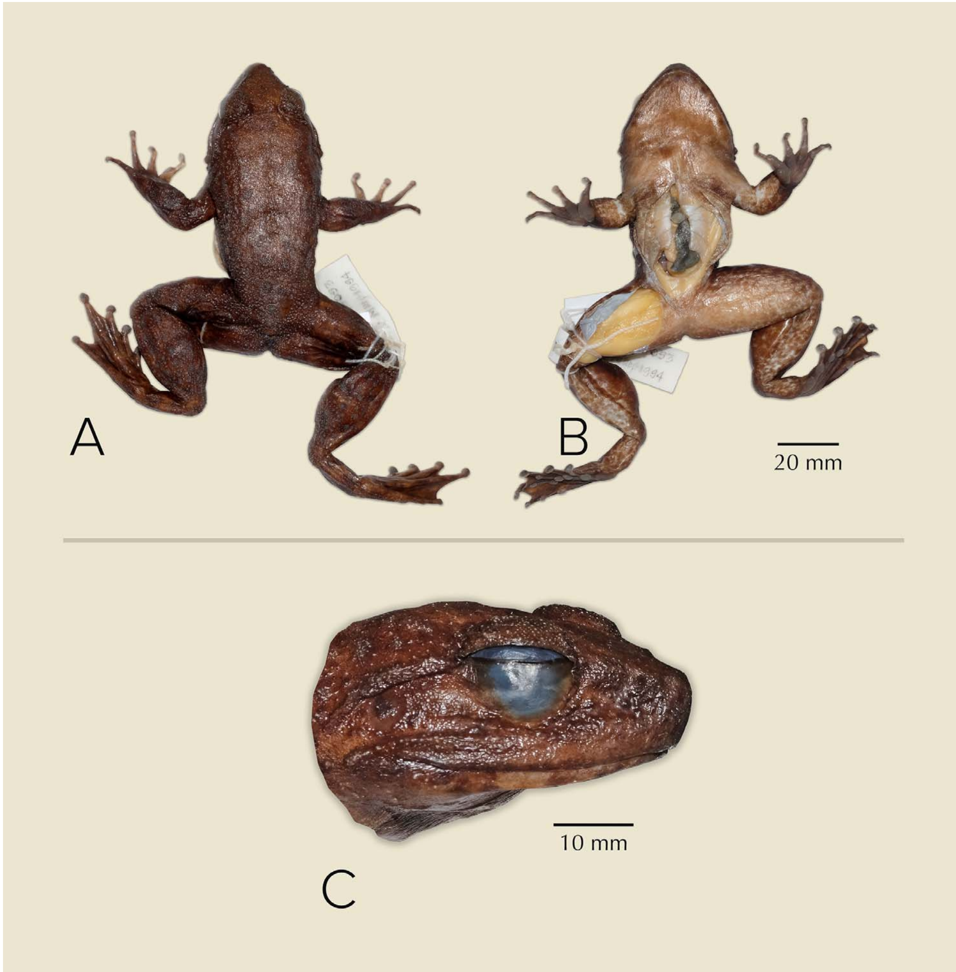

Fig. 7.—Adult male holotype (PNM 9506) of *Limnonectes ferneri* from Mt. Pasian, Municipality of Monkayo, Davao Del Norte Province, Mindanao Island, Philippines (Brown and Alcala 1977). A color version of this figure is available online.

clades) in rapidly coalescing mtDNA (Fig. 1), but shows no such strongly supported geographically based genetic substructure in our multilocus phylogenetic estimate (Fig. 2). Having incorporated examination of the *L. diuatus* type series, and a combined multivariate analysis of the greatly expanded sampling for high-elevation Mindanao Fanged Frogs, we take the absence of group/sample-based structure in our continuous morphometric data (broad overlap in *L. diuatus* and other high-elevation populations in PCA, despite some separation in PC1 of our DAPC analysis, which is somewhat limited by the absence of morphometric data from adults of the Mt. Apo population), shallow genetic divergences in mtDNA (Fig. 1), and the lack of mountain massif-based genetic structure in nuclear DNA (Fig. 2) to conservatively refer all Mindanao Island "sky island" populations to a single species, *L. diuatus* (Brown and Alcala 1977).

Limnonectes ferneri **Siler, McVay, Diesmos and Brown 2009**.—In their description of *L. ferneri,* Siler et al. (2009) described the population of Mindanao Fanged Frogs from the Simulaw River drainage, Mt. Pasian (Municipality of Monkayo, Davao del Norte Province), emphasizing that in contrast to the generally smaller *L. diuatus* with traditional amphibian female-larger sexual size dimorphism, *L. ferneri* possessed reversed sexual size dimorphism, typical of larger-bodied *Limnonectes* (Inger 1954; Brown and Alcala 1977; Setiadi et al. 2011). Characters apparently diagnostic for *L. ferneri* and distinguishing the species from *L. diuatus* included its larger (male SVL 79.6–84.3 mm) versus smaller (male SVL 37.4–58.4) body size, less rugose skin texture, finger I longer than finger II (versus fingers subequal), densely (versus sparsely) distributed dermal asperities, snout round (versus acuminate), and absence of dorsolateral folds/ridges (versus present). With the consideration of larger sample sizes from multiple localities (Fig. 1), and that extend the known range of *L. diuatus* from the original diagnosis of Brown and Alcala (1977), we view most of the character comparisons of Siler et al. (2009) as no longer diagnostic. Aside from the problem of interpreting subjective/categorical characterizations (dense versus sparse; smooth versus rugose), we note—as have many others—that many purportedly diagnostic traditional taxonomic characters in anuran systematics can be demonstrably biased by circumstances of preservation, interpopulational variation, reproductive cycle at time of preservation, and interobserver bias (Hayek et al. 2001). Together with the genetic data presented here, indicating a very close relationship between *L. diuatus* from the species' type locality and the *L. ferneri* type series, we have no hesitation in placing *L. ferneri* Siler, McVay, Diesmos and Brown 2009 in synonymy with *L. diuatus* (Brown and Alcala 1977). It should be noted that although Brown and Alcala (1977) reported *L. diuatus* male body size to vary 37.4–58.4 mm, Siler et al. (2009) were unable to confirm sexual maturity in the type series beyond a single male (SVL 58.4 mm) and a single female (62.3 mm). Excluding immature specimens and combining size variation from both species' type series, we emphasize that *L. diuatus* does in fact exhibit reversed sexual size dimorphism (males on average slightly larger; male SVL 58.4–84.3 mm; females 62.3–69.3).

Taxonomic Summary

Limnonectes magnus (Stejneger) (Figs. 4, 5)

Rana magna: Stejneger 1910:437. Holotype male (USNM 35231) from "Mount Apo, Mindanao, between Todaya and camp, 4000 to 6000 ft altitude" (= Philippines, Mindanao Island, Davao City del Sur Province, Municipality of Bansalan, Barangay Sibulan, Sitio Tudaya) [examined].

Rana (Rana) magna Boulenger 1920:6 (in part, misidentification).

Rana modesta magna Smith 1927:211 (in part, misidentification).

Rana macrodon magna Stejneger: Inger 1954:287 (in part, misidentification).

Rana magna magna Stejneger: Inger 1958:254 (correction, reidentification).

Rana (Euphlyctis) magna Stejneger: Dubois 1981:239 (by implication).

Euphlyctis magna (Stejneger): Poynton and Broadley 1985:124 (transferred to genus *Euphlyctis* Fitzinger by implication).

Limnonectes (Limnonectes) magnus (Stejneger): Dubois 1987:63 "1986" (transferred to genus *Limnonectes* Fitzinger by implication).

Limnonectes cf. *magnus*: Evans, Brown, McGuire, Supriatna, Andayani, Diesmos, Iskandar, Melnick, and Cannatella 2003:794; Setiadi, McGuire, Brown, Zubairi, Iskandar, Andayani, Supriatna, and Evans 2011:221 (misidentification).

Identification.—*Limnonectes magnus* differs from all other Philippine congeners by a combination of the following characters: adult large bodied (males = 59.4–164.4 mm SVL; females = 47.6–130.8); skin on dorsum smooth, slightly rugose laterally with irregular dark markings (Fig. 2); white-tipped asperities limited to sacral region or absent; tympanum not partially concealed by supratympanic fold (Fig. 5C); interdigital webbing of foot complete; subarticular tubercles and ventral surfaces of toe discs pale cream to gray; finger discs nonexpanded; discs of toes slightly expanded (Fig. 5D,E); snout rounded in dorsal and lateral aspect; supralabial region with two or three broad, diffuse, indistinct dark blotches; dorsal coloration variable from light brown or gray to olive brown or dark brown; inguinal region and ventral surfaces of hindlimbs with densely spotted dark pigmentation in ≥88% of specimens; ventral throat, sternal region, and other body surfaces otherwise cream to pale yellow. Male advertisement call amplitude-modulated ("keh-keh-keh-keh…"), with 10–16 rapid, loud, and invariant notes.

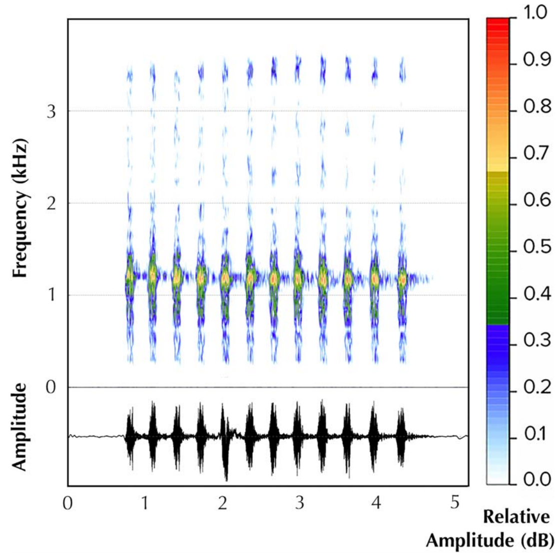

Fig. 8.—Comparative spectrogram (frequency [kHz] versus time [s]) and corresponding oscillogram (relative amplitude [dB] versus time [s]) of the advertisement vocalization of *Limnonectes magnus*. The calls of *L. diuatus* (and its junior synonym, *L. ferneri*) have never been recorded. A color version of this figure is available online.

Distribution and natural history.—*Limnonectes magnus* has been reported from numerous low-elevation habitat types, usually in the vicinity of water (ponds, lakes, seepages, streams, rivers; see also comments by Inger 1954). The species has been recorded most frequently below 1200 m, but a few confirmed *L. magnus* specimens have been collected as high as 1350 m. It exhibits a widespread distribution, and has been documented throughout the Mindanao PAIC, including on the islands of Mindanao, Siargao, Camiguin Sur, Dinagat, Samar, Leyte, Bohol and, Basilan and presumably, Biliran (Taylor 1920; Inger 1954; Diesmos et al. 2015; Sanguila et al. 2016). The tadpole and larval development of this species has not been described.

