*Ichthyology & Herpetology* 112, No. 2, 2024, 270–294

# A Long Overlooked New Species of Fanged Frog, Genus *Limnonectes* (Amphibia: Anura: Dicroglossidae), from Luzon Island, Northern Philippines

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**We describe a new species of fanged frog (genus *Limnonectes*) from the foothills of two, inland, south-to-north oriented, parallel mountain ranges of Luzon Island of the northern Philippines. Although the new species broadly co-occurs with its closest relative at numerous localities within the Luzon Pleistocene aggregate island complex faunal region, it can be readily diagnosed from *Limnonectes macrocephalus* based on its unpigmented (white) ventral surfaces of terminal digital discs, its unexpanded or minimally expanded terminal digital discs, and an allometric growth pattern indicating evidence of sexual dimorphism at a smaller overall body size. The new species, which can also be identified by its divergent 16S ribosomal RNA mitochondrial gene sequence, possesses a curious distribution unlike the range of any Philippine endemic amphibian characterized to date: it is known from nine interior (inland) localities distributed between the two, parallel, south-to-north mountain chains (the Cordillera and Sierra Madre) which characterize mainland Luzon. We interpret the presence of two broadly sympatric, genetically divergent, strongly supported haplotype clades—which correspond to morphologically diagnosable phenotypes, using traditional discrete characters and allometric growth patterns—as prima facia evidence of two, independently evolving evolutionary lineages (species) of giant fanged frogs on Luzon. The description of another new species of large-bodied fanged frog on Luzon from multiple localities in close proximity to the capital city (Manila) emphasizes the degree to which even well-studied larger Philippine landmasses possess unrecognized and overlooked biodiversity.**

THE genus *Limnonectes*, commonly known as the "Fanged Frogs," is composed of nearly 80 described species (Frost, 2021; AmphibiaWeb, 2022). The genus is widely distributed across southeast Asia and ranges from India to China and Indochina, through the Thai–Malaysia Peninsula, and across the Sunda Shelf landmasses (Borneo, Sumatra, Java), throughout the Philippines, the Malukus (Wallacea), the Lesser Sunda island chain, Timor-Leste, and parts of western New Guinea (Taylor, 1920; Smith, 1927; Inger, 1954, 1966, 1999; Duellman, 1993; Zhao and Adler, 1993; Inger and Tan, 1996; Malkmus et al., 2002; Evans et al., 2003; McLeod, 2008; Matsui et al., 2010; McLeod et al., 2011; Diesmos et al., 2015; O'Shea et al., 2015; AmphibiaWeb, 2022).

Over the last two decades, described species diversity has increased steadily (Brown et al., 2002, 2008, 2012a; Brown and Stuart, 2012; Diesmos et al., 2015; Suwannapoom et al., 2016; Phimmachak et al., 2019; Yodthong et al., 2021), and studies have identified numerous unconfirmed, putative, or "candidate" species (Evans et al., 2003; McLeod, 2008; Matsui et al., 2010; McLeod et al., 2011; Köhler et al., 2021). Discussion of unconfirmed candidate species of *Limnonectes* have been standard in summaries of regional species diversity, particularly with regard to underestimated, and potentially morphologically "cryptic," amphibian biodiversity (Inger, 1999; Brown and Diesmos, 2002; Zhang et al., 2005; Stuart et al., 2006; Brown et al., 2008, 2012a; Ron and Brown, 2008; Matsui et al., 2010; Brown and Stuart, 2012). Presumably, knowledge of this undescribed diversity, combined with comprehensive sampling, advancing sequencing technology, statistical approaches to species delimitation, and multidisciplinary approaches to integrative taxonomy would lead to many new species descriptions (Brown and Guttman, 2002; Evans et al., 2003; Padial et al., 2010; Brown and Stuart, 2012; Brown et al., 2012a, 2013a, 2016; Brown and Siler, 2013; AmphibiaWeb, 2022). However, this seemingly "inevitable" outcome has fallen somewhat short in the Philippines, where only one, full, valid new species of fanged frog has been described in the last two decades (Brown and Diesmos, 2002; Brown et al., 2002; Evans et al., 2003; Siler et al., 2009; Abraham et al., 2021; Herr et al., 2021).

Existing studies have suggested that Philippine fanged frog diversification has been essentially geographical (rather than adaptive) in character, mediated by bouts of dispersal (along two or three distinct chains of islands: Taylor, 1928; Inger, 1954; Brown and Alcala, 1970; Diamond and Gilpin, 1983; Brown and Guttman, 2002; Evans et al., 2003; Brown and Siler, 2013; Brown et al., 2013a), island colonization (Brown and Diesmos, 2002), geographical isolation, and steady accumulation of taxa within the archipelago following lineage divergence (Emerson et al., 2000; Brown and Guttman, 2002; Brown et al., 2002, 2013a, 2016; Evans et al., 2003; Setiadi et al., 2011; Brown and Siler, 2013). Recent studies have articulated this non-adaptive, geographical diversification model in contrast to a probable adaptive radiation of *Limnonectes* on the nearby Indonesian island of Sulawesi, possibly involving the absence (on Sulawesi) versus presence (in the Philippines) of incumbent competitors in the form of small-bodied ground frogs of the genus *Platymantis* (Setiadi et al., 2011; Brown et al., 2015).

Eleven Philippine species of *Limnonectes* are currently recognized (Abraham et al., 2021; Herr et al., 2021), with one (Mindoro Island; Herr et al., 2021) to five (Mindanao Island; Brown and Alcala, 1970; Sanguila et al., 2016) species per landmass. On larger islands, body size, feeding niche, microhabitat preference, and elevational stratification all seem to have played a role in the allowance of species coexistence in

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Submitted: 14 October 2022. Accepted: 4 March 2024. Associate Editor: B. L Stuart.

DOI: 10.1643/h2022094

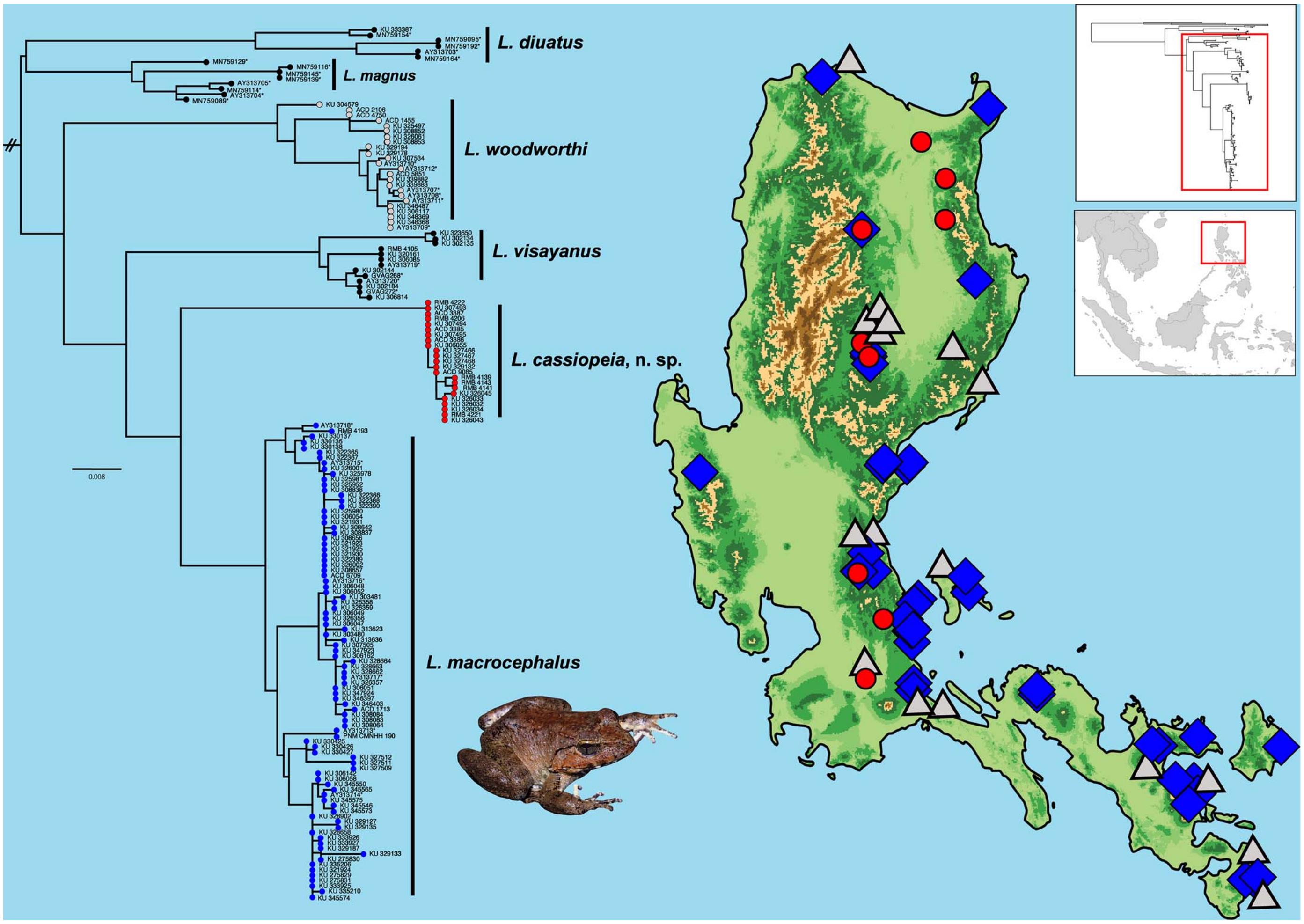

**Fig. 1.** Map of sampling locations on Luzon Island, Philippines (right) and ML phylogenetic tree (left). Red circles on the map represent genetic sampling localities for *Limnonectes cassiopeia*, new species, blue diamonds represent genetic sampling for *L. macrocephalus*, and gray triangles represent genetic samples of *L. woodworthi*. Maximum likelihood tree topology estimated in IQ-TREE. Only the *Limnonectes* clade E (*sensu* Evans et al., 2003) subtree is shown here (see inset; outgroups not shown: *L. finchi*, *L. parvus*, *L. micrixalus*, *L. palavanensis*, *L. leytensis*, *L. acanthi*, and *L. beloncioi*). Black circles at nodes indicate strong support for all ML and BI support metrics (UFBS ≥ 95, SH-LR ≥ 80, PP ≥ 0.95). Branch length scale bar units = substitutions/site. The full ML and BI trees are available in supplementary data (see Data Accessibility).

sympatric (but not necessarily syntopic) ranges/habitats (Siler et al., 2009; Setiadi et al., 2011; Brown et al., 2012a, 2013a; Herr et al., 2021). One curious aspect of these distribution patterns involves the presence of only two species of *Limnonectes* documented on the archipelago's largest island (Luzon), in contrast with five species inhabiting the second largest Island (Mindanao; Inger, 1954; Diesmos et al., 2015). Is this surprising imbalance a true reflection of diversity and biogeography, or could it be a clue that Luzon Island harbors one or more unrecognized species of *Limnonectes*?

In this paper, we describe a new species of *Limnonectes* from Luzon Island, northern Philippines. The new species has been sampled intermittently over the last two decades, with only a few individual specimens collected unknowingly from each site, intermixed with larger series of *Limnonectes macrocephalus*, at a total of nine localities, throughout much of the interior of Luzon Island (Fig. 1). First identified as a divergent mitochondrial gene lineage, the new species is broadly sympatric with *L. macrocephalus* (its sister species), but readily diagnosed by traditional, discrete diagnostic characters, and allometric growth patterns related to the onset of sexual dimorphism at a smaller body size, and apparently the overall smaller maximal body size attained throughout ontogeny.

## MATERIALS AND METHODS

***Species concept.***—We adopt the general lineage species concept (GLSC) as our framework for species delimitation. Under the GLSC model (de Queiroz, 1998, 2005), a logical extension of the evolutionary species concept (Simpson, 1961; Wiley, 1978; Frost and Hillis, 1990), we consider monophyletic, reliably diagnosable, sympatric metapopulations as distinct species if they bear the hallmarks of cohesive, separately evolving lineages: ancestor-descendent series (de Queiroz, 1998) of distinct (from other such series), temporally connected, recognizable populations/generations (Frost and Hillis, 1990; Brown et al., 2000a; de Queiroz, 2005). By "diagnosable" we refer to the presence of fixed (invariant), discrete character difference(s), whether traditional character states (discrete differences of external morphology; presence vs. absence of anatomical features), unique biochemical or molecular characteristics, behavioral or ecological character states, and/or ontogenetic allometric growth pattern differences. Whether allopatric, sympatric, reproductively isolated, or occasionally exchanging alleles via gene flow, we focus on whether putative lineages possess unique evolutionary histories with predictable evolutionary fates (Wiley, 1978; Frost and Hillis, 1990; Brown et al., 2000a; Brown and Guttman, 2002). In this paper, we test such a putative hypothesis within an integrative framework (Dayrat, 2005; Padial et al., 2010; Pante et al., 2015; Herr et al., 2021), addressing genetic variation and phylogenetic relationships, phenotypic variation and traditional character state differences, and body-size adjusted allometric patterns (including body size at onset of sexual dimorphism) as primary lines of evidence.

Given the fact that *Limnonectes cassiopeia*, new species, is broadly sympatric with *L. macrocephalus* at multiple localities in the eastern foothills of Luzon's Cordillera mountain range (Fig. 1), we consider (1) moderate genetic divergence between them, accompanied by (2) phenotypic differentiation (traditional, diagnostic trait differences), and (3) continuous mensural character variation (shape differences, which result in onset of sexual dimorphism at a smaller absolute body size), to constitute strong, integrative (multi-data stream), evidence sufficient for rejecting the hypothesis that the putative new species of *Limnonectes* and *L. macrocephalus* represent a single widespread Luzon Pleistocene aggregate island complex (PAIC; Voris, 2000; Brown and Guttman, 2002; Brown et al., 2002) species.

***Molecular data and phylogenetic analyses.***—We first compiled mitochondrial gene sequences from GenBank of 41 specimens of *Limnonectes* including exemplars of every recognized Philippine species of *Limnonectes* (excepting *L. micrixalus* for which no sequences exist) and one Bornean species (*L. finchi*). These GenBank sequences consist of either a ∼2,400 base pair fragment of the mitochondrial gene regions $tRNA^{phe}$, 12S rRNA, $tRNA^{val}$, and 16S rRNA or an overlapping ∼900 base pair subregion of 16S rRNA. We then generated new sequences of the same 16S rRNA subregion for a large geographic sample of the *L. macrocephalus* complex ($n = 106$), plus additional sequences from its closest known relatives, *L. woodworthi* ($n = 18$) and *L. visayanus* ($n = 11$).

