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Phylogenetic systematics, ecology, and conservation of marsupial frogs (Anura: Hemiphractidae) from the Andes of southern Ecuador, with descriptions of four new biphasic species

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Abstract

We review the systematics of the species of *Gastrotheca* (Anura: Hemiphractidae) in the highlands of the southern Ecuadorian Andes. We analyzed phylogenetic, morphological, ecological, and acoustic data from populations in the region. We provide an updated phylogenetic hypothesis inferred from a database that contains 42 species of *Gastrotheca,* and sequences from mitochondrial (12S, 16S, and ND1) and nuclear (POMC and RAG-1) genes. We describe four new endemic biphasic species for Ecuador (*Gastrotheca cuencana*, *G. elicioi*, *G. turnerorum*, and *G. yacuri*). In addition, we redefine *G. lojana*, recently resurrected from the synonymy of *G. monticola*, and redescribe *G. litonedis*. Furthermore, we describe the tadpoles and ontogenetic color changes in six species (*G. cuencana*, *G. elicioi*, *G. litonedis*, *G. lojana*, *G. pseustes*, and *G. turnerorum*). Also, we describe the calls of seven species (*G. cuencana*, *G. elicioi*, *G. litonedis*, *G. lojana*, *G. pseustes*, *G. testudinea*, and *G. yacuri*). The phylogenetic relationships estimated here are congruent with previous phylogenetic hypotheses for the group, except for the placement of *G. galeata*, *G. plumbea*, *G. orophylax*, *G. nicefori*, and *G. griswoldi*. Because most sister species in *Gastrotheca* are allopatric, the evolutionarly scenarios that likely have intervened in shaping the diversity are the uplift of the Andes and the formation of cross-Andean river valleys, which probably promoted conditions that acted as dispersal barriers that led to speciation. Many species of *Gastrotheca* (44%) are highly threatened. Most monophasic species have not been seen since the late 1980s, whereas the highland biphasic species have survived the catastrophic events that led to the disappearance of many other sympatric anurans. Research and conservation actions are urgently needed for all surviving species treated herein, five of which are either Critically Endangered or Endangered because of their restricted distributions (10–1600 km^2), habitat destruction and fragmentation, climate change, and pathogens. Two of the new species, *G. cuencana*, and *G. elicioi*, mostly are known from the cities of Cuenca and Loja, respectively, where urbanization threatens their survival. In order to call attention to conservation issues, we name one new species to refer to the Yacuri National Park, and the other three in honor of the people from Cuenca, the Turner family, and Elicio E. Tapia, whose actions are helping to halt amphibian extinctions.

Key words: Anura, conservation, Ecuador, new species, *Gastrotheca*, morphology, ontogeny, systematics, tadpoles, vocalizations

Resumen

En este estudio, revisamos la sistemática de las especies del género *Gastrotheca* (Anura: Hemiphractidae) distribuidas en los Andes del sur de Ecuador. Obtuvimos y analizamos información filogenética, morfológica, ecológica y acústica de las poblaciones distribuidas en la región. Proveemos una hipótesis filogenética basada en datos de secuencias mitocondriales (12S, 16S, ND1) y nucleares (POMC, RAG-1) de 42 especies de *Gastrotheca*. Describimos cuatro especies nuevas endémicas para el Ecuador (*Gastrotheca cuencana*, *G. elicioi*, *G. turnerorum* y *G. yacuri*). Adicionalmente, redefinimos a *Gastrotheca lojana*, recientemente removida de la sinonimia de *G. monticola*, y redescribimos a *G. litonedis*. También describimos los renacuajos y cambios de color ontogénicos de seis especies (*G. cuencana*, *G. elicioi*, *G. litonedis*, *G. lojana*, *G. pseustes* y *G. turnerorum*). Además, describimos los cantos de siete especies (*G. cuencana*, *G. elicioi*, *G. litonedis*, *G. lojana*, *G. pseustes*, *G. testudinea* y *G. yacuri*). Las relaciones filogenéticas que presentamos son congruentes con hipótesis filogenéticas previas del grupo, excepto por la posición de *G. galeata*, *G. plumbea*, *G. orophylax*, *G. nicefori* y *G. griswoldi*. Debido a que la mayoría de las especies hermanas en *Gastrotheca* son alopátricas, los escenarios evolutivos que probablemente han intervenido en su diversificación son el levantamiento de los Andes y la formación de valles transversales de ríos Andinos, los cuales probablemente promovieron condiciones que actuaron como barreras a la dispersión y condujeron a la especiación. Muchas especies de *Gastrotheca* (44%) están severamente amenazadas. La mayoría de las especies monofásicas no han sido avistadas desde finales de la década de 1980, mientras que las especies bifásicas de zonas altas han sobrevivido a las extinciones catastróficas que llevaron a la desaparición de muchos otros anuros simpátricos. Se necesitan con urgencia acciones de investigación y conservación para todas las especies sobrevivientes que se discuten en esta publicación, cinco de las cuales están En Peligro Crítico o En Peligro debido a sus áreas extremadamente restringidas (10–1600 km^2), la destrucción y fragmentación del hábitat, el cambio climático y los patógenos. Dos de las nuevas especies, *Gastrotheca cuencana* y *G. elicioi*, son conocidas principalmente en las ciudades de Cuenca y Loja, respectivamente, en donde la urbanización amenaza severamente a su supervivencia. Con el fin de llamar la atención sobre estos temas de conservación, nombramos una especie nueva en referencia al Parque Nacional Yacuri y las otras tres en honor a la gente de Cuenca, la familia Turner y Elicio E. Tapia, cuyas acciones ayudan a detener las extinciones de anfibios.