Advertisement call.—We include the following brief description of the male advertisement call (Fig. 8) of *L. magnus* on the basis of the recordings of two males (specimens not collected) recorded by RMB at Barangay Pasonanca, Municipality of Zamboanga City, western Mindanao Island (1130 m elevation, west side of Pasonanca Natural Park, at an area known locally as "Nancy") in the evening ~1730 to 1900 h (ambient temperature of 21.5°C). To the best of our knowledge this constitutes the first description of vocalizations of the species.

The call of *L. magnus* is a stereotyped, repetitive, rapidly pulsed, amplitude-modulated pulse train, sounding to the human ear like "keh-keh-keh-keh-keh-keh-keh…" and lasting several seconds, followed by several minutes of silence. Call duration 1.64–2.95 s (2.24 ± 0.30, $n = 47$ calls from two specimens; Fig. 8); rise time 80.1–91.4 (86.46 ± 3.1) ms; fall time 1100–1681.9 (1391.79 ± 157.36) ms; notes (pulses) per call 10–16 (13 ± 1.22); note repetition rate 2.7–3.11 (2.8 ± 0.58). Spectral properties of *L. magnus* calls were invariant across recordings available and the majority of call energy was concentrated between 0.6 and 1.5 kHz. Our two recording segments exhibited an invariant dominant frequency of 1.4 kHz for one male and 1.2 kHz in the other; rich harmonic structure was evident up to 3.5 kHz. Over a 4-night survey at this locality, the two focal individuals intermittently called for several hours, starting near sunset (1800 h) and extending for 2–3 h after dark; calling activity was initiated by one male, initially with short calls of two to five notes; then the second male responded, resulting in more intensely alternating call exchanges for 3–8 min, followed by periods of silence of 30–75 min, until another bout of calling began again (RMB, personal observation). During vocalizations, males remained partially concealed beneath boulders (2–4-m diameter) in the immediate vicinity of waterfalls and loudly cascading water.

Limnonectes diuatus (Brown and Alcala)
(Figs. 2, 6, 7)

Rana diuata: Brown and Alcala 1977:669. Holotype male (CAS 133500) from "Taguibo River, south side of Mt. Hilong-hilong, altitude 1000+ m, Diuata Mountains, Cabadbaran Agusan del Norte Province, Mindanao Island, Philippines" [examined].

Limnonectes ferneri Siler, McVay, Diesmos and Brown 2009:106. Holotype male (PNM 9506) from "Simulaw River Drainage, 2.3 km N, 1.0 km E of Peak 1409, Mt. Pasian (7°58′16.26″N, 126°17′50.52″E; datum = WGS-84), Municipality of Monkayo, Davao Del Norte Province, Mindanao Island, Philippines" [examined; **new synonymy**].

Limnonectes (Limnonectes) diuatus (Brown and Alcala), Dubois 1987:63 "1986" (transferred to genus *Limnonectes* Fitzinger by implication).

Limnonectes magnus (Stejneger) Evans, Brown, McGuire, Supriatna, Andayani, Diesmos, Iskandar, Melnick, and Cannatella 2003:794; Setiadi, McGuire, Brown, Zubairi, Iskandar, Andayani, Supriatna, and Evans 2011:221 (misidentifications).

Identification.—*Limnonectes diuatus* differs from all known congeners by a combination of the following characters: medium bodied (SVL males = 58.4–84.3 mm; females = 62.3–69.3); skin of dorsum smooth to shagreened, laterally highly rugose, with two to four longitudinal rows of large dermal tubercles (or tubercular ridges), each associated with a black spot (Fig. 2), with or without spiculate texture from aggregations of white-tipped asperities (Siler et al. 2009:their Fig. 4); tympanum usually fully exposed, or partially concealed along dorsoposterior margin by less-prominent, obtusely angled (posteroventrally) supratympanic fold (Fig. 6C); interdigital webbing of foot complete; subarticular tubercles, toe discs, and ventral surfaces of feet dark gray to black; finger discs slightly expanded; discs of toes moderately expanded (Fig. 8D,E); snout acuminate to round in dorsal view, angled posteroventrally in lateral aspect (Fig. 6C); supralabial region with four to six distinct, round, dark brown spots (Figs. 2, 5, 8); dorsal coloration dark brown to nearly black brown; ventral surfaces of body bright white to pale cream; when present, dark brown ventral pigmentation concentrated on throat, sternal region, and in some specimens, posterior distal surfaces of limbs (Fig. 2); loreal region vertically flat, not concave, pigmented as surrounding lateral head surfaces (medium brown); known from high-elevation riparian habitats (above 900 m, usually above 1200 m) only on Mindanao Island. Male advertisement call unrecorded.

Distribution and natural history.—*Limnonectes diuatus* occurs in high-elevation riparian habitats (montane streams and small, rapidly cascading, high-gradient rivers; Brown and Alcala 1977; Siler et al. 2009; Diesmos et al. 2015; Sanguila et al. 2016) on Mindanao Island, above 900 m (usually ≥1200 m) including Mt. Apo, Mt. Pasian, Mt. Hilong-hilong, Mt. Magdiwata, Mt. Balatucan, Mt. Lumot, and most likely numerous additional montane sites of eastern and possibly central Mindanao. A single unvouchered record for Mt. Kitanglad (Bukidnon, Central Mindanao) exists (Diesmos et al. 2015). The absence of recordings of the vocalizations of this species should be taken as a challenge for future fieldwork—both from sites where it occurs exclusively (high elevations, ≥1400 m) and at lower, mid-elevations (900–1200 m), where it may occur syntopically with *L. magnus*. The tadpole and larval development of this species has not been described.

Discussion

Our re-evaluation of the phylogenetic relationships, clarification of the taxonomy, and consideration of island and elevational distributions of *L. magnus* and allied taxa leads to the conclusion that only two valid giant Fanged Frog species can demonstrably be said to exist on the Mindanao PAIC (Stejneger 1910; Taylor 1920; Inger 1954; Brown and Alcala 1977). Rather than resulting in the previously anticipated increase in species numbers, this exercise argues for the placement of *L. ferneri* (Siler et al. 2009) in synonymy with *R. diuata* Brown and Alcala 1977 (=*Limnonectes diuatus*) and reverses the assignment of Evans et al. (2003) of available names (Brown et al. 2013; Diesmos et al. 2015; Sanguila et al. 2016). Moreover, genetic identification of all insular populations (including name-bearing type specimens and expanded genetic data from relevant type localities) and robust statistical characterizations of phenotypic data failed to identify unambiguous support for additional, unrecognized lineages or putative new species. Our conservative interpretation at this point stems from the lack of agreement among available data streams (e.g., mtDNA phylogeny, multilocus phylogeny, morphometric analyses, traditional characters) and the absence of comparable data from all relevant populations (recordings of advertisement calls are unavailable for *L. diuatus* or from allopatric populations [Bohol vs. Mindanao] of *L. magnus*). Consideration of the Bohol Island population of *L. magnus* illustrates these points. With only a phylogeny estimated from single-locus mitochondrial sequences (Fig. 1) and a morphometric analysis (Fig. 3), one might be tempted to suggest that the allopatric Bohol population could be an example of an unrecognized, morphologically cryptic, new species—embodying a popularly potentially widespread predicted phenomenon in Southeast Asian amphibian systematics and biodiversity science (Bickford et al. 2007; Inger et al. 2009; Matsui et al. 2010)—and which it may very well prove to be. However, analyses from individual and combined nuclear genes (not shown) did not result in strong support for Bohol populations as a distinctive, first-diverging lineage, as observed in the mtDNA gene tree (Fig. 1). Further, our multilocus Bayesian and likelihood estimates differed substantially in support at several nodes relevant to Bohol samples, which were not even inferred to be monophyletic (Fig. 2). Finally, additional lines of evidence germane to the question of the Bohol population, such as ecological information, bioacoustics, or data from larval phenotypes, are unavailable. Although we acknowledge that a markedly divergent or structurally distinctive mate-recognition signal (the male anuran advertisement call; Wells 2007) would cause reconsideration of our interpretation (Herr et al. 2021), at present we hold in abeyance any additional taxonomic changes until a time when changes to synonymy are unavoidable and bolstered with appropriate evidence. Until such gaps in our data and sampling are ameliorated, we would consider it speculative and even irresponsible to assert strong conclusions regarding possible existence of additional species. As such, we refrain from proposing new names or other liberal taxonomic changes, which might cascade into downstream error in synonymy (Frost 2020), create additional misunderstanding for biodiversity information products (AmphibiaWeb 2020) and national Red List summaries (Gonzalez et al. 2018), or result in extraneous, wasteful expenditure of conservation resources (Diesmos and Brown 2011; Leviton et al. 2018). The emergence of conspicuous case studies involving sequential reconsiderations of seemingly straightforward anuran taxonomic revisions, using increasingly sophisticated analytical approaches (e.g., multispecies coalescent-based methods and empirical characterizations of gene flow) and the power of statistical species delimitation procedures coupled with technology allowing locus sampling from across the genome (Hutter et al. 2019) have made clear the weaknesses, pitfalls, and potential for error associated with making strong conclusions on the basis of single-locus studies, and even those on the basis of a handful of loci (Brown and Guttman 2002; Brown and Siler 2014; Chan et al. 2020).

The emergent interpretation of a widespread low-elevation, larger-bodied generalist species (*L. magnus*) distributed on many Mindanao faunal region islands versus a high-elevation montane species (*L. diuatus*) restricted to the higher reaches of isolated "sky island" massifs of Mindanao likely would have become apparent earlier if high-elevation herpetological survey work on Mindanao had not been so infrequent over the last 3 decades (Sanguila et al. 2016). This lack of modern, high-quality biodiversity surveys has resulted in a general lack of genetic material and specimen-associated data (ecology, bioacoustics, larval biology, etc.), all of which have the potential to contribute to the pluralistic, integrative species delimitation standards of today (Fujita et al. 2012; Carstens et al. 2013). Another factor that likely delayed the resolution of Mindanao Fanged Frog taxonomy may have been the small number of sexually mature specimens in the original type series (Stejneger 2010; Brown and Alcala 1977; Siler et al. 2009). In the case of *L. diuatus*, inclusion of immature specimens in the original type series also mistakenly gave the impression of females-larger sexual size dimorphism and small male body size in this species (Brown and Alcala 1977; Siler et al. 2009).