Laboratory protocols for the generation of new sequences follow Herr et al. (2021) and are summarized here. We subsampled 135 preserved Philippine tissues in *Limnonectes* stored in the University of Kansas Biodiversity Institute cryogenic facility (fresh frozen in liquid nitrogen or preserved in $\geq$ 95% ethanol and then frozen, $\leq$ 1 mo following collection). We extracted DNA from tissue samples using a Promega Maxwell® RSC extraction robot with Maxwell® RSC Tissue DNA kits. We amplified a ∼900 base pair fragment of the 16S rRNA mitochondrial gene using polymerase chain reaction (PCR) under a protocol adapted from Quah et al. (2017). We summarize the PCR conditions here: 1.0 μl DNA extract, 1.0 μl (10 μM concentration) forward primer 16Sc 5′–GACCTGTGATMTGAAAAACCAYC–3′, 1.0 μl (10 μM concentration) reverse primer 16Sd 5′–GACCTGTGATMTGAAAAACCAYC–3′ (Evans et al., 2003; Chan et al., 2022), 2.0 μl 5X buffer (1.5 μM), 1.0 MgCl 10X buffer (1.5 μM), 1.0 μl deoxynucleotide pairs (1.5 μM), 0.1 μl Promega Taq polymerase (5u/μl), and 7.4 μl water. We implemented the following thermal PCR protocol in a Bio-Rad gradient thermocycler: initial denaturation at 95°C for 2 min, second denaturation at 95°C for 35 s, annealing at 56°C for 35 s followed by an extension cycle at 72°C for 95 s + 4 s per cycle for 34 cycles. We visualized PCR amplicons via electrophoresis in a 1.0% agarose gel in order to confirm the quality and molecular weight of PCR products. We sent our amplified DNA fragments to GENEWIZ® for contract sequencing (purification, cycle sequencing, clean up, and nucleotide sequence determination). GENEWIZ® produces independent sequences from the 3′ and 5′ ends of the DNA fragment. We edited and assembled the resulting forward and reverse sequences with the software Geneious® version 11.1.5 (Kearse et al., 2012).

We added the newly assembled sequences to those from GenBank for a final combined dataset of 176 sequences which we used for all subsequent molecular analyses. We present a list of all sequences included in this study along with their GenBank numbers and associated information in Supplemental Table A (see Data Accessibility).

We aligned sequences with MAFFT v7.407 (Katoh et al., 2019) on the NGPhylogeny web server (Lemoine et al., 2019) employing the q-ins-I strategy to account for the secondary structure of RNA. MAFFT generated an initial alignment of 2532 base pairs which we then trimmed using trimAl v. 1.4.1 with a consistency threshold of 95% (Capella-Gutierrez et al., 2009). We accessed trimAl through the NGPhylogeny web server (Lemoine et al., 2019) and employed it to identify and excise the hypervariable sections known to occur on the 12S and 16S rRNA genes that cannot be confidently aligned. Trimming resulted in a final 2405 base pair alignment that we used for all downstream molecular analyses.

We performed maximum likelihood (ML) and Bayesian inference (BI) phylogenetic analyses on the molecular dataset to estimate relationships (ML and BI) and divergence timing (BI) among Philippine *Limnonectes*. We performed all phylogenetic analyses on both unpartitioned and partitioned ($tRNA^{phe}$, 12S rRNA, $tRNA^{val}$, and 16S rRNA partitioned separately) datasets and obtained identical topologies and support levels.

We performed the ML analysis in IQ-TREE on the web server (Trifinopoulos et al., 2016; Minh et al., 2020). The Bayesian Information Criterion employed in model selection within IQ-TREE selected $TIM2+F+I+\Gamma4$ as the model of evolution. We evaluated support in IQ-TREE with the Shimodaira-Hasegawa-like approximate likelihood ratio test (SH-LR) and the integral ultrafast bootstrap (UFBS) approximation algorithm with 1,000 pseudoreplicates (Hoang et al., 2018). We considered nodes with SH-LR values equal or greater than 80 and UFBS values equal or greater to 95 to be highly supported (Hoang et al., 2018).

We employed BI phylogenetic analysis in BEAST 2.5.2 (Bouckaert et al., 2019) to estimate a time-calibrated ultrametric phylogeny. We accessed BEAST 2.5.2 on the CIPRES web portal (Miller et al., 2010). We employed a birth–death tree prior and a relaxed log normal clock with rate of mitochondrial evolution set to 0.0065 to estimate a time-calibrated phylogeny. This rate corresponds to a rate of 1.3% sequence divergence per million years and has been used to estimate divergence times in *Limnonectes* (Reilly et al., 2019). We employed the reversible jump (RJ) model to select the most appropriate substitution model while simultaneously estimating model parameters and estimating tree topology; the general time reversible (GTR) model was selected and implemented in subsequent analysis. We implemented two independent runs, each for 100 million generations and sampled every 10,000 generations. We evaluated convergence by visualizing the log file in Tracer v1.7.1 (Rambaut et al., 2014) to ensure that all parameter effective sample sizes reached stationarity (accepted ESS values ≥ 200). We combined the two runs after discarding the first 10% of each run as burn-in and used TreeAnnotator v2.4.8 to generate a maximum clade credibility tree using median heights. We considered nodes with Bayesian posterior probability (PP) support values of 0.95 and above to be well supported (Wilcox et al., 2002; Bouckaert et al., 2019).

***Morphology and analysis of mensural characters.***—Our phylogenetic analyses identified an undescribed mitochondrial lineage (*Limnonectes cassiopeia*, new species) sister to *Limnonectes macrocephalus* (see results of molecular analyses, below). Most of the 23 individuals of *Limnonectes cassiopeia*, new species, uncovered by the genetic data correspond to preserved museum specimens available for examination, all of which we included in our morphological study ($n = 19$; Table 1). We then collected detailed morphological measurements from all specimens of *Limnonectes cassiopeia*, new species, and a sample of genetically confirmed true specimens of *Limnonectes macrocephalus* ($n = 37$), which we obtained by blindly selecting specimens of true *Limnonectes macrocephalus* from the molecular tree, taking care to select samples from across the genetic structure and full geographic range of the species. We then examined these blindly selected specimens to confirm that the sample included an adequate range of individuals of both sexes encompassing the known range of body sizes of the species, which it did. Morphometric data were collected by a single observer (MWH) to avoid inter-observer bias and/or extraneous error quantification of body dimensions (Lee, 1982; Hayek et al., 2001). We identified individuals as adult males, adult females, or juveniles in downstream analyses. We sexed all frogs with snout–vent length (SVL) > 50 mm by dissection and gonadal inspection, excepting obvious adult males possessing large fangs. All of the smallest frogs that we dissected lacked any mature gonads, and we categorized them as juveniles. As a result, we felt no need to dissect frogs with SVL < 50 mm (which can damage small specimens) and categorized them as juveniles as well. We measured specimens on the left side of the body with digital calipers to the nearest 0.1 mm. We measured the following 17 continuous morphometric characters: snout–vent length (SVL), head length (HL), snout length (SL), eye–nostril distance (EN), tympanum diameter (TYM), head width (HW), internarial distance (IND), interorbital distance (IOD), forearm length (FLL), hand length (HAL), Finger IV disk width (Fin4DW), thigh length (THL), tibia length (TL), tarsus length (TAR), foot length (FL), toe IV disk width (Toe4DW), and eye–tympanum distance (ETD). All character definitions and acronyms follow Watters et al. (2016).

Prior to statistical analysis, we generated exploratory plots of *Limnonectes macrocephalus* and *Limnonectes cassiopeia*, new species, morphology depicting raw untransformed character measurements of individuals plotted against their SVL. We used these plots to visualize character differences between the putative species in untransformed morphospace and to examine any possible sexual or allometric differences between them.

We performed all size correction and statistical analyses in R v3.6.3 (R Core Team, 2020) separately on adult males and females to account for sexual dimorphism (juveniles were excluded). We corrected all morphological measurements using the allometric formula (Thorpe, 1975; Chan and Grismer, 2021) using the R package GroupStruct which is specifically designed to assist in species delimitation of amphibians and reptiles (Chan and Grismer, 2022). The allometric formula is as follows: $Xadj = \log(X)–b [\log(BL)–\log(BLmean)]$ where $Xadj$ = size-corrected variable; $X$ = unadjusted trait variable; $b$ = regression coefficient between $\log(X)$ and $\log(BL)$ of each clade; $BL$ = snout–vent length; $BLmean$ = the grand mean of all BLs. We generated corrected measurements using the GroupStruct setting "species," which is parameterized for species delimitation analyses (Chan and Grismer, 2022). All further multivariate and univariate morphological analyses were performed on the allometry-corrected data.

We employed the GroupStruct function ez_pca() to perform principal component analysis (PCA) separately by sex. We used PCA to assess whether *Limnonectes cassiopeia*, new species, and *Limnonectes macrocephalus* differ from one another in multivariate morphospace. We then performed univariate analyses to determine whether *Limnonectes cassiopeia*, new species, differs from *Limnonectes macrocephalus* in any single morphometric characters following the methods outlined by Yodthong et al. (2021). We tested whether data conformed to assumptions of normality and variance homogeneity by performing Shapiro-Wilk tests and F-tests on each variable. We tested for morphometric differences between *Limnonectes cassiopeia*, new species, and *Limnonectes macrocephalus* separately by sex using either two sample independent *t*-tests (data normally distributed with equal variances), Welch's *t*-tests (data normally distributed with unequal variances), or Mann-Whitney U tests (data not normally distributed). We employed an alpha level of 0.05 for all statistical tests.

We also conducted external examinations to determine whether *Limnonectes macrocephalus* and *Limnonectes cassiopeia*, new species, can be reliably distinguished via any discreet diagnostic characters such as those relating to shape, pattern, coloration, skin rugosity, dentition, toe webbing, etc. For formulating our diagnosis, we examined all available genotyped specimens of *Limnonectes cassiopeia*, new species ($n = 19$), and *L. macrocephalus* ($n = 80$). We examined the holotype specimen of *Limnonectes macrocephalus* (FMNH 40519) to ensure that our taxonomic and nomenclatural actions were consistent with the identity of the existing name-bearing type specimen. Finally, we examined a large sample of specimens from throughout Luzon, Polillo, and Catanduanes Islands (purportedly *L. macrocephalus*; $n = 615$; not genotyped) to determine whether any additional specimens of *Limnonectes cassiopeia*, new species, could be identified for inclusion in our description, and to extensively survey phenotypic and color pattern variation to evaluate the reliability of our proposed diagnostic, fixed (shared by all specimens examined) character state differences. For repeatability and objectivity in our description of color pattern and intraspecific variation in the new species, we

**Table 1.** Summary of all genetically confirmed *Limnonectes cassiopeia*, new species, samples included in this study. Field numbers followed by asterisks (*) correspond to 19 vouchered physical specimens (the holotype and 18 paratypes) included in morphological analyses, and for which corresponding DNA sequences were included in molecular phylogenetic analyses—plus four genetic samples for which corresponding physical specimens were not available for this study. Holotype specimen bolded.

| Field number | Catalogue number | Sex | SVL (mm) | Locality | GPS | GenBank |
|---|---|---|---|---|---|---|
| RMB 6116* | KU 307495 | Juvenile | 28.3 | Isabela Province: Barangay Garita | 17.4136667°N, 121.82278333°E | PP923993 |
| RMB 6114* | KU 307493 | Juvenile | 40.6 | Isabela Province: Barangay Garita | 17.4136667°N, 121.82278333°E | PP923990 |
| CDS 2229* | KU 306055 | Juvenile | 42.5 | Kalinga Province: Barangay Poblacion | 17.34711°N, 121.17257°E | PP923986 |
| RMB 6115* | KU 307494 | Juvenile | 51.3 | Isabela Province: Barangay Garita | 17.4136667°N, 121.82278333°E | PP923991 |
| ACD 4559* | KU 327468 | Female | 54.2 | Bulacan Province: Biak-na-Bato National Park | 15.118879°N, 121.085081°E | PP924083 |
| RMB 13558* | KU 326034 | Male | 56.7 | Nueva Vizcaya Province: Barangay Maddiangat | 16.497°N, 121.209°E | PP924071 |
| RMB 13557* | KU 326033 | Female | 58.5 | Nueva Vizcaya Province: Barangay Maddiangat | 16.497°N, 121.209°E | PP924070 |
| RMB 13556* | KU 326032 | Male | 58.6 | Nueva Vizcaya Province: Barangay Maddiangat | 16.497°N, 121.209°E | PP924069 |
| RMB 4221* | PNM 7487 | Female | 62.5 | Cagayan Province: Municipality of Gattaran | 17.975207°N, 121.643398°E | PP924010 |
| RMB 4141* | PNM 7610 | Female | 64 | Rizal Province: Municipality of Tanay | 14.573962°N, 121.336956°E | PP924029 |
| RMB 4139* | PNM 7608 | Male | 65 | Rizal Province: Municipality of Tanay | 14.573962°N, 121.336956°E | PP924030 |
| RMB 13580* | KU 326043 | Female | 65.1 | Nueva Vizcaya Province: Barangay Paitan | 16.438°N, 121.225°E | PP924072 |
| ACD 4540* | KU 327467 | Female | 67.3 | Bulacan Province: Biak-na-Bato National Park | 15.118879°N, 121.085081°E | PP924082 |
| ACD 4539* | KU 327466 | Male | 74.4 | Bulacan Province: Biak-na-Bato National Park | 15.118879°N, 121.085081°E | PP924081 |
| RMB 4143* | PNM 7612 | Female | 74.6 | Rizal Province: Municipality of Tanay | 14.573962°N, 121.336956°E | PP924009 |
| RMB 4222* | PNM 7488 | Male | 74.8 | Cagayan Province: Municipality of Gattaran | 17.975207°N, 121.643398°E | PP924011 |
| RMB 13583* | KU 326045 | Male | 74.8 | Nueva Vizcaya Province: Barangay Paitan | 16.438°N, 121.225°E | PP924075 |
| **RMB 4206*** | **PNM 9871** | **Male** | **75.2** | **Cagayan Province: Callao Caves** | **17.707606°N, 121.8195°E** | **PP924008** |
| DSM 1708* | KU 329132 | Male | 84.6 | Bulacan Province: Bit-bit River | 14.8955333°N, 121.14233333°E | PP924095 |
| ACD 3387 | — | — | — | Cagayan Province: Municipality of Gattaran | 17.975207°N, 121.643398°E | PP923997 |
| ACD 3385 | — | — | — | Cagayan Province: Municipality of Gattaran | 17.975207°N, 121.643398°E | PP923995 |
| ACD 3386 | — | — | — | Cagayan Province: Municipality of Gattaran | 17.975207°N, 121.643398°E | PP923996 |
| ACD 9085 | — | — | — | — | — | PP924028 |

incorporated Köhler's (2012) standardized (numbered) color identities.

## RESULTS

***Molecular analyses.***—Our ML and BI analyses produced phylogenetic trees with identical interspecific topologies (Fig. 1; see ML and BI tree files, Supplemental Figures A and B; see Data Accessibility) which are consistent with published phylogenies of Philippine *Limnonectes* (Evans et al., 2003; Setiadi et al., 2011; Herr et al., 2021). Maximum likelihood and BI trees show high support for all species and all but one deeper node; both trees show *L. magnus* and *L. diuatus* as sister species but lack strong support for that relationship. Both analyses showed strong support for *Limnonectes cassiopeia*, new species, as reciprocally monophyletic to *L. macrocephalus (Limnonectes cassiopeia*, new species, monophyly 100 SH-LR, 100 UFBS, 1.0 PP; *Limnonectes cassiopeia*, new species + *L. macrocephalus* sister relationship 91.6 SH-LR, 98 UFBS, 0.99 PP; Fig. 1). Together, *Limnonectes cassiopeia*, new species, and *L. macrocephalus* are sister to *L. visayanus* (from the West Visayan PAIC) and are nested within a clade also containing *L. woodworthi*, *L. magnus*, and *L. diuatus* (clade E *sensu* Evans et al., 2003). Molecular clock analyses generated an estimated divergence time between *Limnonectes cassiopeia*, new species, and *Limnonectes macrocephalus* of 4.7 million years before present (Ma; 95% HPD 3.3–6.2 Ma; see time-calibrated BI phylogeny in Supplemental Figure B; see Data Accessibility).