Palabras claves: Anura, Ecuador, Especies nuevas, *Gastrotheca*, Morfología, Ontogenia, Renacuajos, Sistemática, Vocalizaciones

Introduction

Marsupial frogs of the genus *Gastrotheca* occur from Costa Rica to Argentina, Cordillera de la Costa of Venezuela, and Brazil (Duellman 2015). Species in this genus vary in size from 30 to 110 mm in snout–vent length. Recent studies have provided hypotheses of evolutionary relationships (Wiens *et al.* 2007; Blackburn & Duellman 2013; Duellman *et al.* 2014; Duellman 2015; Castroviejo-Fisher *et al.* 2015). However, many species remain to be discovered and others are poorly known. For example, the knowledge of *Gastrotheca* diversity is increasing continuously as new collections and studies are conducted in the Andes (Duellman 2013, 2015; Duellman *et al.* 2014). The same is true for the Andean regions of Ecuador that have been a hot spot for the evolution of marsupial frogs (Duellman & Hillis 1987). When one of us, William E. Duellman, began his journey of discovery of *Gastrotheca* in the Andes, about 50 years ago, only two species of biphasic marsupial frogs (*G. riobambae* and *G. lojana*) from the Ecuadorian Andes, and four monophasic species (*G. guentheri*, *G. plumbea*, *G. testudinea*, and *G. weinlandii*) were known from Ecuador. The biphasic life cycle species have free-swimming tadpoles, whereas monophasic species are direct developers that lack the tadpole stage in water. In a systematic review of Ecuadorian marsupial frogs, Duellman & Hillis (1987) recognized eight species of *Gastrotheca* distributed along the Ecuadorian Andes. They described three new species that were previously confused under the single taxon name *Gastrotheca riobambae* (Fowler 1913); these were *G. espeletia*, *G. litonedis*, and *G. pseustes*. In addition, they provided information on *G. plumbea* (Boulenger 1882); *G. psychrophila* Duellman 1974; *G. orophylax* Duellman & Pyles 1980); *G. monticola* Barbour & Noble 1920; and *G. riobambae*. Finally, they placed *Gastrotheca marsupiata lojana* (Parker 1932) in the synonymy of *Gastrotheca monticola*. Among Ecuadorian species with aquatic tadpoles,

the ones of *G. espeletia*, *G. lojana*, *G. pseustes*, *G. psycrophila*, and *G. riobambae* have been described (Duellman 2015). Nevertheless, after Duellman and Hillis's seminal taxonomic review, the data on marsupial frogs from Ecuador has significantly increased by additional collections and field efforts. Recently, Duellman and a team of Ecuadorian scientists from Centro Jambatu de Investigación y Conservación de Anfibios discovered a greater diversity of species of Andean marsupial frogs in Ecuador, which were mentioned by Duellman (2015). This was made possible by the availability of larger series of adults, tadpoles, and ontogenetic series from different localities and new molecular data, combined with modern conceptual and analytical methods. Here we review the taxonomy and phylogenetic relationships of the marsupial frogs from the Andes of southern Ecuador, specifically we: (1) provide a phylogenetic hypothesis that includes 42 species of *Gastrotheca* based on mitochondrial and nuclear sequence data, (2) describe four new species, (3) redescribe *Gastrotheca litonedis*, (4) redefine *Gastrotheca lojana*, resurrected from the synonymy of *G. monticola*, (5) provide additional data on *G. pseustes*, (6) describe the calls of seven species, (7) describe the tadpoles of six species, and (8) describe ontogenetic variation in coloration of six species.

Materials and methods

Species boundaries were assessed under the General Lineage Concept of Species (de Queiroz 1998, 1999). We considered morphological, acoustic, and genetic characters, as sources of evidence when recognizing species. We also estimated their phylogenetic relationships, considering reciprocal monophyly as evidence for independent evolution (see Sites & Marshall 2004). Institutional abbreviations follow Sabaj Pérez (2014) and Frost (2017). Specimens examined are housed at Centro Jambatu de Investigación y Conservación de Anfibios (CJ), Biodiversity Institute at The University of Kansas (KU), Museo de Zoología, Pontificia Universidad Católica del Ecuador (QCAZ), and Museo de Colecciones Biológicas, Universidad Técnica Particular de Loja (MUTPL).