The collection of the original holotype specimen of *L. magnus* at the very upper limit of its elevational distribution (Stejneger 1910) and collection of the type series of *L. diuatus* near the lower extent of its range (Brown and Alcala 1977; precisely at the point where we now conclude they are narrowly sympatric and syntopic) further contributed to biologists' confusion, as did the inadvertent switching of names for "*L. magnus*" and "*L.* cf. *magnus*" on the tips of the first-available phylogenetic estimate (Evans et al. 2003). With our redefinition of each species, clarification of their status with respect to one another via diagnoses presented here, and characterization of their geographic ranges and elevational limits (confirmed with genetic data), we anticipate that field biologists will have the necessary tools to properly identify, further study, and assess the conservation status of these still poorly known taxa.

In addition to full descriptions of the advertisement calls of both species, proper descriptions of tadpoles and larval development of both taxa are long overdue. With careful study of their microhabitats and focus on whether they partition resources in areas of elevational sympatry, it should be possible to characterize their general natural history and true extent of occurrence. It is clear that this study would not have been possible without the existence of (and our access to) the relevant name-bearing type specimens, which provided the crucial clues and other bits of evidence needed to make sense of the historical uncertainty surrounding *L. magnus, L. diuatus, L. ferneri,* and other hypothesized species of Mindanao Fanged Frogs (Brown and Diesmos 2002; Evans et al. 2003), all of which underscores the importance of properly vouchered specimens and specimen-associated data in freely available natural history museums and biodiversity repositories (McLean et al. 2016; Miralles et al. 2020). Given the half-century of confusion that has resulted from indiscriminate acceptance of assumptions from earlier taxonomy and the practice of relying on expert opinions for policy making (IUCN 2020), the case of *L. magnus* provides an important lesson regarding the pitfalls of misinterpretation that may develop when actual biodiversity surveys have not been conducted. In such cases, the data needed to inform conservation status assessments are unavailable (McLean et al. 2016; Miralles et al. 2020), and yet this lack of data is often itself incorrectly interpreted when implementing legal policy (Brown and Diesmos 2002; Hilton-Taylor 2000; Leviton et al. 2018; Gonzalez et al. 2018; Betts et al. 2020; Brown et al. 2020).

The case of Mindanao Fanged Frog classification is compelling for several reasons. *Limnonectes magnus* is one of the most widespread, common, and abundant, supposedly well-studied species in the southern portions of the archipelago (Taylor 1920; Inger 1954; Alcala and Brown 1998; Sanguila et al. 2016). Its distribution is well characterized (Brown and Alcala 1970; Diesmos et al. 2015) and challenges to its conservation have been reasonably well discussed (Diesmos and Brown 2011; Brown et al. 2012; Gonzalez et al. 2018; IUCN 2020). Naturally, we might ask why has it taken so long for biologists to connect the dots from scientific names to name-bearing type specimens (the Linnaen shortfall; Lomolino et al. 2010) and, eventually, to actual biological populations? Our experience suggests that current trends toward increasingly restrictive research permit systems and sociopolitical obstacles to biodiversity research is to blame—and that the latter represents a worrisome trend. Even if recent wholesale reclassification of Philippine amphibians to increasingly higher threatened conservation status categories justifies bureaucratic obstacles to research (Gonzalez et al. 2018), we argue that limiting biologists' access to species occurrence data (the Wallacean shortfall) will always be counterproductive. On the basis of first principles of biodiversity science (taxonomy, species occurrence data), an understanding of species boundaries and their real-world geographic distributions are destined to remain the crucial gold standard for formulation and implementation of effective conservation efforts (Diesmos and Brown 2011; Brown et al. 2014; Diesmos et al. 2015; Leviton et al. 2018).

Acknowledgments.—Support for our work in the Philippines has been generously provided by the US National Science Foundation (NSF EF 0334928, Division of Environmental Biology [DEB] 0073199, 0344430, 0743491, and 0804115); most recent studies focusing on Philippine *Limnonectes* were funded by DEB 1654388 to RMB. We thank J. Vindum, A. Leviton, R. Drewes, D. Blackburn, R. Sison, and A.C. Diesmos (PNM); R. Inger, A. Resetar, and H. Voris (FMNH); K. de Queiroz and R. Crombie (USNM); T. LaDuc and D. Cannatella (TNHC); and J. Hanken, J. Losos, and J. Rosado (MCZ) for access to specimens and provision of workspace during visits to collections where Philippine *Limnonectes* specimens are housed. Special thanks to J.L. Welch (USNM), who photographed and provided digital images of the holotype of *L. magnus*. Phylogenetic analyses were conducted in part on Cornell's Computational Biology Services Unit BioHPC cluster and University of Kansas (KU)'s Center for Research Computing. We especially appreciate the logistical support of the Philippine Biodiversity Monitoring Bureau (BMB; formerly Parks and Wildlife Bureau, PAWB) of the Department of Environment and Natural Resources (DENR) and we thank authorities at DENR for their facilitation of research agreements, collecting permits, and export permits necessary for this and related studies. Specimens were collected by RMB, KU students, and colleagues under the aegis of three formal Memoranda of Agreement (MOA) between KU and the BMB (formerly PAWB) of the Philippine central government (MOAs, 2004, 2009, 2015, endorsed by Chancellor of KU and the Secretary of the DENR, Quezon City, Manila) and a formal Specimen Repository Agreement at the KU Biodiversity Institute (KU-BI) stipulating ownership by the National Museum of the Philippines. With local municipal permissions obtained in the form of Prior Informed Consent certificates (obtained from all collection sites), specimens were subsequently collected under BMB Gratuitous Permits to Collect Biological Specimens (185, 185-renewal, 201, 201-renewal, 212, 212-renewal, 221, 221-renewal, 228, 228-renewal, 228-Amendment, 228-3rd renewal, 228-4th renewal, 246, 246-renewal, 258, 258-renewal, 258-Amendment, 292, 292-renewal and exported under the auspices of DENR Regional Office(s) Wildlife Certification Export permit(s), with coordinated institutional permits (APHIS, CITES, COSE F&W 3-177s) and Designated Port Exemptions archived by the KU-BI's administrative Office of the Director. Authorizations for the handling of live animals were provided to RMB by KU's Institutional Animal Care and Use Committee (IACUC AUS no. 185-05, 2004–2019).

We reserve special thanks for our collaborators in fieldwork: J. and B. Fernandez, A.C. Diesmos, N. Antoque, J. Cantil, and V. Yngente; and we thank the Zamboanga City Water District and provincial, municipal, and local Pasonanca protected area officials who graciously provided access to Pasonanca Natural Park for this and related studies. Finally, thanks are due to P. De Mello for helping with formatting the base map used in Fig. 1 and we thank Chan Kin Onn for constructive critique of an earlier draft of the manuscript.

Supplemental Material

Supplemental material associated with this article can be found online at https://doi.org/10.1655/HERPMONOGRAPHS-D-20-00010.F1.

Literature Cited

Alcala, A.C., and W.C. Brown. 1998. Philippine Amphibians: An Illustrated Field Guide. Bookmark Press, Philippines.

AmphibiaWeb. 2020. AmphibiaWeb Electronic Database. Available at https://amphibiaweb.org. Accessed on 20 October 2020. University of California, USA.

Betts, J., R.P. Young, C. Hilton-Taylor, M. Hoffmann, J.P. Rodríguez, S.N. Stuart, and E.J. Milner-Gulland. 2020. A framework for evaluating the impact of the IUCN Red List of threatened species. Conservation Biology 34:632–643.

Bickford, D., D.J. Lohman, N.S. Sodhi, . . . I. Das. 2007. Cryptic species as a window on diversity and conservation. Trends in Ecology and Evolution 22:148–155. DOI: http://dx.doi.org/10.1016/j.tree.2006.11.004.

Blackburn, D.C., C.D. Siler, A.C. Diesmos, J.A. McGuire, D.C. Cannatella, and R.M. Brown. 2013. An adaptive radiation of frogs in a Southeast Asian island archipelago. Evolution 67:2631–2646.

Blonder, B., C. Lamanna, C. Violle, and B.J. Enquist. 2014. The n-dimensional hypervolume. Global Ecology and Biogeography 23:595–609.

Bouckaert, R., J. Heled, D. Kühnert, T. Vaughan, C.-H. Wu, D. Xie, M.A. Suchard, A. Rambaut, and A.J. Drummond. 2014. BEAST 2: A software platform for Bayesian evolutionary analysis. PLOS Computational Biology 10:e1003537. DOI: http://dx.doi.org/10.1371/journal.pcbi.1003537.

Boulenger, G.A. 1920. A monograph of the South Asian, Papuan, Melanesian and Australian frogs of the genus *Rana*. Records of the Indian Museum 20:1–226.

Brown, R.M. 2016. Biogeography of vertebrates. Pp. 211–220 in The Encyclopedia of Evolutionary Biology, vol. 1 (R.M. Kliman, ed.). Academic Press/Elsevier Incorporated, UK.

Brown, R.M., and A.C. Diesmos. 2002. Application of lineage-based species concept to oceanic island frog populations: The effects of differing taxonomic philosophies on the estimation of Philippine biodiversity. Silliman Journal 42:133–162.

Brown, R.M., and A.C. Diesmos 2009. Philippines, Biology. Encyclopedia of Islands. University of California Press, USA.

Brown, R.M., and S.I. Guttman. 2002. Phylogenetic systematics of the *Rana signata* complex of Philippine and Bornean stream frogs: Reconsideration of Huxley's modification of Wallace's Line at the Oriental–Australian faunal zone interface. Biological Journal of the Linnean Society 76:393–461.

Brown, R.M., and D.T. Iskandar. 2000. Nest site selection, larval hatching, and advertisement calls of *Rana arathooni* from southwestern Sulawesi (Celebes) Island, Indonesia. Journal of Herpetology 34:404–413.

Brown, R.M., and C.D. Siler. 2014. Spotted stream frog diversification at the Australasian faunal zone interface, mainland versus island comparisons, and a test of the Philippine 'dual-umbilicus' hypothesis. Journal of Biogeography 41:182–195.

Brown, R.M., J.A. McGuire, and A.C. Diesmos. 2000. Status of some Philippine frogs referred to *Rana everetti* (Anura: Ranidae), description of a new species, and resurrection of *Rana igorota* Taylor 1922. Herpetologica 56:81–104.

Brown, R.M., A.C. Diesmos, M.B. Sanguila, C.D. Siler, M.L.D. Diesmos, and A.C. Alcala. 2012. Amphibian conservation in the Philippines. FrogLog 104:40–43.

Brown, R.M., C.D. Siler, C.H. Oliveros, . . . A.C. Alcala. 2013. Evolutionary processes of diversification in a model island archipelago. Annual Review of Ecology, Evolution, and Systematics 44:411–435.

Brown, R.M., J.A. Weghorst, K.V. Olson, . . .C.D. Siler. 2014. Conservation genetics of the Philippine tarsier: Cryptic genetic variation restructures conservation priorities for an island archipelago primate. PLOS ONE 9:e104340. DOI: http://dx.doi.org/10.1371/journal.pone.0104340.