***Analysis of morphological data.***—Our exploration of morphological data immediately suggested that *L. macrocephalus* and the new species differ in size, with the new species being the smaller of the two (Figs. 2, 3). The three largest individuals of the new species (all males) had snout–vent lengths of 84.6 mm, 75.2 mm, and 74.8 mm, while the three largest specimens of *L. macrocephalus* measured 137.8 mm (male), 121.3 mm (female), and 116.2 mm (male).

Our exploratory data plots also suggest a possible difference in the onset and/or rate of secondary sexual development in males. Male *Limnonectes* of many species develop large "blocky" (temporal regions characterized by hypertrophied adductor musculature) heads starting at sexual maturity. In both *L. macrocephalus* and the new species, we found that eye–tympanum distance provides a reliable proxy to quantify this change in head shape; juvenile and adult female eye–tympanum distances appear to increase linearly with snout–vent length, while adult male eye–tympanum distances also seem to increase linearly, but with a steeper slope (Fig. 2A, B). We confirmed this difference in slopes with separate analyses of covariance (ANCOVA) for *Limnonectes cassiopeia*, new species ($P = 0.002$), and *L. macrocephalus* ($P < 0.001$; Fig. 2A, B). We then used these data to calculate the approximate body size of each species at the onset of sexual maturity by assuming that head shape should begin to diverge between males and females at that time. We regressed eye–tympanum distance against snout–vent length separately for males and females (combined with juveniles) of each species separately and recorded the slopes of the regression lines and the point at which they intersect (dashed gray lines, Fig. 2A, B). We found that the male and female (plus juvenile) regression lines intersect at 60.8 mm SVL for *Limnonectes macrocephalus* and at 41.6 mm SVL for the new species. These values are only rudimentary estimates of size at sexual maturity, but they do suggest that the new species matures at a smaller body size than *L. macrocephalus*. This finding, combined with the smaller maximum snout–vent length of known specimens of the new species, reinforces the evidence that the two species do indeed vary by size. Additionally, *Limnonectes cassiopeia*, new species, appears to possess relatively smaller toe disks than *Limnonectes macrocephalus* (Fig. 2C).

Our principal component analysis identified major variation in multivariate morphospace between the new species and *Limnonectes macrocephalus*. For both males and females, the two species show no overlap on a plot of the first and second principal components (Fig. 4). The first and second principal components accounted for 91.6% of variation in males and 88.3% of variation in females. The first factor loadings for the first principal component in males and females were all positive and were loaded heaviest for head length, head width, thigh length, and tibia length (Table 2).

Univariate comparisons showed that nearly all of the 16 size-corrected characters and uncorrected SVL displayed statistically significant mean differences between *Limnonectes macrocephalus* and the new species (Fig. 3; Table 3). Only the size-corrected female tympanum diameter was not significantly different between the taxa (Table 3).

Our external specimen examinations identified two discrete characters that unambiguously distinguish *Limnonectes macrocephalus* from the new species, both of which relate to the terminal disks of the digits of the feet. All specimens of *Limnonectes macrocephalus* possess ventrally pigmented terminal toe disks, while all specimens of the new species possess bright, ventrally unpigmented toe disks (Figs. 5, 6, 7). Furthermore, the terminal discs of the toes of *Limnonectes macrocephalus* are distinctly expanded, whereas those of the new species are unexpanded or very slightly expanded (Figs. 5, 6, 7). We examined the holotype of *Limnonectes macrocephalus* (FMNH 40519; Fig. 8) and found that it possessed distinctly expanded, ventrally pigmented terminal toe discs and large body size (snout–vent length approximately 90–100 mm), ruling out the possibility that the name-bearing type could be conspecific with the new species described below.

***Conclusion and justification for the recognition of a new species.***—We identified multiple lines of intersecting, complementary evidence which lead us to conclude that the new species is not conspecific with *Limnonectes macrocephalus*. Further, given that the name-bearing type specimen (FMNH 40519) of Inger's (1954) *Rana macrodon macrocephala* possesses the large body size and traditional, discrete diagnostic character states of moderately expanded, darkly pigmented, terminal toe discs (vs. unpigmented, cream to white, unexpanded to minimally expanded terminal digital discs), we have no hesitation in assigning the name *Limnonectes macrocephalus* to the larger, widespread Luzon giant fanged frog and recognizing the newly discovered genetic lineage and phenotypically diagnosable form as a new species. Although we do not use arbitrary genetic

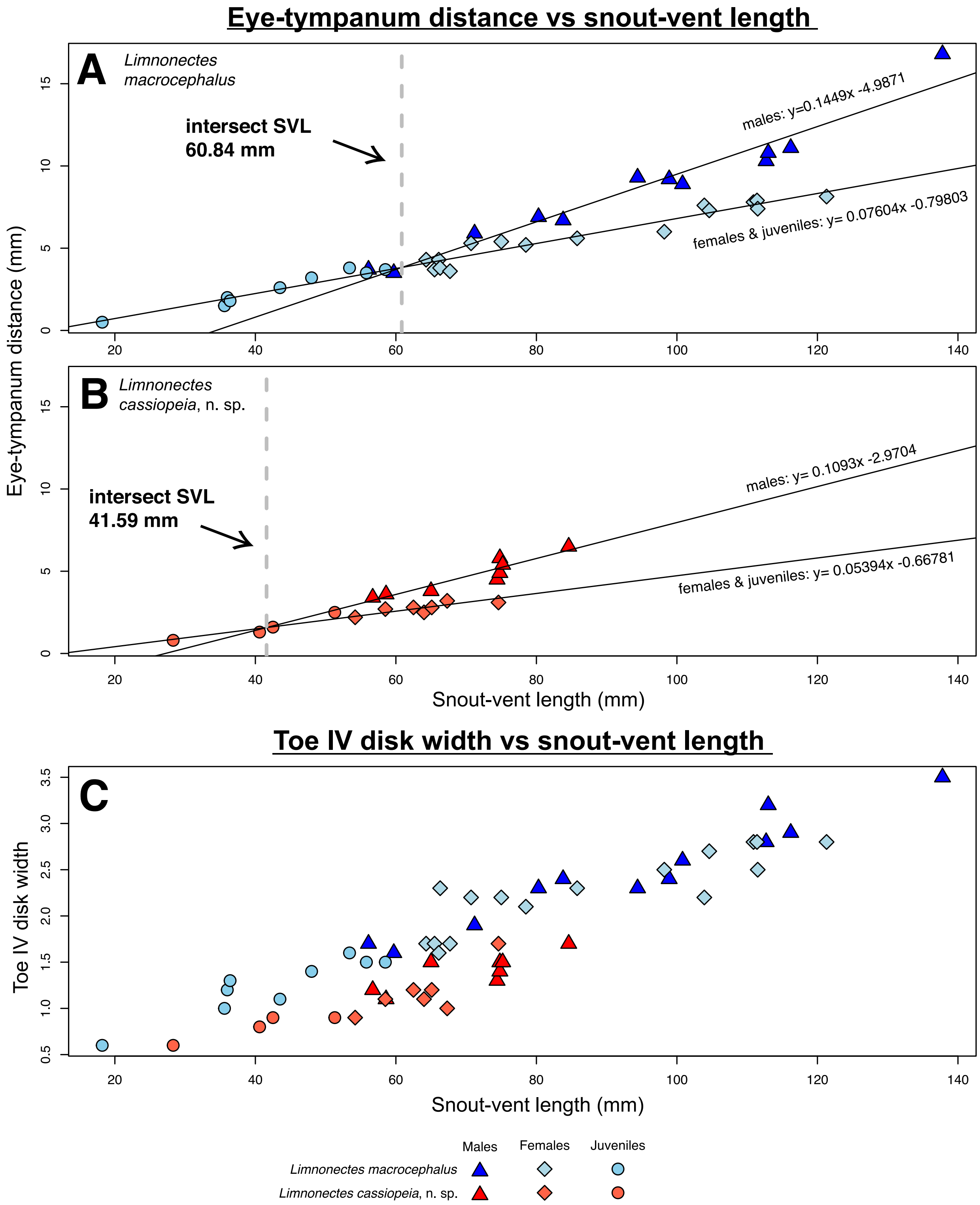

**Fig. 2.** Exploratory plots depicting uncorrected measurements plotted against SVL in specimens of *Limnonectes macrocephalus* (blue shades) and *Limnonectes cassiopeia*, new species (red shades). In all plots, adult males are represented by triangles, adult females by diamonds, and juveniles by circles. Eye–tympanum distance vs. snout–vent length is plotted separately for *L. macrocephalus* (A) and *Limnonectes cassiopeia*, new species (B). Solid black lines in panels A and B show the fitted regression lines for eye–tympanum distance vs. snout–vent length for males and combined females plus juveniles, while the vertical gray dashed line shows the snout–vent length intersect of two regression equations in each taxon. We confirmed that the apparent difference in slopes between sex classes was statistically significant with separate analyses of covariance (ANCOVA) for *Limnonectes cassiopeia*, new species ($P = 0.002$), and *L. macrocephalus* ($P < 0.001$). In *Limnonectes cassiopeia*, new species, the intersection point of the two regressions occurs at a substantially smaller snout–vent length (B: 41.6 mm) than in *L. macrocephalus* (A: 60.8 mm), which suggests that sexual dimorphism begins to emerge at a smaller size in *Limnonectes cassiopeia*, new species, than in *L. macrocephalus*. Panel C shows toe IV disk width vs. snout–vent length in *L. macrocephalus* and *Limnonectes cassiopeia*, new species, plotted together, suggesting that *Limnonectes cassiopeia*, new species, has relatively narrower toe disks than *L. macrocephalus*. All plots depict uncorrected measurements for eye–tympanum distance, toe IV disk width, and snout–vent length.

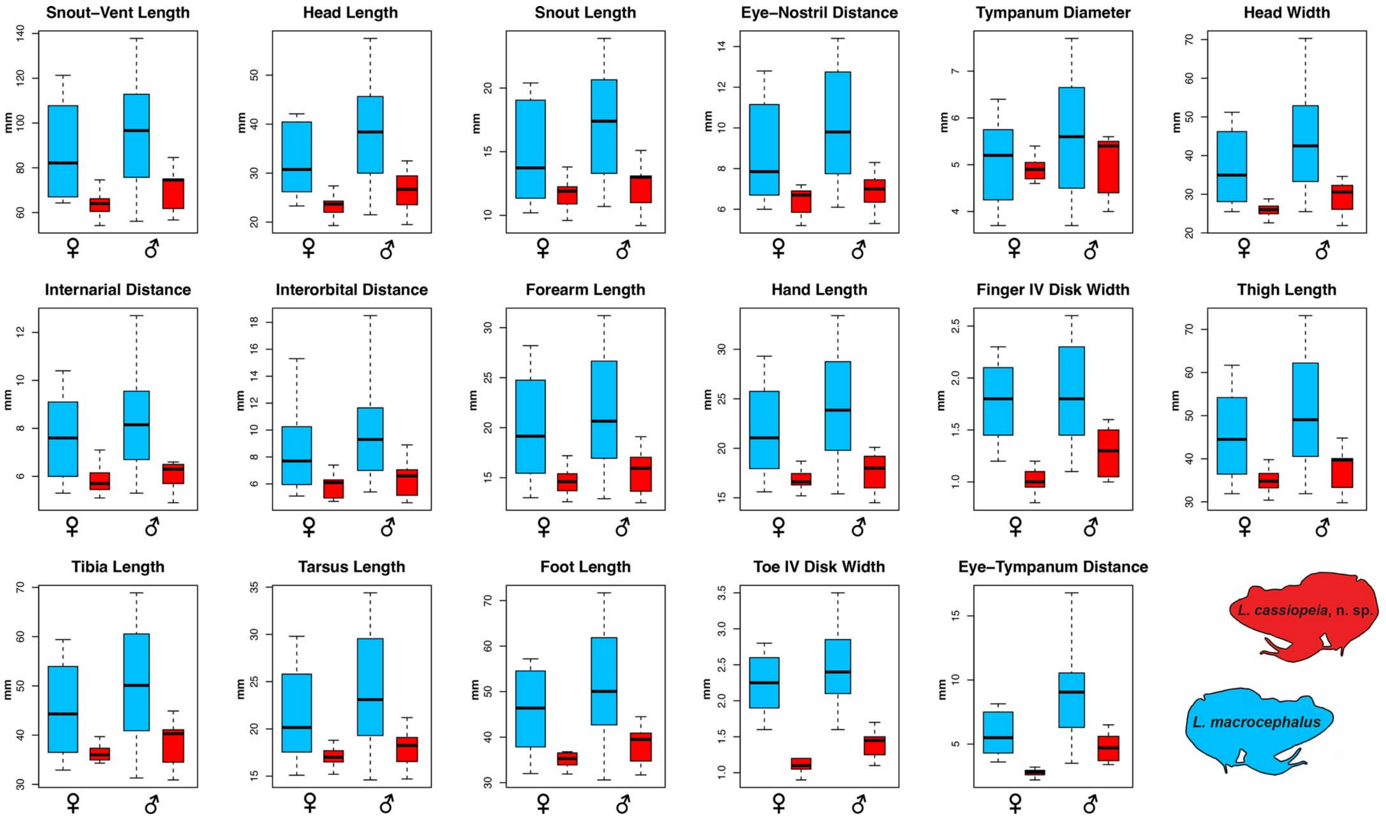

**Fig. 3.** Boxplot summary comparisons for the 17 continuous morphometric variables collected in this study. Each plot depicts morphological variation between *Limnonectes cassiopeia*, new species (red) and *L. macrocephalus* (blue) and between females (left) and males (right). Horizontal lines within boxes represent the median values, upper and lower bounds of boxs represent interquartile ranges, and whiskers represent the full range of measurements.

distances to diagnose the new species, our phylogenetic analyses identified two reciprocally monophyletic, strongly supported clades corresponding to the two species we characterize in this study.

Our time-calibrated BI phylogeny estimated a divergence between *L. macrocephalus* and the new species of approximately 4.7 million years before present (Ma; 95% highest posterior density [HPD] 3.3–6.2 Ma). Although the wide HPD time interval suggests use of caution in interpreting these temporal estimates, we note that this mean divergence date estimate is comparable or older than published estimates of three other, uncontroversially diagnosable and undoubtedly distinct sister species pairs (*L. diuatus*–*L. magnus*; *L. visayanus*–*L. macrocephalus*; and *L. acanthi*–*L. beloncioi*; Evans et al., 2003; Herr et al., 2021).

Our survey of 615 additional, non-genotyped specimens of *L. macrocephalus* from throughout Luzon, Polillo, and Catanduanes Islands, resulted in the identification of ten >additional individuals of the new species (Referred Specimens section); all others ($n = 605$; Material Examined) were unambiguously confirmed as true *L. macrocephalus* (see Diagnosis, below). Further, these ten additional specimens of *Limnonectes cassiopeia*, new species, were confirmed as having been collected from the same localities as our genotyped samples (holotype and paratypes sections, below). Thus, we are confident in our overall characterization, definition, and diagnosis of this geographically, morphologically, and genetically cohesive lineage—a new species of *Limnonectes*—which we describe below.

## *Limnonectes cassiopeia*, new species

urn:lsid:zoobank.org:act:B54414A3-B49F-4338-9911-C8BDFE6C2066
Cassiopeia Fanged Frog
Figures 5–7, 9

*Rana macrodon*: Boulenger 1882:24, in part; Boettger 1886:121, in part.
*Rana magna*: Stejneger 1910:437, in part; Boulenger 1920:45, in part; Taylor 1920:243; 1923:522, in part.
*Rana macrodon macrocephala*: Inger 1954:287, in part.
*Rana magna macrocephala*: Inger 1958:253–255, in part.
*Euphlyctis magna macrocephala*: Poynton and Broadley 1985:124, by implication; in part.
*Limnonectes macrocephalus*: Dubois 1987:63, in part.