Author contributions. SCE, LAC, WED conceived and designed research, analyzed data, and wrote the paper. Fieldwork was mostly done by SCE, LAC, MAM and PS; WED and field parties collected before 1991. MAM described tadpoles. PS described and discussed the calls. JMG aided with part of sequencing and discussion. All authors contributed to manuscript editing and gave final approval for publication.

Phylogenetic relationships. Molecular data were analyzed using a dataset of ~3.9 kb of DNA that include partial sequences of three mitochondrial genes (12S ribosomal RNA; 16S ribosomal RNA; and NADH dehydrogenase subunit 1, ND1) and two nuclear gene (proopiomelanocortin, POMC; and recombination activating gene 1, RAG-1). We used sequences from 53 individuals of 42 species from 49 different localities (Table 1). The species included herein are members of the subgenus *Duellmania* and *Gastrotheca* (*sensu* Duellman 2015); thus, we included samples from *G. microdiscus*, *G. albolineata*, *G. fulvorufa*, *G. guentheri*, and *G. dendronastes* as outgroups. We used sequences published in previous studies (Wiens *et al.* 2007; Duellman *et al.* 2011; Blackburn & Duellman 2013; Duellman *et al.* 2014) and 42 new sequences generated for this study that were deposited in GenBank (www.ncbi.nlm.nih.gov). Information on voucher specimens, associated locality data, and GenBank accession numbers are summarized in Table 1. KU 173171 (cited in Table 1 and Figure 1 as *Gastrotheca* sp.) has been treated as *G. excubitor*, but it is related to *G. ochoai* and *G. pachachacae* (Duellman *et al.* 2011a), and likely a distinct taxon (Duellman 2015). DNA fragments from each gene were amplified independently using the polymerase chain reaction (PCR). Thermal cycle profiles and the primers used for the amplification were those used by Wiens *et al.* (2007). The PCR products were visualized in 1% agarose gel by a horizontal electrophoresis and purified with ExoSap (ExoSap-iT, GE Healthcare). PCR products were sequenced by the Macrogen Sequencing Team (Macrogen Inc., Seoul, Korea). DNA sequences were assembled using GENEIOUS 5.4.4 (Drummond *et al.* 2011), low-quality and ambiguous regions were trimmed. We generated an alignment for each gene using CLUSTAL X 2.0.10 (Larkin *et al.* 2007), and then we concatenated these alignments in a matrix of 3928 aligned characters (available upon request).

Phylogenetic analyses were performed using Maximum likelihood and Bayesian methods. The partitioning scheme used was a partition by gene [12S, 16S, ND1, POMC and RAG1]. We used JMODELTEST 2.1.4 (Darriba *et al.* 2012) to select the best-fit model of sequence evolution for each partition under the Akaike information criterion. Maximum likelihood analyses were performed in GARLI 2.0 (Zwickle 2006). A total of 25 independent search replicates were performed to infer the best tree. Each replicate was terminated when no significant topology

improvement was found in 20,000 generations or until a maximum of 1,000,000 regenerations was reached (the score threshold was set as 0.05 and the significant score improvement for topology as 0.01). Support for the nodes was estimated via 1000 nonparametric bootstrap pseudoreplicates under the same settings used during tree search, but one search per bootstrap replicate. From the 1000 trees we estimated a 50% majority-rule consensus tree using GENEIOUS 5.4.4. Bayesian analyses were performed in MRBAYES 3.1.2 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003). Bayesian phylogenetic analyses consisted of two independent runs of 20 million generations each and four MCMC chains (temperature set to 0.20), with trees sampled every 2000 generations. All parameters were unlinked between partitions, except topology and branch lengths. We confirmed that the two independent runs reached stationarity at a similar likelihood score and that the topologies were similar, using TRACER 1.5 (Rambaut & Drummond 2007). Of the 10,000 trees generated per run, the first 5000 were discarded as "burn in". The remaining 10,000 trees from the two runs were combined to calculate the posterior probabilities in a 50% majority-rule consensus tree.

The proportional genetic distance (p-distance) among species were estimated by pairwise comparisons of sequences of the 16S ribosomal RNA gene (438 bp) using the software Mega v.6.0 (Tamura *et al*. 2013).

Morphology. Morphological characters studied and format of description follow Trueb & Duellman (1978), Duellman & Hillis (1987), and Duellman (2015). In the diagnosis of species, characters 10–14 refer to coloration in life. Sex and maturity of specimens were determined by the presence of brood pouches, vocal sac, vocal slits, and in some cases by examination of gonads. Morphological measurements of adult specimens were taken to the nearest 0.1 mm with digital calipers. Abbreviations of the 14 measurements taken are: snout–vent length (SVL), tibia length (TIBL), foot length—distance from the proximal edge of the inner metatarsal tubercle to the tip of the fourth toe (FL), head length—straight-line distance from the posterior edge of the jaw (HL), head width (HW), interorbital distance—straight-line distance between the inner edges of the upper eyelid (IOD), eyelid width—the greatest width of the upper eyelid, measured from its medial most edge to its outer margin (EW), internarial distance (IND), eye diameter (ED), eye–nostril distance—straight-line distance from the posterior edge of the opening of the nostril to the anterior corner of the orbit (EN), tympanum diameter (TD), thumb length—straightline distance between the proximal edge of the prepollical tubercle and the end of the Finger I (FFL), Finger III length—straight-line distance between the proximal edge of the palmar tubercle and the end of Finger III (TFL) and disc width (TFD). Description of webbing follows (Savage & Heyer 1967, 1997) with modifications of Myers & Duellman (1982). Color in life descriptions are based on photographs taken by LAC and Diego Acosta-López, which are available at AnfibiosEcuador (http://www.anfibiosecuador.ec/index.php?aw,2). Specimens measured and their associated locality data are listed in Appendix I.