Brown, R.M., C.D. Siler, S.J. Richards, A.C. Diesmos, and D.C. Cannatella. 2015. Multilocus phylogeny and a new classification for Southeast Asian and Melanesian forest frogs (family Ceratobatrachidae). Zoological Journal of the Linnean Society 174:130–168.

Brown, R.M., Y.-C. Su, B. Barger, C.D. Siler, M.B. Sanguila, A.C. Diesmos, and D.C. Blackburn. 2016. Phylogeny of the island archipelago frog genus *Sanguirana*: Another endemic Philippine radiation that diversified 'Out-of-Palawan'. Molecular Phylogenetics and Evolution 94:531–536.

Brown, R.M., C.G. Meneses, P.S. Wood, Jr., J.B. Fernandez, M.A. Cuesta, M.A. Clores, C. Tracy, M. Buehler, and C.D. Siler. 2020. Unexpected discovery of another new species of Philippine False Gecko (Gekkonidae; *Pseudogekko*) from the Bicol Peninsula of Luzon Island. Herpetologica 76:315–329.

Brown, W.C., and A.C. Alcala. 1970. The zoogeography of the herpetofauna of the Philippine Islands, a fringing archipelago. Proceedings of the California Academy of Sciences 38:105–130.

Brown, W.C., and A.C. Alcala. 1977. A new frog of the genus *Rana* from the Philippines. Proceedings of the Biological Society of Washington 90:669–675.

Carstens, B.C., T.A. Pelletier, N.M. Reid, and J.D. Saltler. 2013. How to fail at species delimitation. Molecular Ecology 22:4369–4383.

Center for Conservation Bioacoustics. 2014. Raven Pro: Interactive Sound Analysis Software, Version 1.5. Available at http://ravensoundsoftware.com/. The Cornell Lab of Ornithology, USA.

Chan, K.O., C.R. Hutter, P.L. Wood, Jr., L.L. Grismer, I. Das, and R.M. Brown. 2020. Gene flow creates a mirage of cryptic species in a Southeast Asian spotted stream frog complex. Molecular Ecology 29:3970–3987. DOI: https://dx.doi.org/10.1111/mec.15603.

Darriba, D., G.L. Taboada, R. Doallo, and D. Posada. 2012. jModelTest 2: More models, new heuristics and parallel computing. Nature Methods 9:772.

Diesmos, A.C., and R.M. Brown. 2011. Diversity, Biogeography, and Conservation of Philippine Amphibians. Pp. 26–49 in Biology and Conservation of Tropical Asian Amphibians. Biology of the Amphibians in the Sunda Region, South-east Asia (I. Das, A. Haas, and A.A. Tuen, eds.). Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak, Kota Samarahan, Malaysia.

Diesmos, A.C., J.L. Watters, N.A. Huron, … C.D. Siler. 2015. Amphibians of the Philippines, part I: Checklist of the species. Proceedings of the California Academy of Sciences 62:457–539.

Dubois, A. 1981. Liste des genres et sous-genres nominaux de Ranoidea (Amphibiens Anoures) du monde, avec identification de leurs espèces types; consequences nomenclaturales. Monitore Zoologico Italiano. Nuova Serie, Supplemento. Firenze 15:225–284.

Dubois, A. 1987 (1986). Miscellanea taxinomica batrachologica (I). Alytes. Paris 5:7–95.

Emerson, S.B. 1994. Testing patter predictions of sexual selection: A frog example. American Naturalist 143:848–869.

Evans, B.J., R.M. Brown, J.A. McGuire, J. Supriatna, N. Andayani, A.C. Diesmos, D. Iskandar, D.J. Melnick, and D.C. Cannatella. 2003. Phylogenetics of fanged frogs: Testing biogeographic hypotheses at the interface of the Asian and Australian faunal zones. Systematic Biology 52:794–819.

Feng, Y.-J., D.C. Blackburn, D. Liang, D.M. Hillis, D.B. Wake, D.C. Cannatella, and P. Zhang. 2017. Phylogenomics reveals rapid, simultaneous diversification of three major clades of Gondwanan frogs at the Cretaceous–Paleogene boundary. Proceedings of the National Academy of Sciences of the United States of America 114:E5864–E5870. DOI: https://dx.doi.org/10/1073/pnas.1704632114.

Frost, D.R. 2020. Amphibian Species of the World 6.0: An Online Reference. Available at https://amphibiansoftheworld.amnh.org/. Accessed 20 October 2020. American Museum of Natural History, USA.

Fujita, M.K., A.D. Leaché, F.T. Burbrink, J.A. McGuire, and C. Moritz. 2012. Coalescent-based species delimitation in an integrative taxonomy. Trends in Ecology and Evolution 27:480–488.

Gonzalez, J.C.T., C.A.A. Layusa, L.E. Afuang, … P.S. Ong. 2018. Review and update of the 2004 National List of Threatened Terrestrial Fauna of the Philippines. Sylvatrop. Technical Journal of Philippine Ecosystems and Natural Resources 28:73–144.

Hayek, L.-A.C., W.R. Heyer, and C. Gascon. 2001. Frog morphometrics: A cautionary tale. Alytes 18:153–177.

Herr, M.W., J. Goyes Vallejos, C.G. Meneses, R.K. Abraham, R. Otterholt, C.D. Siler, E.L.B. Rico, and R.M. Brown. 2021. A new, morphologically cryptic species of fanged frog, genus *Limnonectes* (Amphibia: Anura: Dicroglossidae), from Mindoro Island, central Philippines. Ichthyology & Herpetology 109:188–210.

Hillis, D.M., and J.J. Bull. 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. Systematic Biology 42:182–192.

Hilton-Taylor, C. 2000. IUCN Red List of Threatened Species. The IUCN Species Survival Commission. Available at https://www.iucnredlist.org/. IUCN, Switzerland.

Hoogstral, H. 1951. Philippine Zoological Expedition 1946–1947: Narrative and itinerary. Fieldiana Zoology 33:1–86.

Huelsenbeck, J.P., and B. Rannala. 2004. Frequentist properties of Bayesian posterior probabilities of phylogenetic trees under simple and complex substitution models. Systematic Biology 53:904–913.

Hutter, C.R., K.A. Cobb, D.M. Portik, S.L. Travers, P.L. Wood, Jr., and R.M. Brown. 2019. FrogCap: A modular sequence capture probe set for phylogenomics and population genetics for all frogs, assessed across multiple phylogenetic scales. bioRxiv. DOI: https://dx.doi.org/10.1101/825307.

Inger, R.F. 1954. Systematics and zoogeography of Philippine Amphibia. Fieldiana Zoology 33:181–531.

Inger, R.F. 1958. A note on the Philippine frogs related to *Rana macrodon*. Fieldiana Zoology 39:253–255.

Inger, R.F., H.K. Voris, and P. Walker. 1986. Larval transport in a Bornean ranid frog. Copeia 1986:523–525.

Inger, R.F., B.L. Stuart, and D.T. Iskandar. 2009. Systematics of a widespread Southeast Asian frog, *Rana chalconota* (Amphibia: Anura: Ranidae). Zoological Journal of the Linnean Society 155:123–147.

IUCN (International Union for the Conservation of Nature). 2020. The IUCN Red List of Threatened Species, Version 2020-1. Available at https://www.iucnredlist.org. Accessed on 19 March 2020. IUCN, Switzerland.

Jombart, T., S. Devillard, and F. Balloux. 2010. Discriminant analysis of principal components: A new method for the analysis of genetically structured populations. BMC Genetics 11:94.

Kaiser, H.F. 1960. The application of electronic computers to factor analysis. Educational and Psychological Measurement 20:141–151.

Katoh, K., and D.M. Standley. 2013. MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. Molecular Biology and Evolution 30:772–780.

Leviton, A.E, C.D. Siler, J.L. Weinell, and R.M. Brown. 2018. A synopsis of the snakes of the Philippines: A synthesis of data from biodiversity repositories, field studies, and the literature. Proceedings of the California Academy of Sciences 64:399–568.

Lleonart, J., J. Salat, and G.J. Torres. 2000. Removing allometric effects of body size in morphological analysis. Journal of Theoretical Biology 205:85–93.

Lomolino, M.V., B.R. Riddle, R.J. Whittaker, and J.H. Brown. 2010. Biogeography. Sinauer Associates, USA.

Matsui, M., N. Kuraishi, J.-P. Jiang, H. Ota, A. Hamidy, N.L. Orlov, and K. Nishikawa. 2010. Systematic reassessments of fanged frogs from China and adjacent regions (Anura: Dicroglossidae). Zootaxa 2345:33–42.

McLean, B.S., K.C. Bell, J.L. Dunnum, B. Abrahamson, J.P. Colella, E.R. Deardorff, J.A. Weber, A.K. Jones, F. Salazar-Miralles, and J.A. Cook. 2016. Natural history collections-based research: Progress, promise, and best practices. Journal of Mammalogy 97:287–297.

Miller, M.A., W. Pfeiffer, and T. Schwartz. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Pp. 1–8 in 2010 Gateway Computing Environments Workshop (GCE). Institute of Electrical and Electronics Engineers, USA. DOI: http://dx.doi.org/10.1109/GCE.2010.5676129.

Minh, B.Q., M.A.T. Nguyen, and A. von Haeseler. 2013. Ultrafast approximation for phylogenetic bootstrap. Molecular Biology and Evolution 30:1188–1195.

Miralles, A., T. Bruy, K. Wolcott, … F.O. Glöckner. 2020. Repositories for taxonomic data: Where we are and what is missing. Systematic Biology 53:1–23.

Paulay, G. 1994. Biodiversity on oceanic islands: Its origin and extinction. American Zoologist 34:134–144.

Plaza, J.L., and M.B. Sanguila. 2015. Preliminary report of anurans of Mount Hilong-hilong, Agusan Del Norte, eastern Mindanao, Philippines. Asian Herpetological Research 6:18–33.

Poynton, J.C., and D.G. Broadley. 1985. Amphibia Zambesiaca 2. Ranidae. Annals of the Natal Museum 27:115–181.

R Core Team. 2019. R: A Language and Environment for Statistical Computing, Version 3.6.1. Available at http://www.r-project.org/. R Foundation for Statistical Computing, Austria.

Rambaut, A., A.J. Drummond, D. Xie, G. Baele, and M.A. Suchard. 2018. Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. Systematic Biology 67:901–904.

Raven, P.H., and E.O. Wilson. 1992. A fifty-year plan for biodiversity surveys. Science 258:1099–1100.

Sabaj, M.H. 2019. Standard Symbolic Codes for Institutional Resource Collections in Herpetology and Ichthyology: An Online Reference. Available at http://www.asih.org. Accessed on 1 June 2020. American Society of Ichthyologists and Herpetologists, USA.