***Holotype.***—PNM 9871 (Field Collector No. RMB 4206), adult male, Philippines, northern Luzon Island, Cagayan Province, Municipality of Peñablanca, boundary of Barangays Magdalo and Quibal, vicinity of Callao Caves Resort, 185 m above sea level, 17.70694°N, 121.81915°E, WGS84, Rafe M. Brown, Renato Fernandez, and Arvin C. Diesmos, 8 August 2002.

***Paratypes.***—KU 306055, juvenile of unspecified sex, Kalinga Province, Municipality of Lubuagan, Barangay Poblacion, Cameron Siler, Charles Linkem, and Kyle Hesed, 13 July 2006; KU 307493–307495, three juveniles of undetermined sex, Isabela Province, Municipality of Cabagan, Barangay Garita, Mitra Ranch, Kyle Hesed, Jason Fernandez, and Jose Edgar, 10 July 2006; KU 326032–326034, two adult males

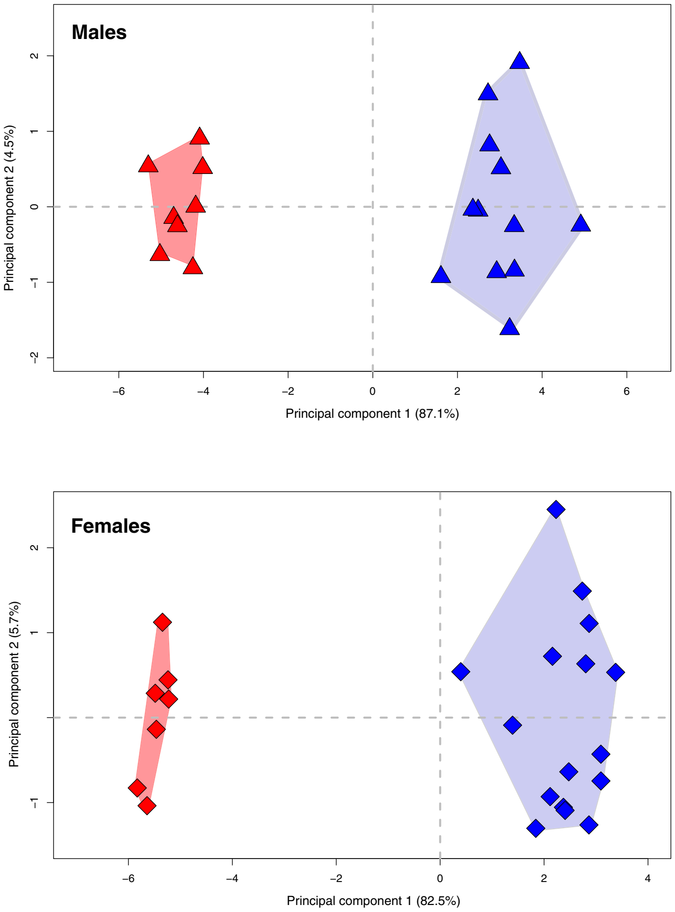

**Fig. 4.** Ordination of principal components one (x-axes) and two (y-axes) from principal component analysis (PCA) of morphometric measurements of *Limnonectes cassiopeia*, new species (red), and *L. macrocephalus* (blue). PCA analyses of males (top) and females (bottom) were conducted separately.

and one adult female, Nueva Vizcaya Province, Municipality of Quezon, vicinity of Barangay Maddiangat, Rafe Brown, Luke Welton, Anthony Barley, Allison Fuiten, and Viscente Yngente, 16 January 2010; KU 326043, 326045, one adult male and one adult female, Barangay Paitan, local MENRO tilapia farm approx. 4 km from barangay on Maddiangat Creek, Rafe Brown, Luke Welton, Anthony Barley, Allison Fuiten, and Viscente Yngente, 17 January 2010; KU 327466–327468, one adult male and two adult females, Municipality of San Miguel, Barangay Biak-na-Bato, Biak-na-Bato National Park, Jason Fernandez, 11 December 2008; KU 329132, adult male, Luzon Island, Bulacan Province, Municipality of Norzagaray, Bit-bit River, Angat Watershed, David McLeod, 29 May 2011; PNM 7487–7488, one adult male and one adult female, Cagayan Province, Municipality of Gattaran, Barangay Nissiping on sandy bank of river, Rafe Brown, Renato Fernandez, and Arvin Diesmos, 10 August 2002; PNM 7608, 7610, 7612, one adult male and two adult females, Rizal Province, Municipality of Tanay, Barangay Sampaloc, Arvin and Mae Diesmos, 24 July 2002.

***Referred specimens.***—Luzon Island, Bulacan Province, Municipality of Norzagaray, Angat Watershed, vicinity of AWAT office: KU 335182–83; Isabela Province, Municipality of Cabagan, Barangay Garita, Mitra Ranch: KU 307502; Nueva Vizcaya Province, Municipality of Quezon, Barangay Maddiangat around barangay proper: KU 326036–39, 326041; Rizal Province, Municipality of Tanay, Barangay Plaza Aldea, Daranak Falls Rest Area: PNM 7625 (Field Collector No. RMB 4156); Rizal Province, Municipality of Tanay, Barangay Sampaloc: PNM 7613 (Field Collector No. RMB 4144).

***Diagnosis and comparisons.***—*Limnonectes cassiopeia* is a medium-sized fanged frog, assigned to the genus *Limnonectes* (family Dicroglossidae) on the basis of well-documented combination of character states shared by most members of *Limnonectes*: prominent, sexually dimorphic odontoid processes of the mandible (“fangs”) present; nuptial pads absent; interphalangeal webbing complete, extending to unexpanded or slightly expanded terminal toe discs; dermal flap along outer edge of the metatarsal and fifth toe present; narrow dermal fringe along either side of the 2nd and 3rd finger present; elongate inner metatarsal tubercle present; outer metatarsal tubercle absent; circummarginal finger and toe disc grooves absent; sexual size dimorphism present, reversed (largest males larger than females); internal, paired, and widely separated subgular vocal sacs present and ovoid vocal sac openings visible in the posterolateral corners of the buccal cavity (Inger, 1954, 1966; Emerson and Berrigan, 1993).

The new species can be distinguished from all other Philippine species of *Limnonectes* (*L. acanthi*, *L. beloncioi*, *L. diuatus*, *L. leytensis*, *L. magnus*, *L. macrocephalus*, *L. micrixalus*, *L. palavanensis*, *L. parvus*, *L. visayanus*, and *L. woodworthi*) by combinations of body size, fang (mandibular odontoid process) length, snout and head shape proportions (particularly eye–tympanum distance relative to eye–nostril distance), relative lengths of the first and second finger, degree of dorsal skin rugosity (dermal torso tuberculation), presence of white-tipped dermal asperities restricted to the posterior quarter of the dorsum (sacral region), absence of dorsolateral torso ridges or folds, presence of supratympanic fold (from posterior corner of eye to insertion of forelimb), and complete interdigital webbing of the foot (extending to terminal discs). Below, we provide morphological comparisons, based in part on characters first identified by Stejneger (1910), Taylor (1923), Inger (1954), and Brown and Alcala (1977), and augmented with our own data (Siler et al., 2009; Abraham et al., 2021; Herr et al., 2021) plus new information presented here.

The new species is morphologically most similar to its broadly sympatric (in interior central and southern Luzon) close relative, *L. macrocephalus*, with which it has been confused until now. However, it can be readily distinguished from this species by the unpigmented, cream to bright white ventral surfaces of its unexpanded terminal toe discs (vs. gray pigmented ventral surfaces of the moderately expanded terminal discs), subarticular tubercles of the foot, and ventral surfaces of terminal discs of its inner three fingers (Figs. 5–8). It also differs from *L. macrocephalus* by a suite of statistically significantly differences in body dimensions, related to its generally smaller body size: the largest males available in our samples of 29 specimens from nine sites do not exceed 90 mm (vs. male body size of *L. macrocephalus* up to of 135–145 mm; Table 3; Fig. 2; Herr et al., 2021).

*Limnonectes cassiopeia* differs from large adult male specimens of *L. magnus* by its smaller adult body size (SVL range 54.2–84.6 vs. 66.3–164.4 mm in *L. magnus*), and by the

**Table 2.** Loadings of 17 allometry-adjusted morphometric characters for the first (PC1) and second (PC2) principal components for males and females of *Limnonectes cassiopeia*, new species, and *Limnonectes macrocephalus*.

| | Adult males | | Adult females | |
|---|---|---|---|---|
| | PC1 | PC2 | PC1 | PC2 |
| Summary statistics | | | | |
| Standard deviation | 3.8482 | 0.8699 | 3.7444 | 0.9988 |
| Proportion of variance | 0.8711 | 0.0445 | 0.8248 | 0.0587 |
| Cumulative proportion | 0.8711 | 0.9156 | 0.8248 | 0.8834 |
| Eigenvalue | 14.808 | 0.7568 | 14.0208 | 0.9975 |
| Characters | | | | |
| Snout–vent length | 0.1347 | –0.9494 | 0.1578 | –0.0119 |
| Head length | 0.2567 | 0.0283 | 0.2608 | –0.0537 |
| Snout length | 0.2551 | 0.0308 | 0.2577 | –0.0923 |
| Eye–nostril distance | 0.2546 | 0.0272 | 0.2483 | 0.0381 |
| Tympanum diameter | 0.1779 | 0.282 | 0.0952 | 0.9271 |
| Head width | 0.256 | 0.0155 | 0.2656 | –0.0136 |
| Internarial distance | 0.2471 | 0.0897 | 0.2397 | 0.138 |
| Interorbital distance | 0.2462 | –0.0269 | 0.2269 | 0.1999 |
| Forearm length | 0.252 | –0.0064 | 0.2526 | –0.0816 |
| Hand length | 0.2547 | 0.0071 | 0.2503 | –0.11 |
| Finger IV disk width | 0.228 | 0.0724 | 0.2511 | –0.1799 |
| Thigh length | 0.2566 | 0.0295 | 0.2638 | –0.0125 |
| Tibia length | 0.2565 | 0.0186 | 0.2636 | 0.0153 |
| Tarsus length | 0.2554 | 0.0154 | 0.2539 | 0.0375 |
| Foot length | 0.2543 | –0.0078 | 0.2569 | –0.1047 |
| Toe IV disk width | 0.2532 | 0.0267 | 0.254 | –0.0574 |
| Eye–tympanum distance | 0.2475 | –0.0065 | 0.2587 | –0.0324 |

much greater extent of reverse sexual size dimorphism (males larger than females) in *L. magnus*, which also has pigmented, dark gray ventral terminal discs, and subarticular tubercles beneath the hands and feet (vs. unpigmented, cream to white toe discs, subarticular tubercles, and inner three finger discs in *L. cassiopeia*). From *L. visayanus*, *L. cassiopeia* differs from its somewhat smaller body size (54.2–84.6 vs. 73.9–94.2 mm) and unpigmented, cream to white toe discs, subarticular tubercles, and inner three finger discs (vs. pigmented, dark gray ventral terminal discs, and subarticular tubercles beneath the hands and feet). Unlike *L. macrocephalus*, *L. magnus*, and *L. cassiopeia*, *L. visayanus* also lacks dark spotting or other pigmentation on ventral surfaces of tibial and tarsal segments of the hind limb (Inger, 1954).

*Limnonectes cassiopeia* is readily distinguished from *L. woodworthi* by its moderately rugose middorsal skin (vs. skin of middorsum smooth in *L. woodworthi*), by its possesion (vs. absence) of white-tipped sacral asperities, by the absence (vs. presence) of continuous dorsolateral folds, and absence of dark lateral head pigmentation (vs. dark "mask" present, to varying degrees, along snout, in loreal region, subocular and postocular region, and eye–tympanic and temporal region below supratympanic fold).

From *L. diuatus*, the new species differs by its Finger I > Finger II relative finger lengths (vs. approximately equivalent length), by possession of white-tipped asperities limited to sacral region and thighs (vs. asperities distributed on most dorsal and lateral body surfaces), and by the absence (vs. presence) of dark ventral upper hindlimb pigmentation (Siler et al., 2009; Abraham et al., 2021).

From *L. acanthi* and *L. beloncioi*, the new species differs by its dorsoposterior edge of its tympanum hidden beneath an overlapping supratympanic dermal fold (vs. tympanum fully exposed in *L. acanthi* and *L. beloncioi*), the presence (vs. absence) of reverse sexual size dimorphism (males larger), and by the unpigmented, cream to bright white ventral surfaces of its unexpanded terminal toe discs (vs. gray pigmented ventral surfaces of moderately expanded terminal discs in *L. acanthi* and *L. beloncioi*).

From *L. leytensis*, the new species can be distinguished by its larger adult body size (SVL range 54.2–84.6 vs. 25.8.2–34.0 mm in *L. leytensis*), Finger I > Finger II (equivalent in *L. leytensis*), complete webbing (webbing incomplete/reduced in *L. leytensis*), and its snout rounded (vs. snout moderately pointed in lateral aspect in *L. leytensis*).

Finally, from the miniature Philippine *Limnonectes* "guardian frogs" *L. parvus*, *L. micrixalus*, and *L. palavanensis*, the new species can be distinguished by its larger adult body size (SVL 54.2–84.6 vs. 24.2–35.5 mm in *L. parvus*; 28.1–30.2 in *L. micrixalus*; 30.0–37.6 in *L. palavanensis*), rugose (vs. smooth) dorsal skin, Finger I > Finger II (vs. equivalent), the absence (vs. presence) of dorsolateral folds (faint, or at times discontinuous in *L. parvus* and *L. palavanensis*; thick and continuous in *L. micrixalus*), and webbing complete (vs. reduced); the new species is additionally distinguished from these species by the absence of unreversed sexual size dimorphism (vs. unreversed sexual size dimorphism present; females larger in *L. parvus*, *L. micrixalus*, and *L. palavanensis*).