The 14 morphological measurements were used in multivariate analyses to assess the degree of morphometric differentiation among species. First, we performed two Principal Component Analyses (PCA) with two groups of closely related species. The first PCA included adult specimens of *Gastrotheca cuencana*, *G. elicioi*, *G. litonedis*, *G. lojana*, and *G. monticola*. The second PCA included adult specimens of *G. turnerorum*, *G. yacuri*, and *G. pseustes* complex (*G. pseustes* 1 from populations nearby the type locality south of the Jubones-Girón river valley in Loja and El Oro provinces and *G. pseustes* 2 from populations north of the Jubones-Girón river valley; see phylogeny in figure 1, map in figure 20, and Appendix I for specimens measured). Each PCA was performed using a variance-covariance matrix of the standardized data (correlation matrix). Variables were log-transformed and then we removed the effect of co-variation with SVL by obtaining the residuals from linear regressions between each one of the 13 variables and SVL. The PCAs were performed with these residuals and SVL scaled to unit variance. Principal components (PC) with eigen values grater than one were retained to visually examine morphological variation among species. To test if morphometric differences among closely related species were statistically significant we used the scores from the retained components to perform multivariate analyses of variance (MANOVA) and compared mean values among species using Tukey contrasts (Herberich *et al.* 2010). *Gastrotheca yacuri* was excluded from the permutational MANOVA because we were able to collect only two individuals of this species. All statistical analyses were performed in R v. 3.4.3.

Tadpoles and ontogeny. Tapoles are described in a Tadpole section within the species accounts. Terminology and description format follow Coloma & Lötters (1996), Castillo-Trenn (2004), Altig & McDiarmid (1999), Lannoo 1987, 1999) and Duellman (2001), with modifications from Duellman & Hillis (1987). Tadpoles are assigned in ecomorphological guilds, as defined by Altig & Johnston (1989). Tadpole descriptions are based on field-collected tadpoles, some of which were lab-reared at Centro Jambatu facilities to document ontogenetic

changes. Parental individuals for the lab-reared lots were collected *in-situ* (see Appendix II for localities). Tadpoles were kept in the lab at a mean temperature of 21°C and pH 6.8. Groups of tadpoles were placed in either glass or plastic tanks about 50 cm long x 30 cm wide x 30 cm deep, with a capacity of 40 liters of water. The water entering the container was filtered to prevent the presence of chlorine, arsenic, bacteria, and other harmful agents. Tadpoles were fed daily with either cooked (5 minutes in boiling water) leaves of *Taraxacum officinale* or food for herbivorous tadpoles with protein (25.16%), fiber (13.08%), and carbohydrates (49.08%). Tadpoles in several stages of development were preserved in a 10% formalin solution. In order to report ontogenetic changes in development and morphology, all developmental stages (sensu Gosner 1960) that were available were described. Body measurements were obtained to the nearest 0.01 using a digital caliper. Small structures, including head and mouth features were measured with a micrometer lens, built in a Zeiss Stemi SV11 stereoscope. Values are presented in millimeters. The measurements taken were: total body length (BL) as the length from tip of snout to the tip of the tail, body length from snout to tail-body junction (BL), tail length (TAL) from point of tail insertion to the tip of the tail, proportion of the body length to tail length—expressed in percentage (TLP), number of ventral papillae (VP), number of lateral papillae (LP), width of the oral disc (WOD), width of the upper jaw—including lateral processes (WUJ), proportion of the upper jaw width related to the oral disc width—expressed in percentage (UJP), body width at the spiracle level (BW), body height behind the eyes level (BH), head width at anterior level of eyes (HWEL), maximum tail height (MTH), width of tail musculature at the body-tail junction level (TMW), height of tail musculature (TMH), snout-nostril distance—taken from tip of snout to anterior border of nostril opening (SND), eye-nostril distance—taken between posterior border of narial opening and anterior border of eye (END), internarial distance—taken from the centers of nostril openings (IND), eye diameter or eye length from anterior to posterior corner of the eye (EL), eye width at the center of the eye (EW), interorbital distance—taken from centers of both eyes (IOD), spiracle length (SL) from the middle of spiracular opening to proximal external evidence of spiracular formation, spiracle width at its widest part (SW), vent tube length (VTL) as the transversal line between basal part and outermost tip of the tube, and vent tube width at the proximal portion (VTW). Oral structures of a single specimen in Gosner Stage 36 or the nearest available stage were stained with Alciane Blue for each species.