Sanguila, M.B., K.A. Cobb, C.D. Siler, A.C. Diesmos, A.C. Alcala, and R.M. Brown. 2016. The amphibians and reptiles of Mindanao Island, southern Philippines, II: The herpetofauna of northeast Mindanao and adjacent islands. ZooKeys 624:1–132. DOI: https://dx.doi.org/10.3897/zookeys.624.9814.

Setiadi, M.I., J.A. McGuire, R.M. Brown, M. Zubairi, D.T. Iskandar, N. Andayani, J. Supriatna, and B.J. Evans. 2011. Adaptive radiation and ecological opportunity in Sulawesi and Philippine fanged frog (*Limnonectes*) communities. American Naturalist 178:221–240.

Siler, C.D., J.D. McVay, A.C. Diesmos, and R.M. Brown. 2009. A new species of fanged frog, genus *Limnonectes* (Amphibia: Anura: Dicroglos-

sidae) from southeast Mindanao Island, Philippines. Herpetologica 65:105–114.
Smith, M.A. 1927. Contributions to the herpetology of the Indo Australian region. Proceedings of the Zoological Society of London 1927:199–225.
Stamatakis, A. 2014. RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30:1312–1313.
Stejneger, L. 1910. Description of a new frog from the Philippine Islands. Smithsonian Miscellaneous Collections 52:437–439.
Sueur, J., T. Aubin, and C. Simonis. 2008. Seewave, a free modular tool for sound analysis and synthesis. Bioacoustics 18:213–226.
Taylor, E.H. 1920. Philippine Amphibia. Philippine Journal of Science 16:213–359.
Thorpe, R.S. 1983. A review of the numerical methods for recognising and analysing racial differentiation. Pp. 404–423 in Numerical Taxonomy: Proceedings of a NATO Advanced Studies Institute NATO ASI series (J. Felsenstein, ed.). Springer Verlag, Germany.
Trifinopoulos, J., L.-T. Nguyen, A. von Haeseler, and B.Q. Minh. 2016. W-IQ-TREE: A fast online phylogenetic tool for maximum likelihood analysis. Nucleic Acids Research 44:W232–W235. DOI: http://dx.doi.org/10.1093/nar/gkw256.
Wells, K.D. 2007. The Ecology and Behavior of Amphibians. University of Chicago Press, USA.

Accepted on 4 March 2021
Published on 9 September 2021

Appendix I Taxa, Museum Repository Catalog Numbers, Localities, and GenBank Numbers for All Samples Included in this Study

						GenBank accession numbers			
Species	Field no.	Catalog no.	Island	Locality	Elevation (m)	16S	LCT[a]	CPT2	POMC
Limnonectes diautus (*L. ferneri* type)	JWF 94091	CMNH 5572	Mindanao	Mt. Pasian, Simulaw River drainage, Municipality of Monkayo, Davao del Norte Province		MN759154			
Limnonectes diautus (*L. ferneri* type)	JWF 94093	PNM 9506 (Holotype)	Mindanao	Mt. Pasian, Simulaw River drainage, Municipality of Monkayo, Davao del Norte Province		MN759153			MT631750
Limnonectes diautus (*L. ferneri* type)	JWF 94094	CMNH 5573	Mindanao	Mt. Pasian, Simulaw River drainage, Municipality of Monkayo, Davao del Norte Province		MN759155			
Limnonectes diautus	RMB 16161	KU 333370	Mindanao	Mt. Hilong-hilong, May-Impit, Municipality of Remedios T. Romualdez, Agusan del Norte Province	1150	MN759175	MZ577259	MT631729	MT631754
Limnonectes diautus	RMB 16164	KU 333373	Mindanao	Mt. Hilong-hilong, May-Impit, Municipality of Remedios T. Romualdez, Agusan del Norte Province	1150	MN759145			
Limnonectes diautus	RMB 16224	KU 333374	Mindanao	Mt. Hilong-hilong, May-Impit, Municipality of Remedios T. Romualdez, Agusan del Norte Province	1150	MN759176			
Limnonectes diautus	RMB 16225	KU 333375	Mindanao	Mt. Hilong-hilong, May-Impit, Municipality of Remedios T. Romualdez, Agusan del Norte Province	1150	MN759144			
Limnonectes diautus	RMB 16232	KU 333381	Mindanao	Mt. Hilong-hilong, May-Impit, Municipality of Remedios T. Romualdez, Agusan del Norte Province	1150	MN759178	MZ577257	MT631728	
Limnonectes diautus	RMB 16235	KU 333384	Mindanao	Mt. Hilong-hilong, May-Impit, Municipality of Remedios T. Romualdez, Agusan del Norte Province	1150	MN759179	MZ577263	MT631725	MT631752
Limnonectes diautus	RMB 16236	KU 333385	Mindanao	Mt. Hilong-hilong, May-Impit, Municipality of Remedios T. Romualdez, Agusan del Norte Province, Mindanao Island.	1150	MN759180			
Limnonectes diautus	RMB 16237	KU 333386	Mindanao	Mt. Hilong-hilong, May-Impit, Municipality of Remedios T. Romualdez, Agusan del Norte Province	1150	MN759181			
Limnonectes diautus	RMB 16238	KU 333387	Mindanao	Mt. Hilong-hilong, May-Impit, Municipality of Remedios T. Romualdez, Agusan del Norte Province	1150	MN759182			
Limnonectes diautus	RMB 16239	KU 333388	Mindanao	Mt. Hilong-hilong, May-Impit, Municipality of Remedios T. Romualdez, Agusan del Norte Province	1150	MN759183			
Limnonectes diautus	RMB 16250	KU 333389	Mindanao	Mt. Hilong-hilong, May-Impit, Municipality of Remedios T. Romualdez, Agusan del Norte Province	1150	MN759184			
Limnonectes diautus	RMB 16278	KU 333393	Mindanao	Mt. Hilong-hilong, May-Impit, Municipality of Remedios T. Romualdez, Agusan del Norte Province	990	MN759186			
Limnonectes diautus	ACD 4274	KU 320079	Mindanao	Mt. Balatukan Natural Park, Sitio San Isidro, Boy Scout Camp, Barangay Lumotan, Municipality of Gingoog, Misamis Oriental Province	1450	MN759095	MZ577264	MT631732	MT631751

Appendix I Continued.

Species	Field no.	Catalog no.	Island	Locality	Elevation (m)	GenBank accession numbers			
						16S	LCT[a]	CPT2	POMC
Limnonectes diautus 1	ACD 4276	KU 320081	Mindanao	Mt. Balatukan Natural Park, Sitio San Isidro, Boy Scout Camp, Barangay Lumotan, Municipality of Gingoog, Misamis Oriental Province	1450	MN759096			MT631753
Limnonectes diautus 1	ACD 4316	KU 320085	Mindanao	Mt. Balatukan Natural Park, Sitio San Isidro, Boy Scout Camp, Barangay Lumotan, Municipality of Gingoog, Misamis Oriental Province	1450	MN759097	MZ577253	MT631739	MT631755
Limnonectes diautus 1	ACD 4324	KU 320090	Mindanao	Mt. Balatukan Natural Park, Sitio San Isidro, Boy Scout Camp, Municipality of Gingoog, Misamis Oriental Province	1450	MN759098			
Limnonectes diautus 1	RMB 16582	KU 333428	Mindanao	Mt. Lumot, Barangay Civoleg, Municipality of Gingoog, Misamis Oriental Province	1236	MN759192	MZ577261	MT631733	MT631749
Limnonectes diautus 1	RMB 16627	KU 333438	Mindanao	Mt. Lumot, Barangay Civoleg, Municipality of Gingoog, Misamis Oriental Province	1236	MN759194			
Limnonectes diautus 2	PNM-CMNH H1197	NA	Mindanao	Mt. Talomo; Mt. Apo Natural Park, Sitio San Roque, Barangay Baracatan, Municipality of Toril, Davao Province	1530–1776	MN759156	MZ577251	MT631727	MT631757
Limnonectes diautus 2	PNM-CMNH H1198	NA	Mindanao	Mt. Talomo; Mt. Apo Natural Park, Sitio San Roque, Barangay Baracatan, Municipality of Toril, Davao Province	1530–1775	MN759157			
Limnonectes diautus 2	PNM-CMNH H1199	NA	Mindanao	Mt. Talomo; Mt. Apo Natural Park, Sitio San Roque, Barangay Baracatan, Municipality of Toril, Davao Province	1530–1770	MN759158			
Limnonectes diautus 2	PNM-CMNH H1200	NA	Mindanao	Mt. Talomo; Mt. Apo Natural Park, Sitio San Roque, Barangay Baracatan, Municipality of Toril, Davao Province	1530–1774	MN759159			
Limnonectes diautus 2	PNM-CMNH H1205	NA	Mindanao	Mt. Talomo; Mt. Apo Natural Park, Sitio San Roque, Barangay Baracatan, Municipality of Toril, Davao Province	1530–1771	MN759160			
Limnonectes diautus 2	PNM-CMNH H1206	NA	Mindanao	Mt. Talomo; Mt. Apo Natural Park, Sitio San Roque, Barangay Baracatan, Municipality of Toril, Davao Province	1530–1778	MN759164	MZ577258	MT631737	MT631758
Limnonectes diautus 2	PNM-CMNH H1244	NA	Mindanao	Mt. Talomo; Mt. Apo Natural Park, Sitio San Roque, Barangay Baracatan, Municipality of Toril, Davao Province	1530–1772	MN759161	MZ577248	MT631741	MT631756
Limnonectes diautus 2	PNM-CMNH H1246	NA	Mindanao	Mt. Talomo; Mt. Apo Natural Park, Sitio San Roque, Barangay Baracatan, Municipality of Toril, Davao Province	1530–1773	MN759162			
Limnonectes diautus 2	PNM-CMNH H1247	NA	Mindanao	Mt. Talomo; Mt. Apo Natural Park, Sitio San Roque, Barangay Baracatan, Municipality of Toril, Davao Province	1530–1777	MN759163			
Limnonectes magnus 1	CDS 4668	KU 323586	Bohol	Raja Sikatuna Natural Park, Magsaysay Park, Barangay Riverside, Municipality of Bilar, Bohol Province	250	MN759130			
Limnonectes magnus 1	CDS 4675	KU 323589	Bohol	Raja Sikatuna Natural Park, Magsaysay Park, Barangay Riverside, Municipality of Bilar, Bohol Province	250	MN759131			

Appendix I Continued.