***Description of holotype.***—A mature male with SVL of 75.2 mm, specimen in good condition, ventral abdomen dissected for gonadal inspection and small portion of liver removed and preserved separately for genetic material; habitus robust; head broader than body, head length 89.8% of

**Table 3.** Summary of univariate statistical comparisons between *Limnonectes cassiopeia*, new species, and *Limnonectes macrocephalus.* Measurements are given by mean ± standard deviation followed by range in parentheses. All measurements presented here are uncorrected values, although statistical tests were conducted on allometry-corrected measurements (see methods). Bold values indicate statistically significant mean differences (alpha level = 0.05; see methods). Following the *P*-value, a * indicates results derived from Welch's T-test and a *** indicates results derived from Mann-Whitney U test. All other results derived from two sample independent T-tests. Only sexually mature, genetically confirmed, positively identified specimens included.

| | Adult males | | | Adult females | | |
|---|---|---|---|---|---|---|
| Characters (mm) | *L. macrocephalus* ($n = 12$) | *L. cassiopeia*, new species ($n = 8$) | *P* | *L. macrocephalus* ($n = 16$) | *L. cassiopeia*, new species ($n = 7$) | *P* |
| Snout–vent length | 93.7±24.5 (56.1–137.8) | 70.5±9.5 (56.7–84.6) | **0.02495** | 87.6±20.6 (64.3–121.3) | 63.7±6.5 (54.2–74.6) | **0.00295*****  |
| Head length | 37.8±10.8 (21.5–57.5) | 26.4±4.2 (19.5–32.5) | <**0.001** | 32.3±7.4 (23.3–42.1) | 23.3±2.6 (19.3–27.4) | <**0.001*** |
| Snout length | 17.1±4.4 (10.7–23.9) | 12.3±1.8 (9.2–15.1) | <**0.001** | 15.1±4 (10.2–20.4) | 11.7±1.4 (9.6–13.8) | <**0.001*** |
| Eye–nostril distance | 10.1±2.9 (6.1–14.4) | 6.9±0.9 (5.3–8.3) | <**0.001** | 8.9±2.5 (6–12.8) | 6.4±0.8 (5.2–7.2) | <**0.001** |
| Tympanum diameter | 5.6±1.4 (3.7–7.7) | 5±0.7 (4–5.6) | **0.004661** | 5.2±1.1 (3.7–8.1) | 4.8±0.4 (4.1–5.4) | 0.112 |
| Head width | 42.9±13.2 (25.5–70.3) | 29.3±4.3 (21.9–34.6) | <**0.001** | 37±9.2 (25.5–51.2) | 25.9±2 (22.6–28.8) | <**0.001** |
| Internarial distance | 8.4±2.2 (5.3–12.7) | 6.2±0.9 (4.9–7.9) | <**0.001** | 7.6±1.7 (5.3–10.4) | 5.9±0.7 (5.1–7.1) | <**0.001** |
| Interorbital distance | 9.7±3.7 (5.4–18.5) | 6.4±1.4 (4.6–8.9) | <**0.001***** | 8.3±2.8 (5.1–15.3) | 5.8±1 (4.7–7.4) | <**0.001** |
| Forearm length | 21.6±5.9 (12.9–31.2) | 15.6±2.2 (12.5–19.1) | <**0.001** | 19.9±5.1 (13–28.2) | 14.7±1.6 (12.6–17.2) | <**0.001** |
| Hand length | 24.1±5.7 (15.4–33.4) | 17.6±2 (14.5–20.1) | <**0.001** | 21.9±4.5 (15.6–29.3) | 16.9±1.2 (15.2–18.7) | <**0.001*** |
| Finger IV disk width | 1.8±0.5 (1.1–2.6) | 1.3±0.2 (1–1.6) | <**0.001** | 1.8±0.4 (1.2–2.3) | 1±0.1 (0.8–1.2) | <**0.001***** |
| Thigh length | 50.4±13.5 (31.9–73.2) | 37.6±4.9 (29.8–44.8) | <**0.001*** | 46±9.9 (31.9–61.7) | 35±3.1 (30.4–39.8) | <**0.001*** |
| Tibia length | 50±12.5 (31.3–68.9) | 38.5±4.7 (30.9–44.9) | <**0.001** | 45.6±9.5 (32.9–59.4) | 35.9±2.7 (31.3–39.7) | <**0.001** |
| Tarsus length | 24±6.3 (14.6–34.4) | 18±2 (14.7–21.2) | <**0.001** | 21.6±4.8 (15.1–29.8) | 17.1±1.2 (15.2–18.8) | <**0.001** |
| Foot length | 50.7±12.7 (30.6–71.7) | 38.3±4.2 (31.7–44.5) | <**0.001** | 46.2±9.1 (32–57.2) | 35.7±3.1 (31.9–41.6) | <**0.001** |
| Toe IV disk width | 2.5±0.6 (1.6–3.5) | 1.4±0.2 (1.1–1.7) | <**0.001** | 2.3±0.4 (1.6–2.8) | 1.2±0.3 (0.9–1.7) | <**0.001** |
| Eye–tympanum distance | 8.6±3.6 (3.5–16.8) | 4.7±1.1 (3.4–6.5) | <**0.001** | 5.8±1.6 (3.6–8.14) | 2.8±0.3 (2.2–3.2) | <**0.001** |

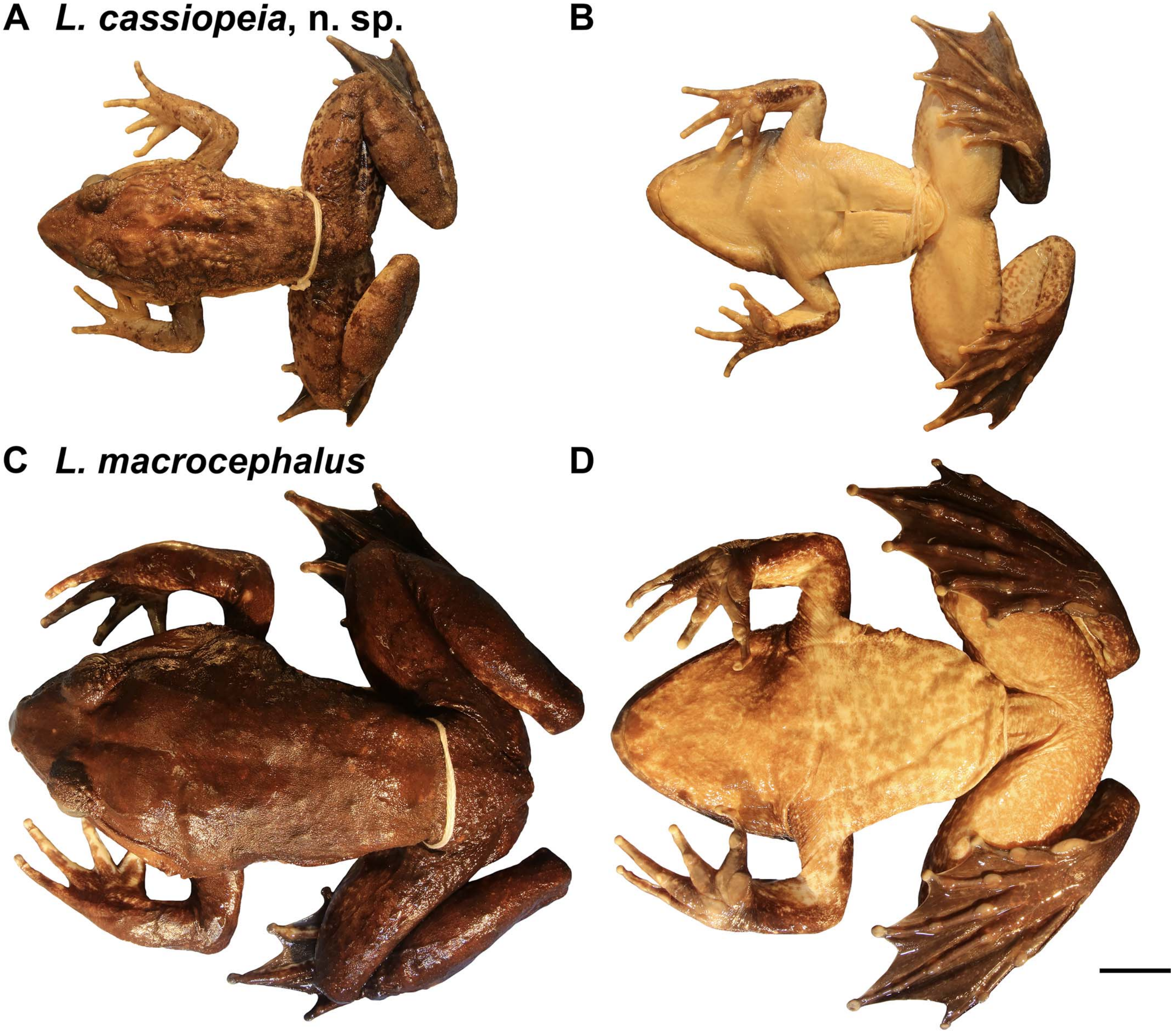

**Fig. 5.** Dorsal (left) and ventral (right) comparison of adult male *Limnonectes cassiopeia*, new species, holotype (PNM 9871; A, B) and adult male *L. macrocephalus* (KU 345550; C, D). Scale bar = 20 mm.

its width and 39.8% of SVL; snout tip nearly rounded, slightly protruding, slanting posteroventrally (Fig. 2); supralabial region moderately swollen, increasingly protuberant towards angle of jaw; interorbital region and dorsal rostrum nearly flat; eye diameter 8.7 mm, 66.1% snout length, 1.3X eye–nares distance, 1.6X eye–tympanum distance; pupil horizontally sub-elliptical, discontinuous posterior margin; canthus rostralis distinct, nearly straight; loreal region concave; nostrils oriented dorsolaterally; internarial region flat; tympanum exposed, its annulus slightly distinct, diameter 63.2% of eye diameter; supratympanic fold protuberant, rugose, extending from posterior corner of eye, overlapping and concealing dorsal margin of tympanic annulus, curving at obtuse angle to supra-axillary region, where it is discontinuous with post-rictal tubercle. Tongue subovoid, tapered anteriorly at attachment and laterally expanded, at free, moderately notched, bilobed posterior margin (anterior edge when tongue projected); choanae situated at anterolateral edge of palate, subcircular, their anterolateral edge partially concealed in ventral view by palatal shelf of maxilla; choanae widely separated by distance four times greater than diameter of single choana, each located just anterolaterally to (by distance half the diameter of single choana) lateral tip of dentigerous process of vomer; dentigerous processes of vomers distinct, with three (left) to four (right) conical teeth on each; dentigerous process angled anterolaterally (rostrally), approximately at 45° orientation, with closest (posterior) points separated by distance approximately equal to one choana, their most distant (anterior) ends separated by distance equal to three choanae; odontoid "fangs" large, recurved, unsheathed for entirety of their length, situated on either side of mandibular symphysis, total length 1.5 mm when measured at natural inclination (dorsoposteriorly), their tips sharply pointed, tips 0.9 mm perpendicular from dorsal, fleshy mandible surface, 5.0 mm apart; maxillary fang "sockets" anteromedial to choanae, large, round, slightly smaller

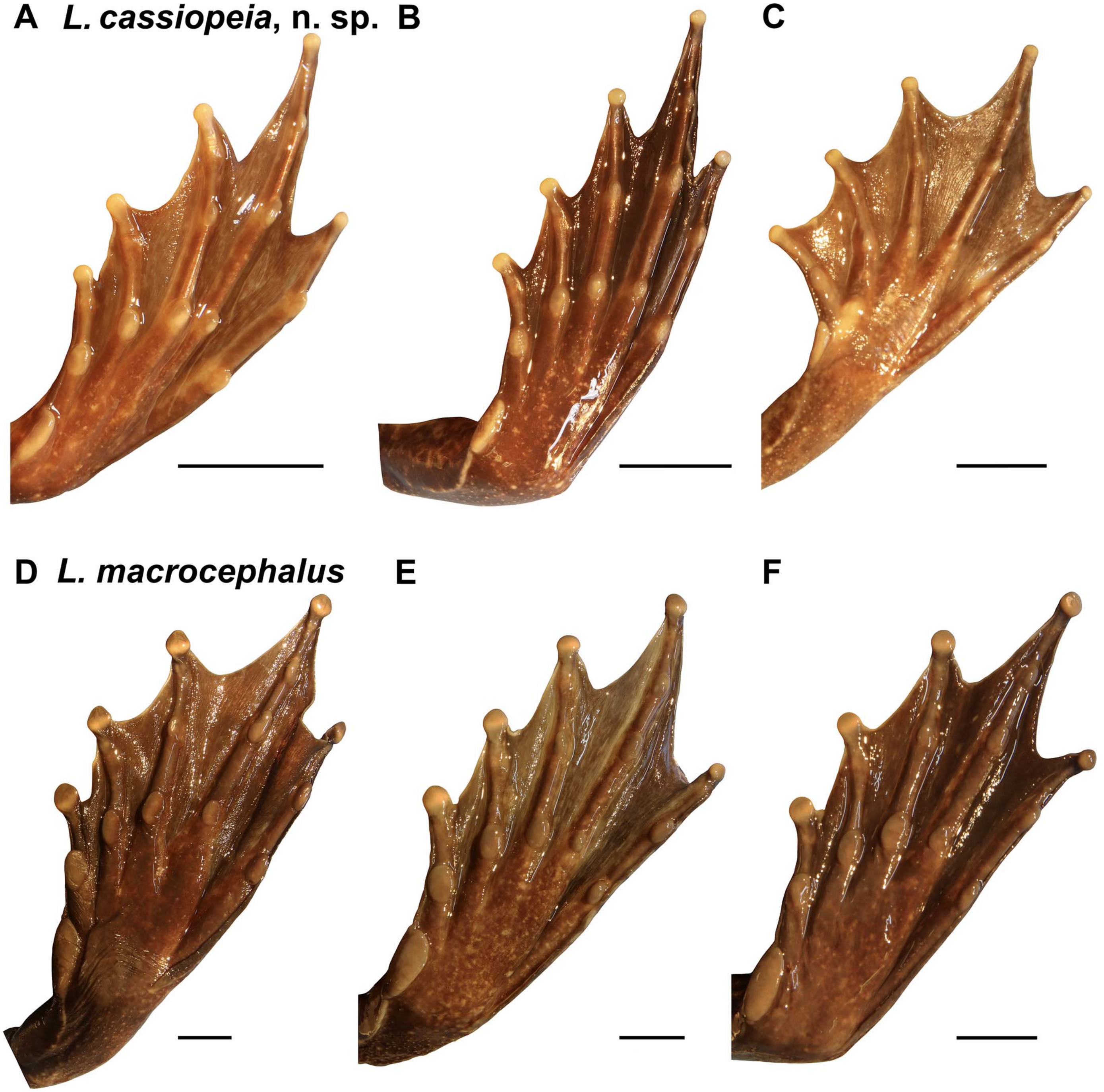

**Fig. 6.** Comparisons of plantar view of the left foot of *Limnonectes cassiopeia*, new species (top row), and *L. macrocephalus* (bottom row) showing differences in toe disk pigmentation between the two species. *Limnonectes cassiopeia*, new species, depicted are: PNM 7610 (A), KU 327466 (B), and PNM 7612 (C). *Limnonectes macrocephalus* depicted are KU 306058 (D), KU 326359 (E), and KU 326358 (F). Scale bars = 10 mm.

than choanae; vocal apertures large, elongate, surrounded by extensive mucosal invaginations, situated at posteroventral margin of floor of buccal cavity, just medial to angle of jaw.