Color descriptions were produced from color photographs taken of live tadpoles and metamorphs under photo studio conditions on black and white backgrounds. When possible, changes in colors and an ontogeny revealing changes in color patterns are presented.

Vocalizations. We analysed 130 calls from 43 males for the seven of the nine known *Gastrotheca* species of the southern Ecuadorian Andes (Appendix III). Calls were recorded in the field or in Centro Jambatu (outdoor enclosures), using the following combinations of recorders and microphones: (1) a Sony MZ-NH1 recorder and a Sennheiser K6-ME66 microphone, (2) an Olympus LS-10S recorder and a Sennheiser ME66 microphone, (3) an Olympus LS-11 recorder and a RØDE NTG2 microphone, or an Olympus LS-14 recorder and a Sennheiser ME66 microphone. The recordings were made at 44.1 or 48 kHz sampling frequency and 16-bit resolution, in WAV or AIFF file formats. Air temperature and humidity were measured with a data logger (Lascar Electronics, model EL-USB-2-LCD, accuracy:±0.5°C;±5%), when available (Appendix III). The original, analysed call recordings are deposited in full length in the Fonoteca Zoológica (www.fonozoo.com) of the Museo Nacional de Ciencias Naturales (CSIC), Madrid, Spain and in the sound library of Centro Jambatu (records ID are provided in Appendix III).

Acoustic analysis was conducted using Raven Pro 1.4 (http://www.birds.cornell.edu/raven). We measured the temporal parameters from the oscillograms and the spectral parameters from spectrograms obtained through Hanning window function, DFT: 512 samples, 3 dB filter bandwidth: 124 Hz, and 50% overlap. The terminology and procedures for measuring call parameters follow Cocroft & Ryan (1995), Toledo *et al.* (2015), and Köhler *et al.* (2017). We used a note-centered approach to define what is considered a call and what a note (sensu Köhler *et al.* (2017). Typically, the advertisement calls of the *Gastrotheca* species consists of one or several long, pulsed notes followed by one or several short, single-pulsed notes (Duellman 2015). These are considered complex calls, as are composed of different types of notes (Toledo *et al.* 2015; Köhler *et al.* 2017). However, in some species (e.g., *G. litonedis* or *G. cuencana*) the calls are composed only of short, single-pulsed notes, being considered as such simple calls. We use the term long note for the pulsed, longer notes of the calls and the term short note, for the shorter single-pulsed ones.