Species	Field no.	Catalog no.	Island	Locality	Elevation (m)	GenBank accession numbers			
						16S	LCT[a]	CPT2	POMC
Limnonectes magnus 1	CDS 4678	KU 323591	Bohol	Raja Sikatuna Natural Park, Magsaysay Park, Barangay Riverside, Municipality of Bilar, Bohol Province	250	MN759132			
Limnonectes magnus 1	CDS 4468	KU 323612	Bohol	Raja Sikatuna Natural Park, Magsaysay Park, Barangay Riverside, Municipality of Bilar, Bohol Province	250	MN759129	MZ577255	MT631740	MT631745
Limnonectes magnus 1	CDS 4778	KU 323615	Bohol	Raja Sikatuna Natural Park, Barangay Danicop, Municipality of Sierra Bullones, Bohol Province	250	MN759133			
Limnonectes magnus 1	CDS 4821	KU 323619	Bohol	Raja Sikatuna Natural Park, Barangay Danicop, Municipality of Sierra Bullones, Bohol Province	250	MN759134	MZ577252	MT631734	MT631760
Limnonectes magnus 1	CDS 4856	KU 323622	Bohol	Raja Sikatuna Natural Park, Barangay Danicop, Municipality of Sierra Bullones, Bohol Province	250	MN759135			
Limnonectes magnus 1	CDS 4867	KU 323627	Bohol	Raja Sikatuna Natural Park, Barangay Danicop, Municipality of Sierra Bullones, Bohol Province	250	MN759136			
Limnonectes magnus 1	CDS 4989	KU 323634	Bohol	Raja Sikatuna Natural Park, Barangay Danicop, Municipality of Sierra Bullones, Bohol Province	250	MN759137	MZ577262	MT631726	MT631744
Limnonectes magnus 1	RMB 2887	KU 327507	Bohol	Raja Sikatuna Natural Park, Barangay Danicop, Bohol Province	390	MN759219			
Limnonectes magnus 2	CDS 1804	KU 306022	Samar	Barangay Poblacion, Municipality of San Jose de Buan, Northern Samar Province		MN759107			
Limnonectes magnus 2	CDS 1826	KU 306024	Samar	Taft Forest, Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759108			
Limnonectes magnus 2	CDS 1827	KU 306025	Samar	Taft Forest, Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759109			
Limnonectes magnus 2	CDS 1828	KU 306026	Samar	Taft Forest, Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759110			
Limnonectes magnus 2	CDS 1839	KU 306028	Samar	Taft Forest, Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759111			
Limnonectes magnus 2	CDS 1840	KU 306029	Samar	Taft Forest, Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759112			
Limnonectes magnus 2	CWL 149	KU 306039	Samar	Taft Forest, Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759143			
Limnonectes magnus 2	CWL 161	KU 306041	Samar	Catbalogan City, Samar Province		MN759246			
Limnonectes magnus 2	CWL 162	KU 306042	Samar	Catbalogan City, Samar Province		MN759247			
Limnonectes magnus 2	CWL 163	KU 306043	Samar	Catbalogan City, Samar Province		MN759248			
Limnonectes magnus 2	CWL 164	KU 306044	Samar	Catbalogan City, Samar Province		MN759249			
Limnonectes magnus 2	CWL 165	KU 306045	Samar	Catbalogan City, Samar Province		MN759146			
Limnonectes magnus 2	CDS 1929	KU 306063	Dinagat	Barangay San Juan, Municipality of Loreto, Dinagat Province		MN759116			
Limnonectes magnus 2	CDS 1934	KU 306068	Dinagat	Barangay San Juan, Municipality of Loreto, Dinagat Province		MN759118			

Appendix I Continued.

Species	Field no.	Catalog no.	Island	Locality	Elevation (m)	GenBank accession numbers			
						16S	LCT[a]	CPT2	POMC
Limnonectes magnus 2	RMB 8548	KU 310190	Samar	Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759233			
Limnonectes magnus 2	RMB 8640	KU 310212	Samar	Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759234			
Limnonectes magnus 2	CDS 2805	KU 310587	Samar	Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759121			
Limnonectes magnus 2	CDS 2833	KU 310591	Samar	Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759122			
Limnonectes magnus 2	CDS 3078	KU 310604	Samar	Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759123			
Limnonectes magnus 2	CDS 3106	KU 310615	Samar	Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759124			
Limnonectes magnus 2	CDS 3216	KU 310969	Leyte	Pilim, San Vicente, Municipality of Baybay, Leyte Province		MN759125			
Limnonectes magnus 2	CDS 3301	KU 310972	Leyte	Pilim, San Vicente, Municipality of Baybay, Leyte Province		MN759126			
Limnonectes magnus 2	CDS 3304	KU 310975	Leyte	Pilim, San Vicente, Municipality of Baybay, Leyte Province		MN759127			
Limnonectes magnus 2	CDS 3395	KU 310979	Leyte	Pilim, San Vicente, Municipality of Baybay, Leyte Province		MN759128			
Limnonectes magnus 2	RMB 8947	KU 326360	Leyte	Visayas State University Campus, Municipality of Baybay, Leyte Province		MN759236			
Limnonectes magnus 2	RMB 8953	KU 326361	Leyte	Visayas State University Campus, Municipality of Baybay, Leyte Province		MN759237			
Limnonectes magnus 2	CDS 6992	KU 337806	Samar	Mt. Huraw, Barangay Uno, Municipality of San Jose de Buan, Northern Samar Province		MN759139	MZ577260	MT631738	MT631743
Limnonectes magnus 2	CDS 7071	KU 337809	Samar	Mt. Huraw, Barangay Uno, Municipality of San Jose de Buan, Northern Samar Province		MN759140			
Limnonectes magnus 2	CDS 7072	KU 337810	Samar	Mt. Huraw, Barangay Uno, Municipality of San Jose de Buan, Northern Samar Province		MN759141			
Limnonectes magnus 2	CDS 7174	KU 337811	Samar	Mt. Huraw, Barangay Uno, Municipality of San Jose de Buan, Northern Samar Province		MN759142			
Limnonectes magnus 2	RMB 18467	KU 337814	Samar	Kadakan River, Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759204			
Limnonectes magnus 2	RMB 18471	KU 337818	Samar	Kadakan River, Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759205			
Limnonectes magnus 2	RMB 18475	KU 337822	Samar	Kadakan River, Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759206			
Limnonectes magnus 2	RMB 18478	KU 337825	Samar	Kadakan River, Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759207			
Limnonectes magnus 2	RMB 18482	KU 337829	Samar	Kadakan River, Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759208			

APPENDIX I Continued.

Species	Field no.	Catalog no.	Island	Locality	Elevation (m)	GenBank accession numbers			
						16S	LCT[a]	CPT2	POMC
Limnonectes magnus 2	RMB 18696	KU 337833	Samar	Kadakan River, Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759209			
Limnonectes magnus 2	RMB 18744	KU 337837	Samar	Kadakan River, Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759210		MT631736	MT631759
Limnonectes magnus 2	RMB 19080	KU 337852	Samar	DENR House, Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759212			
Limnonectes magnus 2	RMB 19101	KU 338896	Samar	Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759213			
Limnonectes magnus 2	CDS 6439	KU 340593	Samar	Kadakan River, Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759138	MZ577254		MT631748
Limnonectes magnus 3	ACD 7076	Deposited at PNM	Siargao	Barangay del Carmen, Surigao del Norte Province		MN759106			
Limnonectes magnus 3	CDS 2005	KU 306004	Dinagat	Barangay Esperanza, Municipality of Loreto, Dinagat Province		MN759120			
Limnonectes magnus 3	CDS 1841	KU 306030	Samar	Taft Forest, Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759113			
Limnonectes magnus 3	CDS 1844	KU 306033	Samar	Taft Forest, Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759114			
Limnonectes magnus 3	CDS 1928	KU 306062	Dinagat	Barangay San Juan, Municipality of Loreto, Dinagat Province		MN759115			
Limnonectes magnus 3	CDS 1931	KU 306065	Dinagat	Barangay San Juan, Municipality of Loreto, Dinagat Province		MN759117			
Limnonectes magnus 3	CDS 1979	KU 306072	Dinagat	Barangay Esperanza, Municipality of Loreto		MN759119			
Limnonectes magnus 3	CWL 252	KU 306076	Dinagat	Barangay San Juan, Municipality of Loreto, Dinagat Province		MN759147			
Limnonectes magnus 3	CWL 253	KU 306077	Dinagat	Barangay San Juan, Municipality of Loreto, Dinagat Province		MN759148			
Limnonectes magnus 3	CWL 257	KU 306081	Dinagat	Barangay San Juan, Municipality of Loreto, Dinagat Province		MN759149			
Limnonectes magnus 3	CWL 299	KU 306082	Dinagat	Barangay Esperanza, Municipality of Loreto, Dinagat Province		MN759150	MZ577249	MT631730	MT631747
Limnonectes magnus 3	CWL 300	KU 306083	Dinagat	Barangay Esperanza, Municipality of Loreto, Dinagat Province		MN759152			
Limnonectes magnus 3	CWL 324	KU 306084	Dinagat	Barangay Esperanza, Municipality of Loreto, Dinagat Province	340	MN759245			
Limnonectes magnus 3	RMB 8540	KU 309273	Samar	Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759232			
Limnonectes magnus 3	RMB 8707	KU 309274	Samar	Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759235			
Limnonectes magnus 3	RMB 7956	KU 309687	Camiguin Sur	Sitio Kampana, Barangay Pandan, Municipality of Mambajao, Camiguin Province		MN759220			
Limnonectes magnus 3	RMB 7971	KU 309691	Camiguin Sur	Sitio Kampana, Barangay Pandan, Municipality of Mambajao, Camiguin Province		MN759221			

APPENDIX I Continued.