Manus length 45.5% pes length; pes 98.5% tibia length; tibia length 54.5% SVL; Fingers II and III laterally ovoid in cross section, due to presence of slight lateral dermal flange, extending from base of each digit, on either side, to proximal margins of terminal finger discs; terminal discs not expanded beyond widths of penultimate phalanges (Fig. 7), their relative descending lengths: III > I > II = IV; circummarginal finger disc grooves absent; subarticular tubercles evident, low and rounded, their ventral surfaces not sharply pointed or protuberant; Fingers I and II each with one subarticular tubercle, Fingers III and IV each with two subarticular tuvercles; terminal discs and subarticular tubercles with cream, velvety, thickened surfaces; distal margins of tubercle not distinctly raised relative to proximal margins; supernumerary tubercles absent, but articular surfaces of fingers between subarticular tubercles and at base of all digits covered with thickened tubercular swelling; palmar surface with large thenar tubercular swelling beneath Finger I; enlarged, flattened, subcircular "inner" metacarpal tubercle

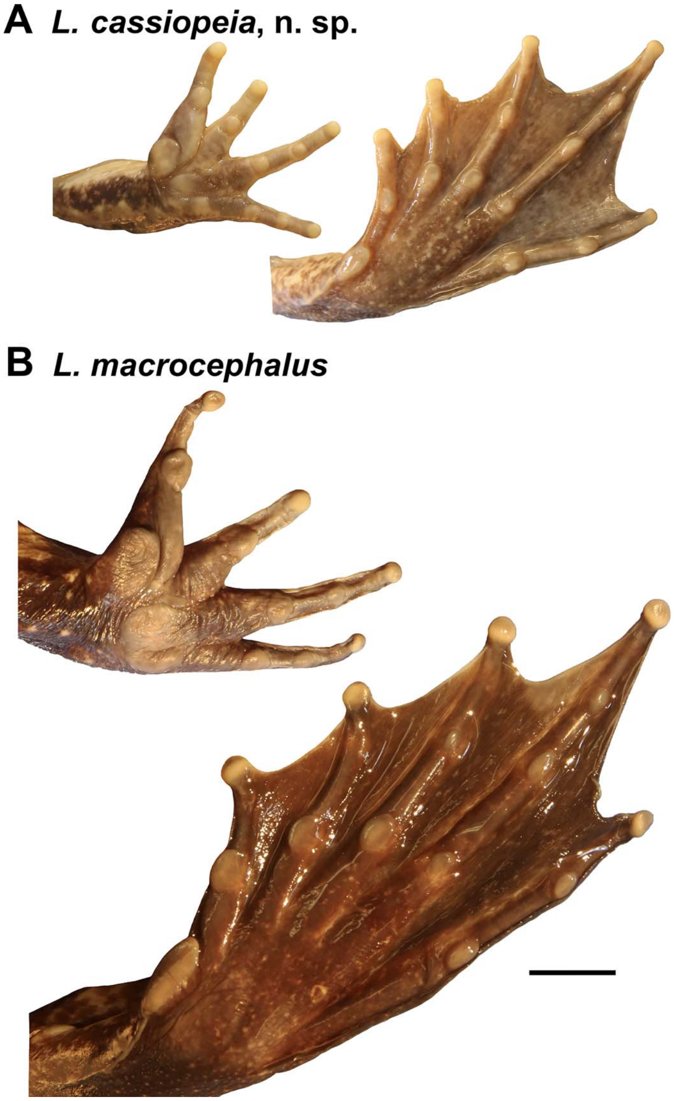

**Fig. 7.** Comparison of palmar view of the left hand (left) and plantar view of the left foot (right) of adult male *Limnonectes cassiopeia*, new species, holotype (PNM 9871; A) and adult male *L. macrocephalus* (KU 345550; B). Scale bar = 10 mm.

at base of Finger I, and small, flat, circular, outer (base of Finger IV) metacarpal tubercle; inner three times diameter of outer metacarpal tubercle, separated by small medial tubercular swelling; surface of palmar structures and intervening surrounding surfaces all covered with similar, thickened, velvety dermis layer; nuptial pads absent; interphalangeal webbing absent; forearm musculature not hypertrophied.

Terminal discs of toes unexpanded to very slightly expanded; circummarginal grooves absent; plantar surfaces of foot smooth, with distinct, velvety-textured, slightly protruding, rounded subarticular tubercles (Figs. 6, 7); descending relative lengths of toes: IV > III > V > II > I; toes fully webbed (interdigital webbing extending to proximal margins of terminal discs of all toes); postaxial flap of skin running along entire outer edge of Toe V; inner metatarsal tubercle prominent, elongate, continuous with dermal ridge extending one-third distal length of tarsus; outer metatarsal tubercle absent.

Skin of head, dorsum, and trunk smooth to slightly shagreened; skin of lateral body surfaces (flanks) rugose, with skin densely wrinkled between irregularly distributed fleshy dermal tubercles; tubercles convex to conical, round to ovoid or slightly elongate, intermittently weakly keratinized; similar fleshy dermal tubercles also present in supraocular (dorsal surfaces of palpebra), supratympanic, and post-tympanic regions; mid-dorsum bearing singly distributed, low, rounded dermal tubercles; white-tipped dermal asperities, distributed evenly, not in clusters, present on dorsum, from just anterior (10 mm) to sacrum, continuously distributed to vent; asperities also present on dorsal surfaces of legs, from insertion of femur to tarsus; dorsal, lateral, and ventral surfaces of limbs smooth to slightly shagreened, with occasional low tubercles; cloacal region rugose, with smooth laterally and ventrally surrounding skin.

***Coloration of holotype in preservative.***—Dominant dorsal color on head, body, and hindlimbs ground cinnamon (color 270; Köhler, 2012) with lighter, irregular, diffuse, drab-gray (256) patches concentrated on dorsal surfaces of trunk and posterior head; lateral head surfaces light buff (2) with diffuse drab-gray (256) markings; canthal bar and pigmentation associated with supratympanic ridge sepia (279); three mottled olive-gray (265) labial bars alternate with lighter, light buff (2) labial region coloration; diffuse light drab (269) color bar spanning interorbital region; tympanum mottled smoke gray (267) with smoky white (261) central spot; dorsal surfaces of hindlimbs clay (18) color to robin rufous (29), with dark drab (45) diffuse transverse crossbars; posterior flash surfaces of femoral and tibial segments of hindlimbs with large, bold, mottled natal brown (49) blotches on smoky white (261) background; dorsal surface of outer (Finger III–IV) manus and toes light buff (2) to cinnamon drab (50) with diffuse olive-gray (265) crossbars; inner dorsal surfaces of manus (Fingers I–II) pale buff (1); infralabial region, ventral body and proximal limb segment surfaces light buff (2) to pale pinkish buff (3), approaching cream (12) on upper ventral thigh surfaces; lateral surface of sacral region with densely mottled natal brown (49) blotches on smoky white (261) background; ventral surfaces of manus and pes smoke gray (266) to grayish horn (268), approaching ground cinnamon (270) on the distal portions of the pes, with post-brachial surfaces of forearms and ventral tarsal (shank) surfaces brown (277); ventral surfaces of inner metatarsal tubercle and subarticular tubercles of pes smoke gray (266); ventral surfaces of subarticular tubercles of manus and terminal discs of fingers and toes uniform pale horn (11). Coloration in life unrecorded.

***Measurements of holotype (in mm).***—Snout–vent length 75.2, head length 29.9, snout length 13.2, eye–nostril distance 7.0, tympanum diameter 5.5, eye–tympanum distance 5.4, head width 33.3, internarial distance 6.6, interorbital distance 6.8, forearm length 15.4, hand length 18.4, Finger IV disc width 1.6, thigh length 40.0, tibia length 41.0, tarsus length 19.0, foot length 40.4, Toe IV disc width 1.5.

***Variation.***—Summaries of univariate morphological variation in the type series are presented in Table 3. Overall ground color and pattern variation in the new species is remarkably uniform. No sexually dimorphic color variation was evident in the type series and referred specimens. Some specimens (e.g., KU 327466; Fig. 9B) have slightly darker dorsal pigmentation, whereas others (PNM 9871; Fig. 5A, B; KU 329132; Fig. 9D) are somewhat lighter, but all specimens possess dark markings on dorsal surfaces, transverse

**Fig. 8.** Holotype specimen of *Limnonectes macrocephalus* (FMNH 40519; adult male) showing dorsal (A) and ventral (C) views of the body, the plantar view of the left foot (B), and the palmar view of the left hand (D). Scale bars = 20 mm (A, C) and 10 mm (B, D).

hindlimb bars, forearm blotches, and a black interorbital bar. Ventral body surfaces are generally pale cream to more yellowish in the inguinal region and on the posterior surfaces of the thighs (PNM 9871, KU 326033, 327467, 327468, 329132); in these specimens, ventral labial markings, faint gular and sternal spots, are diffuse (KU 326032, 326043). In others, dark ventral pigmentation congregates into a more densely spotted throat and sternal region, or to a more uniform dusty brown in these same areas (KU 326045, 327466); in two specimens, ventral

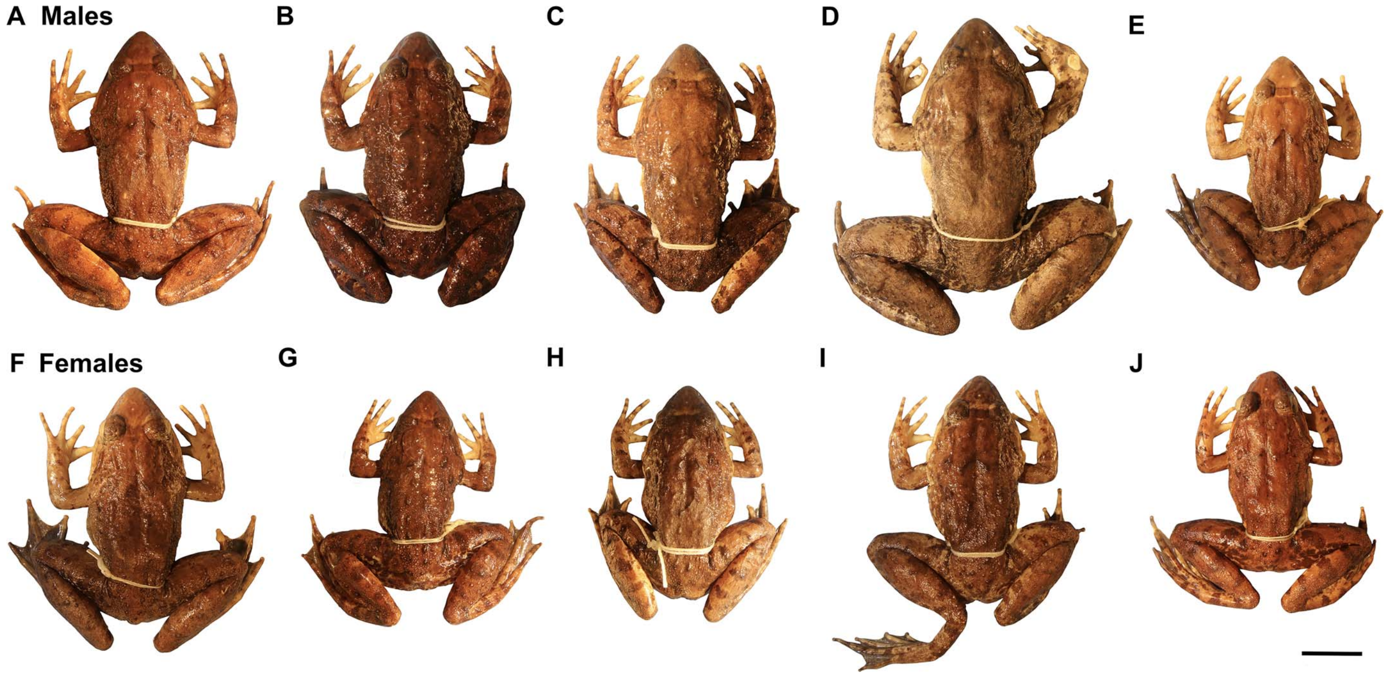

**Fig. 9.** Dorsal variation among adult male (top row) and adult female (bottom row) paratypes of *Limnonectes cassiopeia*, new species. Specimens depicted are PNM 7488 (A), KU 327466 (B), KU 326045 (C), KU 329132 (D), PNM 7608 (E), PNM 7612 (F), PNM 7487 (G), KU 326043 (H), KU 327467 (I), and PNM 7610 (J). Scale bar = 20 mm.

labial bars are particularly bold and distinct (KU 326043, 326045).

***Distribution.***—Currently *Limnonectes cassiopeia* is known from nine localities distributed around the interior foothills of the Cagayan River Valley of central and northern Luzon, and in the foothills of the southern Sierra Madre Mountain range (Fig. 1). At all these locations, it co-occurs with *L. macrocephalus*, and at locations in the southern Sierra Madre it is also sympatric with *L. woodworthi* (Taylor, 1923, 1928; Diesmos et al., 2015). Confined to the interior eastern foothills of the Cordillera (apparently absent on the western, coastal slopes; Brown et al., 1996, 2012b; Diesmos et al., 2004; Devan-Song and Brown, 2012) and the interior western foothills of the Sierra Madre (apparently absent on the eastern, coastal slopes; Brown et al., 2000b, 2013b; Siler et al., 2011; Fig. 1), the entirely interior Luzon geographical range of the new species is unique among Philippine amphibians (RMB, pers. obs.; Alcala, 1986; Duellman, 1993; Alcala and Brown, 1998; Brown, 2007; Diesmos and Brown, 2011; Diesmos et al., 2015; AmphibiaWeb, 2022; IUCN, 2022).

***Etymology.***—We derive the specific epithet, used as a modern simple noun in apposition in the nominative case, from the name collectively given to the five stars of the constellation Cassiopeia—used in reference to the species' five bright, ventrally unpigmented, cream to white toe disks (the principal diagnostic character state difference distinguishing it from *Limnonectes macrocephalus*). In the Philippines, the constellation Cassiopeia is most visible in clear night skies over central and northern Luzon in an area encompassing the known distribution of the new species. Suggested common name: Cassiopeia Fanged Frog.

***Ecology and natural history.***—To date, all specimens of *Limnonectes cassiopeia* have been misidentified by field collectors, identified as—and collected amidst—series of *L. macrocephalus*. The fact that nearly all 29 confirmed specimens have been collected in groups, with *L. macrocephalus* immediately preceding or following the order of individual specimen observation or capture, suggests to us that the new species lives intimately associated with *L. macrocephalus*. Field notes by RMB and field colleagues identify no unique circumstances of collection or structural microhabitat differences, and so we assume the new species is not only sympatric with *L. macrocephalus* throughout the interior of Luzon Island, but also intimately syntopic with its much more locally abundant sister species. We are unaware of any sites at which the new species occurs exclusively (with *L. macrocephalus* locally absent). Due to the new species having been overlooked by collectors, we have no specific observations regarding its behavior or natural history. A single tantalizing clue may be present in field notes which mention "frogs that sounded like *woodworthi* but looked like female *macrocephalus*" (R. Brown field catalogue, July 2002) at a locality and on a night when several specimens of the new species were collected. Circumstantial as it may be, this two-decade-old anecdote should not be dismissed out of hand, considering the recent acoustically based description of a new species of *Limnonectes* from nearby Mindoro island (Herr et al., 2021).

Other potentially sympatric species of amphibians (in similar habitats, at the same elevations but different latitudes, and also in the immediate vicinity of the nine localities of *L. cassiopeia*, but in very different habitats at higher elevations) of Luzon Island include *Platymantis* (subgenus *Platymantis*) *corrugatus*, *P.* (*Lupacolus*) *cagayanensis*, *P.* (*L.*) *dorsalis*, *P.* (*L.*) *indeprensus*, *P.* (*L.*) *mimulus*, *P.* (*L.*) *naomii*, *P.* (*Tahanapuno*) *luzonensis*, *P.* (*Lahatnanguri*) *biak*, *P.* (*L.*) *cornutus*, *P.* (*L.*) *pygmaeus*, *P.* (*L.*) *banahao*, *P.* (*Tirahanulap*) *polillensis*, *P.* (*T.*) *sierramadrensis* (Ceratobatrachidae), *Limnonectes woodworthi*, *Fejervarya moodiei*, *F. vittigera*, *Occidozyga laevis* (Dicroglossidae), *Kaloula conjuncta*, *K. kalingensis*, *K. picta*, and *K. rigida* (Microhylidae), *Hylarana similis*, *Sanguirana luzonensis*, *S. igorota*, and *S. aurantipuntata* (Ranidae), and *Polypedates leucomystax*, *Philautus surdus*, *Rhacophorus pardalis*, *R. bimaculatus*, and *Kurixalus appendiculatus* (Rhacophoridae). Co-occurring, introduced, and invasive frog species include *Rhinella marina* (Bufonidae), *Kaloula pulchra* (Microhylidae), *Hylarana erythraea* (Ranidae), *Hoplobatrachus rugulosus* (Dicroglossidae), and *Eleutherodactylus planirostris* (Eleutherodactylidae; Diesmos et al., 2015). The new species occupies a known (vouchered) elevational range between 60 m and 1430 m ASL.