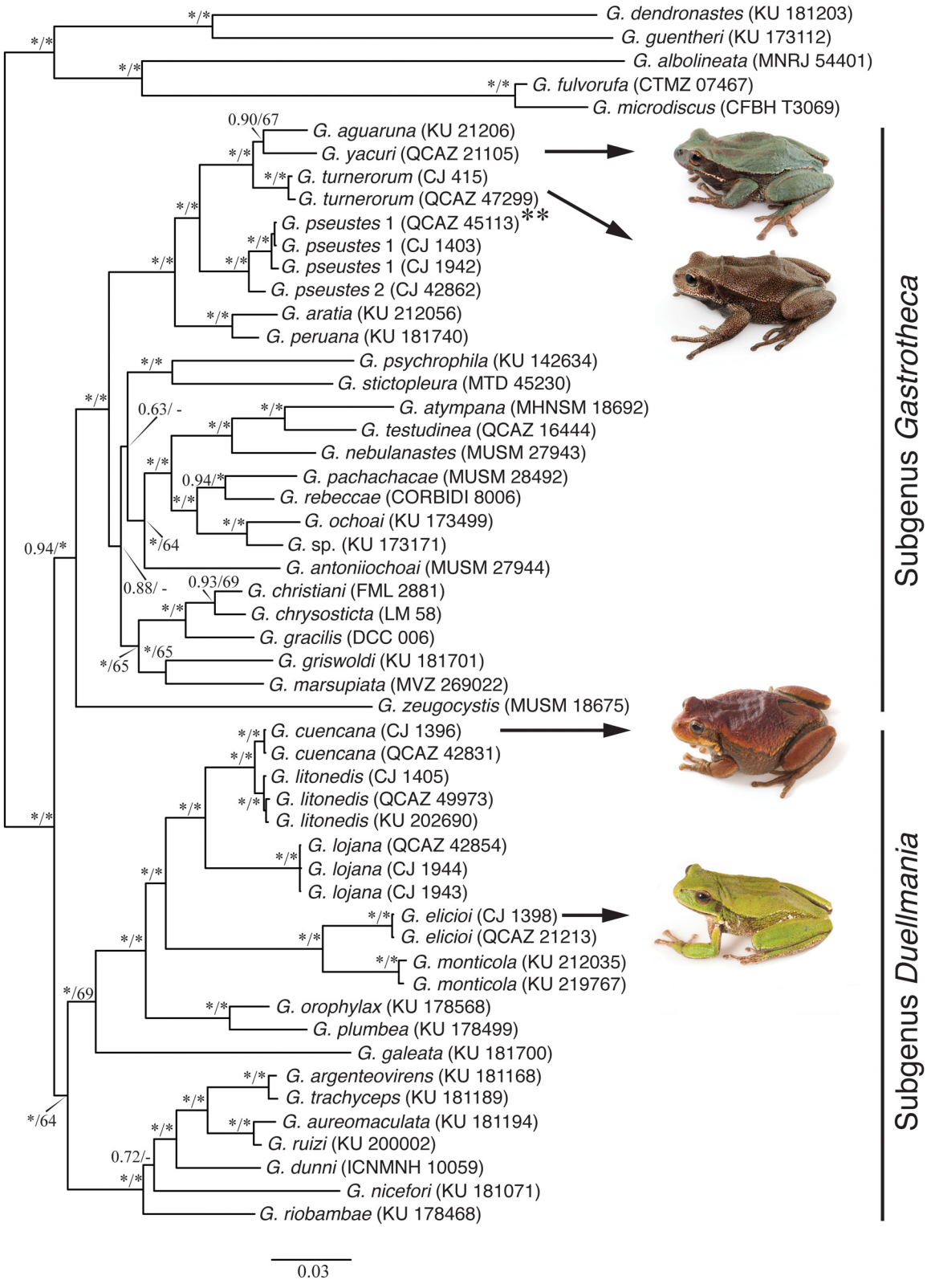

FIGURE 1. Phylogenetic relationships of *Gastrotheca* species depicted from the Majority-rule consensus tree resulted from Bayesian analyses. Node support values are from Bayesian and Maximun likelihood analyses are shown (Bayesian posterior probalilities/bootstrap support). Asterisks incdicate that support values were greater than 0.95 and 70% repectively. Two asterisks (**) indicate an individual identified as *G. lateonota* by Blackburn and Duellman (2013), Duellman *et al.* (2014), and Duellman (2015).

TABLE 1. Taxa included in the phylogenetic analysis, specimen museum numbers, collecting localities, and Genbank accession numbers.

Species	Museum number	Locality	12S	16S	ND1	POMC	RAG1
Gastrotheca aguaruna	KU 212026	PERU: Amazonas: Chachapoyas: 5 km N Levanto, 2850 m	NA	KF723438.1	KF723462.1	KF723484.1	NA
Gastrotheca albolineata	MNRJ 54401	BRAZIL: Rio de Janeiro, Cachoeira de Macacu, Parque Estadual Tres Picos"	NA	KC844924	KC844949	KC844971	KC844992
Gastrotheca antoniiochoai	MUSM 27944	PERU: Cusco, Paucartambo-Shintuya Rd	NA	JN157622	KC844950	KC844972	KC844993
Gastrotheca aratia	KU 212056	PERU: Cajamarca: Cutervo: vicinity of Cutervo, 2620 m	NA	KF723443.1	KF723467.1	KF723489.1	NA
Gastrotheca argenteovirens	KU 181168	COLOMBIA: Cauca: 2 km E Silvia, 2550 m	DQ679233	DQ679383	DQ679342	DQ679311	NA
Gastrotheca atympana	MHNSM 18692	PERU: Junín: Tarma: Pampa Hermosa, 1540 m	DQ679234	DQ679384	DQ679343	DQ679312	DQ679276
Gastrotheca aureomaculata	KU 181194	COLOMBIA: Cauca: Moscapan, 14.7 km W Leticia, 2050 m	DQ679235	DQ679385	DQ679344	NA	DQ679277
Gastrotheca christiani	FML 2881	ARGENTINA: Jujuy: Quebrada Abra de Cañas, Parque Nacional Calilegua, 1700 m	DQ679236	DQ679386	DQ679345	DQ679313	DQ679278
Gastrotheca chrysosticta	LM 58		DQ679237	DQ679387	DQ679346	NA	DQ679279
Gastrotheca cuencana	CJ 1396	ECUADOR: Azuay: Cuenca, 2579 m	MG948912	MG948923	MH223473	NA	NA
Gastrotheca cuencana	QCAZ 42831	ECUADOR: Cañar: Papaloma de la Nube, 3011 m	MG948913	MG948924	MH223474	MH223466	NA
Gastrotheca dendronastes	KU 181203	COLOMBIA: Valle: Río Calima, 1.5 km W Lago Calima, 1230 m	DQ679239	DQ679389	DQ679348	DQ679315	DQ679281
Gastrotheca dunni	ICNMNH 10059	COLOMBIA: Antioquia: 3.5 km N Llanos de Cuiva, 2700 m	DQ679240	DQ679390	DQ679349	DQ679316	DQ679282
Gastrotheca elicioi	CJ 1398	ECUADOR: Loja: Loja, Parque Nacional Podocarpus entrance, 2456 m	MG948914	MG948925	MG948935	NA	NA
Gastrotheca elicioi	QCAZ 21213	ECUADOR: Loja:10 km from Loja, 2250 m	NA	KC844922	KC844947	NA	NA
Gastrotheca fulvorufa	CTMZ 07467	BRAZIL: São Paulo, Parque Natural Municipal Nascentes de Paranapiacaba	NA	KC844929	KC844954	KC844977	KC844997
Gastrotheca galeata	KU 181700	PERU: Piura: 15 km E Canchaque, 1850 m	DQ679242	DQ679392	DQ679351	DQ679318	DQ679284
Gastrotheca gracilis	DCC 006		DQ679243	NA	NA	DQ679319	NA
Gastrotheca griswoldi	KU 181701	PERU: Junín: 6 km ENE Paccha, 3840 m	DQ679244	NA	DQ679352	DQ679320	NA
Gastrotheca guentheri	KU 173112	ECUADOR: Pichincha: 5 km ESE Chiriboga, 2010 m	DQ679245	DQ679393	DQ679353	DQ679321	DQ679285