Species	Field no.	Catalog no.	Island	Locality	Elevation (m)	GenBank accession numbers 16S	LCT[a]	CPT2	POMC
Limnonectes magnus 3	RMB 7976	KU 309696	Camiguin Sur	Sitio Kampana, Barangay Pandan, Municipality of Mambajao, Camiguin Province		MN759222			
Limnonectes magnus 3	RMB 8065	KU 309702	Camiguin Sur	Sitio Kampana, Barangay Pandan, Municipality of Mambajao, Camiguin Province		MN759223			
Limnonectes magnus 3	RMB 8096	KU 309707	Camiguin Sur	Sitio Pamahawan, Barangay Pandan, Municipality of Mambajao, Camiguin Province		MN759224			
Limnonectes magnus 3	RMB 8292	KU 309975	Dinagat	Sitio Cambinlia (Sudlon), Barangay Santiago, Municipality of Loreto, Dinagat Islands Province		MN759225			
Limnonectes magnus 3	RMB 8295	KU 309978	Dinagat	Sitio Cambinlia (Sudlon), Barangay Santiago, Municipality of Loreto, Dinagat Islands Province		MN759226			
Limnonectes magnus 3	RMB 8365	KU 309981	Dinagat	Sitio Cambinlia (Sudlon), Barangay Santiago, Municipality of Loreto, Dinagat Islands Province		MN759227			
Limnonectes magnus 3	RMB 8389	KU 309985	Dinagat	Sitio Cambinlia (Sudlon), Barangay Santiago, Municipality of Loreto, Dinagat Islands Province		MN759228			
Limnonectes magnus 3	RMB 8482	KU 309989	Dinagat	Sitio Cambinlia (Sangay 2), Barangay Santiago, Municipality of Loreto, Dinagat Islands Province		MN759229			
Limnonectes magnus 3	RMB 8520	KU 310181	Samar	Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759230			
Limnonectes magnus 3	RMB 8523	KU 314384	Mindanao	Pasonanca Natural Park, Sitio Canucutan, Barangay Pasonanca, Municipality of Zamboanga, Zamboanga del Sur Province		MN759089	MZ577250	MT631735	MT631746
Limnonectes magnus 3	ACD 3714	KU 314385	Mindanao	Pasonanca Natural Park, Sitio Canucutan, Barangay Pasonanca, Municipality of Zamboanga, Zamboanga del Sur Province		MN759151			
Limnonectes magnus 3	ACD 3728	KU 314387	Mindanao	Pasonanca Natural Park, Sitio Canucutan, Barangay Pasonanca, Municipality of Zamboanga, Zamboanga del Sur Province		MN759090			
Limnonectes magnus 3	ACD 3772	KU 314391	Mindanao	Pasonanca Natural Park, Sitio Canucutan, Barangay Pasonanca, Municipality of Zamboanga, Zamboanga del Sur Province		MN759238			
Limnonectes magnus 3	RMB 8982	KU 314394	Mindanao	Pasonanca Natural Park, Tumaga River, Municipality of Zamboanga, Zamboanga del Sur Province		MN759239			
Limnonectes magnus 3	RMB 9116	KU 314396	Mindanao	Pasonanca Natural Park, Tumaga River, Municipality of Zamboanga, Zamboanga del Sur Province		MN759240			
Limnonectes magnus 3	RMB 9118	KU 314399	Mindanao	Pasonanca Natural Park, Sitio Canucutan, Barangay Pasonanca, Municipality of Zamboanga, Zamboanga del Sur Province		MN759241			

APPENDIX I Continued.

Species	Field no.	Catalog no.	Island	Locality	Elevation (m)	GenBank accession numbers			
						16S	LCT[a]	CPT2	POMC
Limnonectes magnus 3	RMB 9258	KU 314402	Mindanao	Pasonanca Natural Park, Sitio Canucutan, Barangay Pasonanca, Municipality of Zamboanga, Zamboanga del Sur Province		MN759242			
Limnonectes magnus 3	RMB 9316	KU 314404	Mindanao	Pasonanca Natural Park, Sitio Canucutan, Barangay Pasonanca, Municipality of Zamboanga, Zamboanga del Sur Province		MN759243			
Limnonectes magnus 3	RMB 9330	KU 314406	Mindanao	Pasonanca Natural Park, Sitio Canucutan, Barangay Pasonanca, Municipality of Zamboanga, Zamboanga del Sur Province		MN759244			
Limnonectes magnus 3	RMB 9332	KU 314428	Mindanao	Pasonanca Natural Park, Sitio Kilometer 24, Barangay Baluno, Municipality of Zamboanga, Zamboanga del Sur Province		MN759165			
Limnonectes magnus 3	RMB 10034	KU 314438	Mindanao	Pasonanca Natural Park, Sitio Zambales, Barangay Baluno, Municipality of Zamboanga, Zamboanga del Sur Province		MN759166			
Limnonectes magnus 3	RMB 10374	KU 314446	Mindanao	Pasonanca Natural Park, Sitio Zambales, Barangay Baluno, Municipality of Zamboanga, Zamboanga del Sur Province		MN759167			
Limnonectes magnus 3	RMB 10484	KU 319384	Mindanao	Mt. Magdiwata, Barangay Bayugan II, Municipality of San Francisco, Agusan del Sur Province		MN759091			
Limnonectes magnus 3	ACD 3856	KU 319385	Mindanao	Mt. Magdiwata, Barangay Bayugan II, Municipality of San Francisco, Agusan del Sur Province		MN759092			
Limnonectes magnus 3	ACD 3908	KU 319395	Mindanao	Mt. Magdiwata, Barangay Bayugan II, Municipality of San Francisco, Agusan del Sur Province		MN759093			
Limnonectes magnus 3	ACD 4108	KU 320078	Mindanao	Mt. Balatukan Natural Park, Sitio San Isidro, Boy Scout Camp, Municipality of Gingoog, Misamis Oriental Province		MN759094			
Limnonectes magnus 3	ACD 4237	KU 321148	Mindanao	Pasonanca Natural Park, Sitio Nancy, Barangay La Paz, Municipality of Zamboanga, Zamboanga del Sur Province		MN759168			
Limnonectes magnus 3	RMB 11148	KU 321160	Mindanao	Pasonanca Natural Park, Sitio Nancy, Barangay La Paz, Municipality of Zamboanga, Zamboanga del Sur Province		MN759169			
Limnonectes magnus 3	RMB 11178	KU 326655	Mindanao	Barangay Kimlawis, Municipality of Kiblawan, Davao del Sur Province		MN759100			
Limnonectes magnus 3	ACD5263	KU 326656	Mindanao	Sitio Dasal Mangisi, Barangay Tablu, Municipality of Zamboanga, Zamboanga del Sur Province		MN759105			
Limnonectes magnus 3	ACD 5427	KU 327476	Mindanao	Barangay Kimlawis, Municipality of Kiblawan, Davao del Sur Province		MN759099			

APPENDIX I Continued.

Species	Field no.	Catalog no.	Island	Locality	Elevation (m)	GenBank accession numbers			
						16S	LCT[a]	CPT2	POMC
Limnonectes magnus 3	ACD 5252	KU 327479	Mindanao	Barangay Kimlawis, Municipality of Kiblawan, Davao del Sur Province		MN759101			
Limnonectes magnus 3	ACD 5265	KU 327482	Mindanao	Barangay Kimlawis, Municipality of Kiblawan, Davao del Sur Province		MN759102			
Limnonectes magnus 3	ACD 5268	KU 327485	Mindanao	Barangay Kimlawis, Municipality of Kiblawan, Davao del Sur Province		MN759103			
Limnonectes magnus 3	ACD 5271	KU 327499	Mindanao	Sitio Dasal Mangisi, Barangay Tablu, Municipality of Zamboanga, Zamboanga del Sur Province		MN759104			
Limnonectes magnus 3	ACD 5415	KU 333344	Mindanao	Mt. Hilong-hilong, intersection of Dayhopan and Agay rivers, Eye Falls, Municipality of Remedios T. Romualdez, Agusan del Norte Province		MN759170			
Limnonectes magnus 3	RMB 15737	KU 333350	Mindanao	Mt. Hilong-hilong, intersection of Dayhopan and Agay rivers, Eye Falls, Municipality of Remedios T. Romualdez, Agusan del Norte Province	470	MN759171			
Limnonectes magnus 3	RMB 15785	KU 333355	Mindanao	Mt. Hilong-hilong, intersection of Dayhopan and Agay rivers, Eye Falls, Municipality of Remedios T. Romualdez, Agusan del Norte Province	470	MN759172			
Limnonectes magnus 3	RMB 15790	KU 333360	Mindanao	Mt. Hilong-hilong, intersection of Dayhopan and Agay rivers, Eye Falls, Municipality of Remedios T. Romualdez, Agusan del Norte Province	470	MN759173			
Limnonectes magnus 3	RMB 15891	KU 333365	Mindanao	Mt. Hilong-hilong, intersection of Dayhopan and Agay rivers, Eye Falls, Municipality of Remedios T. Romualdez, Agusan del Norte Province	470	MN759174			
Limnonectes magnus 3	RMB 15896	KU 333380	Mindanao	Mt. Hilong-hilong, May-Impit, Municipality of Remedios T. Romualdez, Agusan del Norte Province	470	MN759177			
Limnonectes magnus 3	RMB 16231	KU 333390	Mindanao	Mt. Hilong-hilong, May-Impit, Municipality of Remedios T. Romualdez, Agusan del Norte Province	1150	MN759185			
Limnonectes magnus 3	RMB 16275	KU 333395	Mindanao	Mt. Hilong-hilong, May-Impit, Municipality of Remedios T. Romualdez, Agusan del Norte Province	990	MN759187			
Limnonectes magnus 3	RMB 16280	KU 333400	Mindanao	Mt. Hilong-hilong, Municipality of Remedios T. Romualdez, Agusan del Norte Province	990	MN759188			
Limnonectes magnus 3	RMB 16357	KU 333404	Mindanao	Mt. Hilong-hilong, Municipality of Remedios T. Romualdez, Agusan del Norte Province	170	MN759189			
Limnonectes magnus 3	RMB 16361	KU 333414	Mindanao	Mt. Hilong-hilong, Municipality of Remedios T. Romualdez, Agusan del Norte Province	170	MN759190			
Limnonectes magnus 3	RMB 16372	KU 333423	Mindanao	Mt. Lumot, Haribon Site, Municipality of Gingoog, Misamis Oriental Province	170	MN759191			
Limnonectes magnus 3	RMB 16419	KU 333433	Mindanao	Mt. Lumot, Camp 2, Municipality of Gingoog, Misamis Oriental Province		MN759193			

APPENDIX I Continued.