## DISCUSSION

On most of the separate Philippine geological (island bank) platforms or PAICs (Pleistocene Aggregate Island Complexes; Brown and Diesmos, 2002, 2009; Brown et al., 2002, 2013), Fanged Frogs of the genus *Limnonectes* co-occur in curious general categories of species' ecological attributes, habitat types, and distributions that may inform us about how multiple frog taxa may coexist and presumably alleviate interspecific competition for habitat, food, and other resources (Stebbins and Cohen, 1995; Wells, 2007; Araújo et al., 2009; Costa-Pereira et al., 2018). First, a large-bodied species may co-occur with a small-bodied species (e.g., *L. acanthi* and *L. palavanensis* on Palawan; *L. visayanus* and *L. leytensis* throughout the islands of the West Visayan PAIC, and the Romblon Island Group) and differ further in reproductive mode or microhabitat type. In the first example (fanged frogs of the Palawan PAIC), *L. acanthi* is a large-bodied river- and stream-breeding generalist, abundant in the immediate vicinity of these riparian habitats, whereas *L. palavanensis* is a small-bodied, terrestrial forest floor-breeding form, with male parental care and larval transport; Inger et al., 1986; Inger and Voris, 1988; Goyes Vallejos et al., 2019). In the second case (fanged frogs codistributed throughout the numerous islands of the West Visayan PAIC and Romblon Island Group; Diesmos et al., 2015), *L. visayanus* is the large-bodied generalist common in rivers and streams, but *L. leytensis* is a smaller species, typically breeding in the vicinity of swamps (Alcala and Brown, 1988; Gaulke, 2011). On the Mindanao PAIC landmasses (Basilan, Bohol, Leyte, Mindanao, and Samar Islands), five fanged frog species are present, but they co-occur in subsets of two or three species, partitioning geography and environmental resources differently. Pairs of large and small species occur together on Bohol, Leyte, and Samar (*L. magnus* and *L. leytensis*), but on Mindanao, where extensive topological relief, expansive mountain ranges, and the highest mountains in the country are found, an additional, large-bodied, high-elevation species occurs (*L. diuatus*), seemingly replacing the large-bodied form *L. magnus*, found throughout low-elevation riparian habitats (Brown and Alcala, 1977; Siler et al., 2009; Abraham et al., 2021). *Limnonectes leytensis* is widely distributed on Mindanao as well, inhabiting low-elevation swamps, but in many dry forests from low- to mid-elevation, a second small-bodied species, *L. parvus*, is present. Closely related to *L. palavanensis* (Evans et al., 2003; Setiadi et al., 2011), *L. parvus* is another terrestrial, forest floor-breeding form, with male parental care and larval transport (Lama and Senarillos, 2023; RMB, pers. obs.); on Basilan Island and the tip of Mindanao's extreme western Zamboanga Peninsula, *L. parvus* is replaced by its ecological equivalent sister species *L. micrixalus* (Taylor, 1920; Brown et al., unpubl. data). Overall, these patterns of distribution suggest that species pairs with differing body sizes (possibly associated with divergent dietary requirements), microhabitats, and reproductive patterns can coexist on small to moderately sized islands and those of limited habitat variation or environmental heterogeneity (islands without high elevation forests), but that additional species may be accommodated by geographical divergence (the *L. parvus*–*L. micrixalus* case) or elevational stratification (*L. diuatus* vs. *L. magnus*). And, of course, on islands that are smaller, or lack substantial habitat heterogeneity, species may exist alone (*L. leytensis* on the Sulu PAIC, *L. beloncioi* on Mindoro; Herr et al., 2021).

With the recognition of *Limnonectes cassiopeia*, an additional piece of the Philippine fanged frog distribution puzzle falls into place. Until two decades ago, biologists' general perception was that two species existed on the Luzon PAIC: the widespread *L. macrocephalus* and the more range-restricted species *L. woodworthi*, documented only from the Bicol Faunal Region (the Bicol Peninsula of southern Luzon and the adjacent, smaller, land-bridge islands of Polillo and Catanduanes) and the immediately adjacent southern portion of mainland Luzon, just north of the Tayabas Isthmus, and including portions of Laguna and Quezon provinces (Taylor, 1920, 1922, 1923; Brown and Alcala, 1970; Alcala and Brown, 1998; Evans et al., 2003; Devan-Song and Brown, 2012). However, with increased frequency and geographic scope of field-based faunal survey work, it became clear that *L. woodworthi* was present at localities farther west (Zambales Mountains; Brown et al., 1996; Devan-Song and Brown, 2012) and northward (Brown et al., 2000b; Siler et al., 2011), possibly as far as the mid-Sierra Filter Zone (an arid, low elevation valley, situated over a geological fault, and which bisects and interrupts the otherwise continuous south-to-north continuity of the Sierra Madre Mountain Range; Yumul et al., 2003, 2009; Welton et al., 2010)—but that it was infrequently detected (uncommonly collected). When *L. woodworthi* was encountered, only a few individuals have been reported, suggesting reduced local abundance (Brown et al., 1996, 2000b; Siler et al., 2011; Devan-Song and Brown, 2012). Today, and with the benefit of a much more comprehensive survey-and-resurvey field-based biodiversity inventory effort (Brown et al., 2013a) and the accumulation of specimen-associated data in biodiversity repositories (Brown et al., 2000b, 2012b, 2013b; Oliveros et al., 2011; Siler et al., 2011; Devan-Song and Brown, 2012), *L. woodworthi* has been documented at a few additional localities along the eastern foothills of the Sierra Madre, as far north as Luzon's northern coast, Palaui Island, and Camiguin Norte Island (Oliveros et al., 2011; Brown et al., 2012b, 2013b). Yet a puzzling question remained: why is *L. woodworthi* so clearly absent from the interior of central inland Luzon (the broad Cagayan valley, and all central low-elevation habitats between the parallel Cordillera and Sierra Madre mountain ranges)? The discovery of an overlooked fanged frog in broad sympatry (and possibly, intimate syntopy) with the giant species *L. macrocephalus*—in precisely this same interior Luzon region—seems to be the answer. As a final point, we note that *L. cassiopeia* and *L. woodworthi* are both medium-sized species that attain approximately the same maximal body size (and, as a result, might compete for resources such as food), whereas *L. macrocephalus* attains a much larger maximum size—which may allow for reduction of interspecific competition (between *L. macrocephalus* and either *L. cassiopeia* or *L. woodworthi*) in the different parts of its range which are shared with either of the two smaller species.

At present, the task of identifying potential conservation threats to the new species would be plagued by guesswork and the same absence of validated information that has prevented the recognition of this species until now. Nevertheless, we know that large-bodied fanged frogs represent an important source of protein for the diets of many indigenous Philippine human communities (Jenks, 1904; Willcox, 1912; Cole, 1922; Nance, 1975; Kikuchi, 1984; Schult, 1991; Stuart et al., 2008; Diesmos and Brown, 2011; Scheffers et al., 2012; Diesmos et al., 2014; IUCN, 2022), and overharvesting has been identified as a potential threat to other Philippine fanged frog species (Diesmos and Brown, 2011; Diesmos et al., 2014, 2015; Gonzalez et al., 2018; IUCN, 2022). Depending on the intensity of the local human population's consumption of *L. cassiopeia* at particular locations, hunting for sustenance or sport may be a threat to the new species. However, without any actual data—except for its general geographic distribution and the fact that it apparently continues to coexist sympatrically with *L. macrocephalus* and *L. woodworthi* (and in heavily disturbed, well-developed, lowland habitats surrounded by dense human habitation)—we find that the new species does not qualify for any biologically meaningful, or concrete, threat-derived conservation status (IUCN, 2022), nor arbitrary, social, or politically associated threat "category" (Gonzalez et al., 2018), and so we propose to designate it "Least Concern" (LC; *sensu* IUCN, 2022), with the caveat that "Data Deficient" (DD) might be more appropriate, given how little we know about the natural history of the new species. Characterizing other axes of differentiation (e.g., larval biology, ecological characteristics, reproductive season phenology, acoustic mate-recognition signal variation) that have facilitated its coexistence in such apparent close sympatry with *L. macrocephalus* is a major priority for a more nuanced future understanding and appreciation of the natural history of *L. cassiopeia*.

## MATERIAL EXAMINED

Institutional abbreviations follow Sabaj (2020, 2022).

*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: PNM 6694, 7607, TNHC 59903; Palawan Island, Palawan Province: FMNH 51185–96, 51199–51220, 51222–40; Municipality of Puerto Princesa, Mt. Bloomfield: PNM 6280, 6295, 6301; Barangay Lamod, sitios Kayasan & Tagabinet: PNM 6375–77, 6390–94, 6409–10, 6431–33, 6440–43; Municipality of Iwahig, WNW of Iwahig Town, Malatgaw River: CAS-SU 21432–34, 21437, 21439–41, 21444–49, 21465; Tugbuni Creek, ca 10 km S Iwahig: CAS-SU 21496–501; ca. 8 km S. of Iwahig: CAS-SU 21525–26; Malatgaw River tributary, ca. 5 km W. of Iwahig: CAS-SU 21502–08; 9 km SW of Iwahig: CAS-SU 21520–24; ca. 9 km SSW of Iwahig: CAS-SU 21509–17, 21519, 21527–41; Malatgaw River tributary, ca. 1.5 km SSW of Iwahig: CAS-SU 21453–60; Malabosog Creek, 95.5 km NE of Puerto Princesa: CAS 157215–16, 158100–04, 158131–33; W of coast road, 96.5 km NE of Puerto Princesa: CAS 158136–40; Pelotan Creek, 94 km NE of Puerto Princesa: CAS 158144–48; Langogan River tributary, 1.5 km upstream from mouth, 85 km NE Puerto Princesa: CAS 158151–53; Puerto Princesa District, Municipality of Iwahig, Iwahig Penal Colony, Sitio Balsahan: USNM 229492–93; Municipality of Narra, Taritien Barrio, Estrella Falls: USNM 287281–83, 287342–45; Municipality of Quezon, National Museum compound: USNM 287370–73; Municipality of Brooke's Point, Barangay Macagua: USNM 158204–09; 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: CAS 62577 (holotype), FMNH 51205–17, 51219–20, 51222–40, KU 79043, 79045, 79059–60; Siñgai: CAS-SU 5986–6003, 6026–29, 6038–40, 14710–13, MCZ A-14067–69 (paratypes); Coron Island, Palawan Province: CAS 158154–77, CAS-SU 5943–45, 5954, 13965–67; Wayan Creek, 1–3 km N of San Nicolas: CAS 62133–35, 62562 (paratypes); 6 km NE San Nicolas: KU 79041–60; Culion Island, Palawan Province: CAS-SU 3284, FMNH 51241–79; 6.5 km SW Culion Town: KU 79061–68.

*Limnonectes beloncioi* (type series): Philippines: Mindoro Island, Oriental Mindoro Province: Municipality of Bongabong, Barangay Carmundo, Sitio Paypay-Ama, Paypay-Ama River: KU 302084–89, 303369–78 (paratopotypes), PNM 9870 (holotype); Barangay Formon: 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, 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, 303345; Municipality of Magsaysay, Barangay Nicolas, Sitio Banban: KU 303404–30, 304131–32; Municipality of Sablayan, Barangay Batong Buhay, Sitio Batulai, Mt. Siburan: KU 303430–52, 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 508558–72; Municipality of Tarogin, ca. 30 km S of Calapan Town, Mt. Halcon SE slope: CAS-SU 22145–50, 22576–77, 23485, 23487, 23489, 23496–99, 23501–02, 23505, 23508, 23512–15, 23519–20, 23522, 23525; Municipality of Tarogin, Mt. Halcon: CAS-SU 22240, 22288–95, 23500, 23510–11, 23517–18, 23521; E side of Mt. Halcon, SE slope of Barawanan Peak, 830 m: CAS-SU 22151; Semirara Island, Oriental Mindoro Province: Municipality of Caluya, Barangay Tinogboc: KU 302105–07; non-type specimens: Mindoro Island, Oriental Mindoro Province: Municipality of Baco, Mt. Baco, Alangsa River: USNM 508534–57; Occidental Mindoro Province: Municipality of Paluan, Barangay Harrison, Sitio Ulasan, local name "Mat-ingaram": 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: CAS 133430–32, 133434, 139389–93, FMNH 197934, MCZ A-88036 (paratypes), 133500 (holotype); Municipality of Remedios T. Romualdez, Mt. Hilong-hilong, Barangay San Antonio, 1130 m, local area name "May Impit": KU 333325, 333369–75, 333381–89, 333392–93; Davao Del Norte Province: Municipality of Monkayo, Simulaw River Drainage, Mt. Pasian: CMNH 5572–73 (paratypes of *Limnonectes ferneri*), PNM 9506 (holotype of *L. ferneri*);

*Limnonectes leytensis*: Philippines: Mindanao Island, "Mindanao": FMNH 14868 (batch of 16 specimens), MCZ A-14137–41 (+11 duplicates); "Zamboanga Province": FMNH 63200; "Zamboanga" MCZ A-10480; Zamboanga Del Norte Province: Katipunan: CAS-SU 13960; 1 km S of Gumay, 7 km SE Buena Suerte, Dapitan River: CAS 147303; "Cotobato Province": 50060–131; "Takayan, near Saub, Cotobato Coast" (=S. Cotobato and/or Sulturan Kudarat Provinces): MCZ A-23198–99, 14134–36; Davao City Province: Municipality of Kalinan, Barangay Malagos, Malagos Eagle Station: TNHC 61940–41; Lanao Del Norte Province: Municipality of Kolambugan, Marata Bogan: CAS-SU 6060; Lanao del Sur Province: Municipality of Marawi, "Viscar Landing, Lake Lanao": MCZ A-25755; Misamis Occidental Province: Municipality of Misamis: CAS-SU 13956; Misamis Oriental Province: Municipality of Cartegena Bo, Plaridel: CAS-SU 16910–12; Leyte Island, Leyte Province: FMNH 42855–84, 54121–22, 60789–91; Leyte City: CAS-SU 15483; Calabian: MCZ A-14099; Camiguin SUR Island, Camiguin Province: Mambajao: CAS-SU 23088–91; Negros Island, Negros Oriental Province: Dumaguete City: KU 306006, 306008–09, 306011–12, 306014, 306016–18; "Philippines": FMNH 99212–24; "Negros Island": FMNH 61524–29; Municipality of Dumaguete City, Barangay Valinad: MCZ A-45654, 45660–61; Samar Island, “Samar Isl.”: 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-14125–33; Basilan Province, Port Holland: CAS 60377–78, MCZ A-14103–10; Mt. Abung-abung, “NE of Maluso”: MCZ A-22741–42; Jolo Island, FMNH 40538–39; Jolo Isl., Sulu Archipelago: MCZ A-10481; Bohol Island, Bohol Province: Municipality of Sierra Bullones, ca. 13 km SE Sierra Bullones Town, Cantaub; CAS-SU 23243, 23246–47, 23252, 23258, 23274, 23280, 23283, 23293, 23330–01; Municipality of Sierra Bullones, 10 km SE of Sierra Bullones Town, Dusita: CAS 131950–51, CAS-SU 23140–42, 23144, 23241, 23251, 23265, 23272, 23284, 23287, 23291, 23299, 23307, 23317, 23326–30, 23331–35; Dinagat Island, Dinagat Province: MCZ A-14100–02, 14270; Tawi-tawi Island, Sulu Archipelago: MCZ A-10479, 14111–19, 14271–72.