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TABLE 1. (Continued)

Species	Museum number	Locality	12S	16S	ND1	POMC	RAG1
Gastrotheca litonedis	KU 202690	ECUADOR: Azuay: 10 km (by the road) NE of Girón, 2854 m	NA	MG948926	MH223475	NA	NA
Gastrotheca litonedis	CJ 1405	ECUADOR: Azuay: San Fernando, Laguna de Busa, 2834 m	MG948915	MG948927	MH223476	NA	NA
Gastrotheca litonedis	QCAZ 49973	ECUADOR: Azuay: San Gerardo, 2854 m	MG948916	MG948928	MH223477	MH223467	NA
Gastrotheca lojana	CJ 1944	ECUADOR: Azuay: Oña, 2272 m	MG948917	MG948929	MH223478	MH223468	NA
Gastrotheca lojana	QCAZ 42854	ECUADOR: Azuay: San Fernando, Laguna de Busa, 2834 m	MG948919	MG948930	MH223479	MH223469	NA
Gastrotheca lojana	CJ 1943	ECUADOR: Loja: Paraíso del Celén, 2680 m	MG948918	MG948931	MH223480	NA	NA
Gastrotheca marsupiata	MVZ 269022	PERU: Cusco: Calca	NA	KC844925	KC844951	KC844973	KC844994
Gastrotheca microdiscus	CFBH T3069	Brazil: Parana, Mananciais da Serra	NA	KC844933	KC844958	KC844981	KC845000
Gastrotheca monticola	KU 219767	PERU: Piura: 1.8 km N Huancabamba, 1980 m	NA	KF723446	KF723470	KF723492	KF723513
Gastrotheca monticola	KU 212035	PERU: Amazonas: Pomacochas (Florida), 2180 m	NA	KJ489471.1	KF723465.1	KF723487.1	NA
Gastrotheca nebulanastes	MUSM 27943	PERU: Cusco, Rocotal	NA	JN157621	KC844959	KC844982	KC845001
Gastrotheca nicefori	KU 181071	VENEZUELA: Táchira: 11 km S Delicias, 1750 m	DQ679249	DQ679399	DQ679357	DQ679325	DQ679291
Gastrotheca ochoai	KU 173499	PERU: Cusco: Chilca, 10 km N Ollantaytambo, 2760 m	DQ679250	DQ679400	DQ679358	DQ679326	DQ679292
Gastrotheca orophylax	KU 178568	ECUADOR: Napo: 11 km ESE Papallacta, 2660 m	DQ679251	DQ679401	DQ679359	DQ679327	DQ679293
Gastrotheca pachachacae	MUSM 28492	PERU: Apurímac: Cerabamba-Andina Chinchay cloud forest	NA	JN157620	NA	KC844983	KC845002
Gastrotheca peruana	KU 181740	PERU: Cajamarca: 23 km SW Celendín, 3050 m	DQ679253	DQ679402	DQ679361	NA	NA
Gastrotheca plumbea	KU 178499	ECUADOR: Cotopaxi: Pilaló, 2410 m	DQ679254	DQ679403	DQ679362	DQ679328	DQ679294
Gastrotheca pseustes 1	CJ 1942	ECUADOR: Loja, Manu, 2876 m	MG948920	MG948932	MH223481	MH223470	NA
Gastrotheca pseustes 1	CJ 1403	ECUADOR: Loja: Loja, Parque Nacional Podocarpus entrance, 2456 m	MG948921	MG948933	MH223482	MH223471	NA
Gastrotheca pseustes 1	QCAZ 45113	Ecuador: El Oro, Chillacocha, 8 km SW Chilla	NA	KC844923	KC844948	KC844970	NA

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TABLE 1. (Continued)