Species	Field no.	Catalog no.	Island	Locality	Elevation (m)	GenBank accession numbers			
						16S	LCT[a]	CPT2	POMC
Limnonectes magnus 3	RMB 16587	KU 333480	Mindanao	Mt. Lumot, Camp 3, Sitio Kibuko-Boundary with Barangay Lawaan, Gingoog River, Municipality of Gingoog, Misamis Oriental Province	1236	MN759195			
Limnonectes magnus 3	RMB 16958	KU 333481	Mindanao	Mt. Lumot, Camp 3, Sitio Kibuko-Boundary with Barangay Lawaan, Gingoog River, Municipality of Gingoog, Misamis Oriental Province	420	MN759196			
Limnonectes magnus 3	RMB 16982	KU 333482	Mindanao	Mt. Lumot, Camp 3, Sitio Kibuko-Boundary with Barangay Lawaan, Gingoog River, Municipality of Gingoog, Misamis Oriental Province	420	MN759197			
Limnonectes magnus 3	RMB 16983	KU 333483	Mindanao	Mt. Lumot, Camp 3, Sitio Kibuko-Boundary with Barangay Lawaan, Gingoog River, Municipality of Gingoog, Misamis Oriental Province	420	MN759198			
Limnonectes magnus 3	RMB 16984	KU 333485	Mindanao	Mt. Lumot, Camp 3, Sitio Kibuko-Boundary with Barangay Lawaan, Gingoog River, Municipality of Gingoog, Misamis Oriental Province	420	MN759214			
Limnonectes magnus 3	RMB 20765	KU 333487	Mindanao	Mt. Lumot, Camp 3, Sitio Kibuko-Boundary with Barangay Lawaan, Gingoog River, Municipality of Gingoog, Misamis Oriental Province		MN759215			
Limnonectes magnus 3	RMB 20767	KU 333488	Mindanao	Mt. Lumot, Camp 3, Sitio Kibuko-Boundary with Barangay Lawaan, Gingoog River, Municipality of Gingoog, Misamis Oriental Province	420	MN759216			
Limnonectes magnus 3	RMB 20862	KU 333490	Mindanao	Mt. Lumot, Camp 3, Sitio Kibuko-Boundary with Barangay Lawaan, Gingoog River, Municipality of Gingoog, Misamis Oriental Province	420	MN759217			
Limnonectes magnus 3	RMB 20883	KU 333491	Mindanao	Mt. Lumot, Camp 3, Sitio Kibuko-Boundary with Barangay Lawaan, Gingoog River, Municipality of Gingoog, Misamis Oriental Province	420	MN759218			
Limnonectes magnus 3	RMB 20884	KU 335041	Mindanao	Pasonanca Natural Park, Sitio Catala, Catala Creek, Municipality of Zamboanga City, Zamboanga del Sur Province	420	MN759199			
Limnonectes magnus 3	RMB 17312	KU 335043	Mindanao	Pasonanca Natural Park, Sitio Catala, Catala Creek, Municipality of Zamboanga City, Zamboanga del Sur Province		MN759200			
Limnonectes magnus 3	RMB 17314	KU 335045	Mindanao	Pasonanca Natural Park, Sitio Catala, Catala Creek, Municipality of Zamboanga City, Zamboanga del Sur Province		MN759201			
Limnonectes magnus 3	RMB 17316	KU 335049	Mindanao	Pasonanca Natural Park, Sitio Catala, Catala Creek, Municipality of Zamboanga City, Zamboanga del Sur Province		MN759202			

Appendix I Continued.

Species	Field no.	Catalog no.	Island	Locality	Elevation (m)	GenBank accession numbers			
						16S	LCT[a]	CPT2	POMC
Limnonectes magnus 3	RMB 17320	KU 335052	Mindanao	Pasonanca Natural Park, Sitio Catala, Catala Creek, Municipality of Zamboanga City, Zamboanga del Sur Province		MN759203			
Limnonectes magnus 3	RMB 17376	KU 337842	Samar	Kadak-an River, Barangay San Rafael, Municipality of Taft, Eastern Samar Province		MN759211	MZ577256	MT631731	MT631742
Limnonectes magnus 2	RMB 18843	CMNH 5513	Mindanao	Mt. Apo, Barangay Ilomavis, Municipality of Kidapawan, Davao del Norte Province		AY313703			
Limnonectes magnus 1	NA	PNM 7829	Bohol	Municipality of Bilar, Bohol Province		AY313706			
Limnonectes magnus 1	NA	USNM 534311	Samar	Bagakay Mines, Municipality of Bagakay, Samar Province		AY313704			

[a] LCT, lactase; CPT-2, carnitine palmitoyltransferase II; POMC, pro-opiomelanocortin.

Appendix II

Specimens Examined

Limnonectes acanthi.—PHILIPPINES: 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 (TNHC 59903, PNM 6694, 7607); Palawan Island, Palawan Province (FMNH 51185–89, 51190–95, 51196, 99, 51200–04; 51205–17, 51219–20, 51222–29, 51230–40); KU Palawan Island, Palawan Province (FMNH 51185–95); Municipality of Puerto Princesa, Mt. Bloomfield (PNM 6280, 6295, 6301); Barangay Lamod, Sitios Kayasan and 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 21496–21501); ca. 8 km S. of Iwahig (CAS–SU 21525–26); Malatgaw River tributary, ca. 5 km W. of Iwahig (CAS–SU 21502–21508); 9 km SW of Iwahig (CAS–SU 21520–24); ca. 9 km SSW of Iwahig (21509–17, 21519, 21527–41); Malatgaw River tributary, ca. 1.5 km SSW of Iwahig (CAS–SU 21432–24, 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 (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, 6026–29, 6038–40, 14710–13; CAS-SU 6000–03, MCZ A–14067–69, paratypes); Coron Island Palawan Province (CAS-SU 5943–45, 5954, 13965–67 CAS 158154–77); 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 (FMNH 51241–79, CAS–SU 3284); 6.5 km SW Culion Town (KU 79061–68).

Limnonectes beloncioi—PHILIPPINES: Mindoro Island, Oriental Mindoro Province, Municipality of Bongabong, Barangay Carmundo, Sitio Paypay-Ama, Paypay-Ama River (PNM 9870, holotype; KU 302084–88 KU 302085–86, 302089; 303343, 303369–78, paratopotypes; KU 302090–91, 302093, 302095, 302097, 302100, 302109–11); Municipality of Victoria, Barangay Loyal (KU 302112–18); Barangay Loyal, Sitio Panguisan, Panguisan River (KU 303470–78); Municipality of Gloria, Barangay Malamig (KU 302108, 303344; KU 303346–54); Sitio Balogbog, Cueba Simbahan (KU 303379–80); Sitio Pastohan, Tanguisian Falls (KU 303381–402); Occidental Mindoro Province, Municipality of Calintaan, Barangay New Dagupan (KU 303266); Municipality of Magsaysay, Barangay Nicolas, Sitio Banban (KU 303404–30; KU 304131–32); Municipality of Sablayan, Barangay Batong Buhay, Sitio Batulai, Mt. Siburan (KU 303430–52; KU 305450–51, 306637); Barangay Malisbong, Sitio Aruyan (KU 335863–83); Barangay Burgos, Sitio Posoy, Posoy River (KU 303453–69); 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); Municipality of Puerto Galera, Barangay San Isidro, Sitio Minolo, Ponderosa Golf Resort (TNHC 54920); Municipality of San Teodoro, Barangay Villaflor, Tamaraw Falls, approximately km 15 from Puerto Galera on Calapan-to-Puerto Galera road (TNHC 54921–29, 55023, 55025, 55029, 55033, USNM 556073–94); Municipality of Baco, Barangay Lantuyan, near Cabinuangang River (USNM 508558–63, USNM 508564–72); Municipality of Tarogin, ca. 30 km S of Calapan Town, Mt. Halcon SE slope (CAS-SU 22146, CAS-SU 22145, CAS-SU 22147–49, CAS–SU 22150, CAS-SU 22576, CAS-SU 22577, 23508, CAS-SU 23499, 23501, 23525, 23505, 23514–15, 23519–20, CAS-SU 23485, 23487, 23496–97, 23512–13, 23522, 23489, 23498, 23502); Municipality of Tarogin, Mt. Halcon (CAS-SU 22240, CAS–SU 22288–

22295, 23500, 23510–11, 23517–18, 23521, CAS-SU 22151); Semirara Island, Oriental Mindoro Province, Municipality of Caluya, Barangay Tinogboc (KU 302105–07); 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).

Limnonectes diuatus.—PHILIPPINES: Mindanao Island, Agusan del Norte Province: Municipality of Cabadbaran, Tagibo River, south side of Mt. Hilong-hilong (FMNH 197934, CAS 133430–32, 133434, 139389–93, 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); Davao Del Norte Province: Municipality of Monkayo, Simulaw River Drainage, Mt. Pasian (CMNH 5572, 5573, PNM 9506 paratypes and holotype of *Limnonectes ferneri*); Dinagat Island, Dinagat Islands Province: Municipality of Loreto, Barangay Santiago, Sitio Cambinlia (Sudlon) (KU 309992–310000).

Limnonectes leytensis.—PHILIPPINES: Mindanao Island, "Mindanao" FMNH (14868, batch of 16 specimens); MCZ A-14137–14141, + 11 duplicates); "Zamboanga Province" (63200, 6900); "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:" 50060–131; "Takayan, near Saub, Cotabato Coast (=S. Cotabato 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 60789–91, 42855–84, 54121–22); Leyte City (CAS-SU 15483); Calabian (MCZ A-14099); Camiguin SUR Island, Camiguin Province: Mambajao (CAS-SU 23088–23091); 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 174049–51, 174034); Basilan Province (MCZ A-14125-14133); Basilan Province, Port Holland (CAS 60377–78, MCZ A-14103–14110); 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-SU 23140–42, 23144, 23251, 23272, 23284, 23287, 23291, 23299, 23307, 23317, 23326–30, 23331–35, 23241, 23265, CAS 131950–51); 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, 175264–66, 175267, 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, CAS-SU 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 306036, 306041–42, 306077, 306082–84, 306028–30, 306033, 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 16800, CAS-SU 16799); 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 Taguibo 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 17170–17211; 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 *R. micrixalus* Taylor 1923).

Limnonectes palavanensis.—PHILIPPINES: Palawan Island, Palawan Province, Municipality of Brooke's Point, Barangay Mainit (KU 309133–36, 309138); S slope of Thumb Peak, 330–660 m, WNW of Iwahig (CAS 14744, CAS-SU 20421–26, CAS 20432–34, CAS 20438, CAS 20445–47, CAS 20449, CAS 20451, CAS-SU 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 kn SE Buena Suerte (CAS–SU 20411).

Limnonectes visayanus.—PHILIPPINES: Masbate Island, Masbate Province, Municipality of Mobo (KU 302171, CAS-SU 144253–59); Mt. Mobo, Tugbo watershed (CAS-SU 1442609–61, CAS-SU 144327, CAS-SU 14482–84; CAS 144345); 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 139164–139166); Municipality of Makato, Castillo Barrio (CAS-SU 137590); Calagna-an Island, Iloilo Province: Barangkalan (CAS 124121, 124293–97); Siquijor Island, Siquijor Province (FMNH 61439–43, CAS-SU 23126; Municipality of Lazi, Po-o (CAS-SU 16796–97); 1.5 km N of Maria Town (CAS-SU 23908); Municipality of San Jua, Tag-ibo Barrio, 2 km from coast (CAS-SU 16777, 16779, 16780, 16783–85, 16787–88, 16790, 16792, 16794); Sicogon Island, Iloilo Province: Buaya area (CAS 124950–58, CAS 12442–44); 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 (TNHC 62880–82, KU 302189–90, 302192, 302196, 302203–04); Tahiro River, 120 m asl (MCZ A-110944–48; Municipality of Bayanan, Malyong (CAS 17078–81); "Negros Island" (FMNH 61504–23, 57204–33, 57234–41, 57244, 57246–47, 61403–09, 61444–48, 77721–22); Municipality of Sibulan Lake Balinsasaayo, 1000 m asl, 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 16685–16736); 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 (KU 302224, 302227, 302228, 303483–85, 307528, 307531–34; CAS 61001, paratype): 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 (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).