*Limnonectes macrocephalus*: Philippines: Catanduanes Island, Catanduanes Province: Municipality of Bato, Barangay Buenavista: KU 308047; Municipality of San Miguel, Sulong: KU 308060, 308064, 308083–87; Luzon Island, “Luzon”: KU 4488; Albay Province: Municipality of Malinao, Barangay Sugcad, Sitio Kumagingking, “Sugcad Plaza”: KU 328662–64; Municipality of Tabaco, Barangay Comon: KU 306050–51, 306162; Municipality of Tiwi, Barangay Banhaw, Sitio Purok 7, Mt. Malinao: KU 326357; Aurora Province: Municipality of Maria Aurora, Barangay Villa Aurora, Aurora Memorial National Park, “Siete” area, Mt. Dayap: KU 321929–52; Sitio Dimani, Aurora Memorial National Park: KU 321923–28, 323420; Municipality of San Luis, Barangay Lipimental, “waterfall site”: KU 322364–87; Barangay Real, Sitio Minoli, limestone forest: KU 322388–92; Bulacan Province: Municipality of Dona Remedios Trinidad, Barangay Kabayunan, Sitio Langud, Langud River, Angat Watershed: KU 329133–88; Municipality of Norzagaray, Angat Watershed; AWAT office: KU 329127, 329451, 335184–85, 335193, 335196–206, 335210; Barangay San Lorenzo, Angat Dam: KU 327465, 328647–58; Barangay San Lorenzo, Sitio Langud, Angat Watershed: KU 328659–61, 328896–928; Bit-bit River, Angat Watershed: KU 329128–31; Cagayan Province: Municipality of Gonzaga, Barangay Magrafil, Site 1, Mt. Cagua: KU 330425–54; Site 2, Mt. Cagua: KU 330455–69; Camarines Norte Province: Municipality of Labo, Barangay Tulay Na Lupa: KU 313634–36; Barangay Tulay Na Lupa, Mt. Labo camp 1: KU 313621–33, 313644; Camarines Sur Province: Municipality of Caramoan, Barangay Hanopol, Hanopol River (Dam vicinity): KU 350138–53; Municipality of Naga City, Barangay Panicuasan, edge of Isarog National Park, Mt. Isarog: KU 326356; Municipality of Naga City: KU 306047–49, 306056–57; Municipality of Presentacion, Barangay Bantugan, Halabang Bukid: KU 350154; Barangay Lidong: KU 350162; Barangay Lidong: lower slopes of Saddle Peak Mountain Range, above Tariktik River drainage, local area name = “Palalihun”: KU 350180–81; Tariktik River drainage, at the base of Saddle Peak Mountain Range: KU 350155–61, 350163–79; Barangay Maangas: KU 306052; Ilocos Norte Province: Municipality of Adams, Barangay Adams, Site 1, Mt. Pao: KU 330136–60; Site 2, Mt. Pao: KU 330161–63; Site 3, Mt. Pao: KU 330164–67; Isabela Province: Municipality of Cabagan, Barangay Garita, Mitra Ranch: KU 307498–99, 307501, 307503; Municipality of San Mariano, Barangay Dibuluan, Sitio Apaya, Apaya Creek area: KU 327509–17; Kalinga Province: Municipality of Lubuagan, Barangay Poblacion: KU 306053–54, 306059, 306061; Laguna Province: “Purok 9, Adelina Peak Resort Area”: KU 333907–08; Municipality of Los Banos, Barangay Batong Malake, UPLB Forestry Campus: KU 327463; UPLB Forestry campus: KU 327469–70; Municipality of Paete, Barangay Saray, University of the Philippines Laguna Land Grant: KU 345543, 345565–72; Municipality of Siniloan, Barangay Magsaysay, University of the Philippines Quezon Land Grant, Lalawinan River Drainage: KU 345557–64, 345631; Barangay Maunlad, University of the Philippines Quezon Land Grant, Lalawinan River Drainage: KU 345544–50; Nueva Ecija Province: Aurora Memorial National Park “tower site”: KU 321922; Nueva Vizcaya Province: Municipality of Quezon, Barangay Maddiangat, in and around barangay proper: KU 326032, 326035, 326040, 326042; Mount Palali: KU 308642, 308656–60, 308663, 308689, 308703–04, 308767–68, 308770–72, 308802; Sitio Dayog: KU 308837–46, 308855–57, 308862–64, 308929; Sitio Parola: KU 325978–99, 326048, 326054; Sitio Upper Dayog: KU 325952, 326001–31; Barangay Paitan, local MENRO’s tilapia farm approx. 4 km from barangay on Maddiangat Creek: KU 326044, 326046; Quezon Province: Tayabas City, Barangay Kamaisa: KU 306058, 306142; “Sitio Kipagringau”: KU 333909–24; Municipality of Infanta, Barangay Magsaysay, Infanta-Marikina Highway, Southern Sierra Madre Mountain Range: KU 275829–67; Municipality of Real, Barangay Maunlad, University of the Philippines Quezon Land Grant: KU 345573–76; Sitio New Baguio, Jarrels Peak Area: KU 333925–35; Sorsogon Province: Municipality of Bulusan, Barangay Salvacion: KU 346391–404, 346445; Barangay San Francisco, Bayugin Falls: KU 346446–49; Municipality of Irosin, Barangay Cawayan, Mt. Cawayan: KU 345552, 347923–24; Tayabas Province: Sampaloc: FMNH 40519 (holotype); Polillo Island, Quezon Province: “Polillo”: KU 303480–81; Municipality of Burdeos, Barangay Aluyon, Sitio Malinao: KU 326358–59; “Burdeos”: KU 331719; Municipality of Polillo, Barangay Pinaglubayan: KU 307504–05.

*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 24056–57, 24059, 24078, 24119–20, 24122–24; Nasawa Crater, Mt. Hibok-hibok: CAS-SU 22862; 4.5 km S of Mambajao Town, Catibawasan Falls: CAS-SU 22856; Barrio Naasag, Sitio Vulcan: CAS-SU 23095–96; Dinagat Island: Suriago del Norte Province: Municipality of Loreto: KU 306003, 306062–63, 306068–70; Samar Island: Eastern Samar Province: Municipality of Taft: KU 306028–30, 306033, 306036, 306041–42, 306077, 306082–84, 309272–74; Western Samar Province: Municipality of Paranat, Barangay San Isidro, Sitio Nasarang: TNHC 54947–50; Municipality of Tarabucan, Matuquinao: CAS-SU 18174–79, 18182–83, 18188–90, 18192, 18194–95, 18198; Sequinan: CAS 11235; Mindanao Island: Bukidnon Province: Mt. Kitanglad: FMNH 258974; Municipality of Malaybalay, Kalasungay: CAS-SU 16799, 16800; Davao City Province: Mt. Apo: MCZ A-2597 (paratype); Municipality of Gumay, W side of Dapitan Peak, 6 km SE of Buena Suerte: CAS 19981; Municipality of Calinan, Barangay Malagos, Baguio District, Eagle Foundation Malagos Eagle camp: TNHC 59904–05, 59941; Davao Del Sur Province: Municipality of Toril, Barangay Baracatan (“Upper Baracatan”), Sitio San Roque: TNHC 59906, 59942; Misamis Occidental Province: Mt. Malindang: CAS-SU 13968; Zamboanga City Province: Municipality of Zamboanga City, Barangay Pasonanca: CAS 61870–71; Agusan Del Norte Province: W side of Mt. Hilong-hilong: CAS

133792, 133554, CAS-SU 133673–74; Municipality of Cabadbaran, S side of Mt. Hilong-hilong Peak, crossing of Tagibo and Dalaydayan rivers: CAS-SU 186128; Zamboanga Del Norte Province: Municipality of Katipunan, Labao: CAS-SU 16804; Bohol Island: Bohol Province: Municipality of Carmen, Chocolate Hills Complex, Barangay Buena Vista: TNHC 56397–402; Municipality of Sierra Bullones, 11 mi SE Sierra Bullones Town: CAS 23415, 23417, 23420; Sandayong Barrio: CAS 17170–211; Cantub Barrio: CAS 17135–37; Cantub, 15 km SE Sierra Bullones Town: CAS-SU 23429–30; 11 mi SE Sierra Bullones, Dusita: MCZ A-23167–70, "Bohol Island": CAS 23416, 23418–19, 23424; Leyte Island, Leyte Province: Municipality of Calabian: MCZ A-14152 (paratype of *Rana magna visayanus* Inger 1954); Basilan Island, Basilan Province: Basilan Isl.: MCZ A-14152–54, 14267.

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

*Limnonectes palavanensis*: Philippines: Palawan Island: Palawan Province: Municipality of Brooke's Point: Barangay Mainit: KU 309133–36, 309138; S slope of Thumb Peak, 330–660 m, WNW of Iwahig: CAS 14744, 20432–34, 20438, 20445–47, 20449, 20451, CAS-SU 20421–26, 20448; 7–8 km SW of Santiago: CAS 20466–71; Municipality of Iwahig, Thumb Peak, Iwahig Penal Colony: MCZ A-14214–16.

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

*Limnonectes visayanus*: Philippines: Masbate Island: Masbate Province: Municipality of Mobo: CAS-SU 144253–59, KU 302171; Mt. Mobo, Tugbo watershed: CAS 144345, CAS-SU 14482–84, 144260–61, 144327; Panay Island: Antique Province: Municipality of Culasi: KU 302157–59, 302161, 302165; Municipality of Pandan: KU 302176, 302180–84; Municipality of San Remigio: KU 306816; Municipality of Valderrama, Barangay Lublub, base of Mt. Baloy: TNHC 56337; Aklan Province: Municipality of Makato, Castillo Barrio: CAS 139164–66; Municipality of Makato, Castillo Barrio: CAS-SU 137590; Calagna-an Island, Iloilo Province: Barangkalan: CAS 124121, 124293–97; Siquijor Island, Siquijor Province: CAS-SU 23126, FMNH 61439–43; Municipality of Lazi, Po-o: CAS-SU 16796–97; 1.5 km N of Maria Town: CAS-SU 23908; Municipality of San Jua, Tag-ibo Barrio, 2 km from coast: CAS-SU 16777, 16779–80, 16783–85, 16787–88, 16790, 16792, 16794; Sicogon Island, Iloilo Province: Buaya area: CAS 12442–44, 124950–58; Poro Island, Cebu Province: 0.4 km N of Poro Town: CAS 124515; Negros Island: Negros Occidental Province: Municipality of Cauayan: KU 302145; Negros Oriental Province: Municipality of Sibulan, Barangay Janya-janay, Sitio Balinsasayo, Cuenos, Lake Balinsasyo: TNHC 61911, 61921, 62879; Municipality of Valencia, Barangay Bongbong, Camp Lookout, Mt. Talinis, in Cuernos de Negros range: KU 302189–90, 302192, 302196, 302203–04, TNHC 62880–82; Tahiro River, 120 m above sea level: MCZ A-110944–48; Municipality of Bayanan, Malyong: CAS 17078–81; "Negros Island": FMNH 61504–23, 57204–41, 57244, 57246–47, 61403–09, 61444–48, 77721–22; Municipality of Sibulan Lake Balinsasaayo, 1000 m above sea level, Cuernos de Negros Range: MCZ A-110949; Municipality of Luzuriaga, Barangay Palinpino: MCZ A-28295 (paratype); Municipality of Dumaguete, Dumaguete City: MCZ A-26809; 15 km from Dumaguete City, Camp Lookout: CAS 14723; ca. 35 km W of Bais Town, along Mamagyan River, sitio Panyabunan: CAS 17091; Municipality of Siaton: CAS 156051–56; Hacienda Louisiana: CAS-SU 14725–30; ca. 23 km W of Bais Town, 0.5 km W of Mayaposi Hill, upper Mabaja Creek: CAS 16671, 16776, CAS-SU 16672–83; W. of Mariposi Hill, 20 km W of Bais Town, Mabaja River: CAS 17074–76; ca. 20 km W of Bais, Pagyabunan: CAS 16749–51; ca. 3 km W of Palimpinon, Ocoy River: CAS 16685–736; Pulopaantao, SE slope of Makawili Peak, Mt. Canlaon: CAS 16650–70; Cebu Island, Cebu Province: 3 km NW of Cebu City: CAS-SU 23857, 23861, 23913; Minglanilla area: CAS-SU 131911–13; Municipality of Carmen, Matinao-an: CAS 131903; Guimaras Island, Guimaras Subprovince: near Buenavista: CAS 125305–07; Jordan area: CAS 125308–09.

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

## DATA ACCESSIBILITY

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## ACKNOWLEDGMENTS

First and foremost, we thank the Biodiversity Management Bureau (BMB; formerly Parks and Wildlife Bureau, PAWB) of the Philippine Department of Environment and Natural Resources (DENR) for their assistance facilitating research permits (Memoranda of Agreement), scientific collecting permits (Gratuitous Permits to Collect Biological Specimens), and international Wildlife Certifications (export permits), necessary for this and related studies. The University of Kansas Institutional Animal Care and Use Committee approved live animal handling protocols (IACUC AUS 185-05 to RMB). We are grateful to BMB officers T. M. Lim, C. Custodio, J. de Leon, and A. Tagtag for enthusiastic logistical support, and we thank A. C. Alcala (Silliman University), A. C. Diesmos (ACEAN University Network), the late R. V. Sison (PNM), and C. Custodio (DENR) for their early and consistent support of this work. We thank R. K. Abraham for his conceptual assistance on this work and for reviewing the manuscript. For loans of specimens, we thank J. Vindum, A. Leviton, and R. Drewes (CAS), R. I. Crombie, A. Wynn, and K. de Queiroz (USNM), J. Rosado and J. Hanken (MCZ), J. W. Ferner and R. S. Kennedy (CMNH), R. V. Sison and A. C. Diesmos (PNM), and A. Resetar, H. Voris, R. F. Inger, and J. Mata (FMNH). Visits to CAS were facilitated by the C. Stearns Fellowship of the California Academy of Sciences (awarded to RMB), and we particularly appreciate the Field Museum's Alan Resetar and Joshua Mata for their help photographing the holotype of *Limnonectes macrocephalus* (FMNH 40519). Support for fieldwork was provided by the Society for the Study of Amphibians and Reptiles (SSAR grants-in-aid of research to RMB), The Society of Systematic Biologists (RMB), Fulbright and Fulbright-Hayes grants (to C. D. Siler), the U.S. National Science Foundation (DEB 073199, 0743491, 1418895, 0910341, 0804115, and 0334952 and EF-0334952 to RMB and KU-based students), and the University of Kansas General Research Fund. During the course of this research, MWH was supported by an NSF Graduate Research Fellowship, and while preparing this manuscript, we were supported by a grant from the U.S. National Science Foundation (DEB 1654388 + Pandemic Supplement), a KU College of Liberal Arts and Sciences Graduate Assistantship in Support of Faculty Research award, a KU Biodiversity Institute Research and Exploration Fund grant, and funding from the South, Southeast, and East Asia Fund of the KU Office of International Affairs, University of Kansas.

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