Species	Museum number	Locality	12S	16S	ND1	POMC	RAG1
Gastrotheca pseustes 2	QCAZ 42862	ECUADOR: Azuay: San Fernando, Laguna de Busa, 2834 m	NA	KC844936	KC844962	KC844986	NA
Gastrotheca turnerorum	CJ 415	ECUADOR: Loja: Laguna Negra de Jimbura, 3406 m	MG948922	MG948934	MH223483	MH223472	NA
Gastrotheca turnerorum	QCAZ 47299	ECUADOR: Loja: Parque Nacional Podocarpus, Lagunas El Compadre	NA	KC844934	KC844960	KC844984	NA
Gastrotheca psycrophila	KU 142634	ECUADOR: Zamora-Chinchipe: 13.5 km E Loja, 2800 m	DQ679255	DQ679404	DQ679363	DQ679329	DQ679295
Gastrotheca rebeccae	CORBIDI 08006	PERU: Cordillera de Vilcabamba	NA	KC844937	KC844963	KC844987	NA
Gastrotheca riobambae	KU 178468	ECUADOR: Imbabura: Laguna Cuicocha, 3010 m	DQ679256	DQ679405	DQ679364	NA	DQ679296
Gastrotheca ruizi	KU 200002	COLOMBIA: Putumayo: Santiago, 2250 m	DQ679257	DQ679406	DQ679365	NA	DQ679297
Gastrotheca stictopleura	MTD 45230	PERU: Pasco: Huanchón: Puagmaray, 2500 m	DQ679258	DQ679407	DQ679366	DQ679330	DQ679298
Gastrotheca sp. (*aff. excubitor*)	KU 173171	PERU: Cusco: 1.5 km SW Amparaes, 3580 m	DQ679241	DQ679391	DQ679350	DQ679317	DQ679283
Gastrotheca testudinea	QCAZ 16444	ECUADOR: Morona-Santiago, Cerro Bosco	NA	KC844940	KC844966	NA	NA
Gastrotheca trachyceps	KU 181189	COLOMBIA: Cauca: W slope Cerro Munchique, 29 km WNW El Tambo, 2530 m	DQ679259	DQ679408	DQ679367	DQ679331	DQ679299
Gastrotheca yacuri	QCAZ 21105	ECUADOR: Loja: El Salado de Jimbura, 2712 m	NA	KC844939	KC844965	KC844989	NA
Gastrotheca zeugociystis	MUSM 18675	PERU: Pasco: Cordillera de Carpish, 2700 m	DQ679262	DQ679411	NA	DQ679334	DQ679302

The following temporal and spectral parameters were measured and analyzed: Call duration: duration of a single call, measured from beginning to the end of the call; inter-call interval: the interval between two consecutive calls, measured from the end of the call to the beginning of the consecutive call; call rate: number of calls per minute, measured as the time from beginning of first call to beginning of last call; long notes/call: number of long notes present in a call; short notes/call: number of short notes present in a call; long note rate: number of long notes per second, measured as the time between the beginning of the first long note and the beginning of the last long note; short note rate: number of short notes per second, measured as the time between the beginning of the first short note and the beginning of the last short note; long notes duration: the duration of a single long note within a call, measured from beginning to the end of the note; short notes duration: the duration of a single short note within a call, measured from beginning to the end of the note; inter-note interval: the interval between two consecutive notes (no matter if long or short) within the same call, measured from the end of one note to the beginning of the consecutive note; number of pulses: number of pulses per long notes; pulse rate: number of pulses per second, measured as the time from beginning of first pulse to beginning of last pulse; dominant frequency: the frequency containing the highest sound energy, measured along the entire call; and the 90% bandwidth, reported as Frequency 5% and Frequency 95%, or the minimum and maximum frequencies, excluding the 5% below and above the total energy in the selected call.

Distribution and Conservation status. Geographic and climate calculations were done with QGIS 2.18 (QGIS Team 2018). GPS coordinates were obtained during fieldwork. Additional localities were obtained from published articles; when geographic coordinates were not provided, localities were georeferenced, using digital maps. For each reviewed species, we calculated the area of extent of occurrence by generating a minimum convex polygon, which is the smallest polygon in which no internal angle exceeds 180 degrees and that contains all the sites of occurrence. The ecosystems in which each species occur were determined following the classification by Ministerio de Ambiente del Ecuador (2012). For the description of environmental properties of species distribution we extracted mean annual temperature and mean annual precipitation from the WORLDCLIM dataset (http://www.worldclim.org; Fick & Hijmans 2017). The localities used in this study are listed in Appendix II. The conservation status of the new species was evaluated by applying IUCN categories, criteria and guidelines (IUCN 2001).

Results

Phylogenetic relationships. The evolution models selected under the AIC criterion were: GTR + I + Γ for 12S, TIM2 + I + Γ for 16S, TIM3 + I + Γ for ND1, TIM3 + Γ for POMC and TrN + Γ for RAG 1 partition. The resulting ML tree and the majority-rule consensus tree obtained under Bayesian criterium showed the same topology and similar support for most of the nodes (Fig. 1).

All species reviewed herein are part of Northern or Central Andean clades (*sensu* Blackburn & Duellman (2013). Genetic distances estimated from pairwise uncorrected comparisons of the 16S gene (partial sequences, 438 bp) showed that the divergence between species of the Andean clades (subgenus *Duellmania* and *Gastrotheca*) ranged from < 0.6% (*G. argenteovirens* vs *G. trachyceps*, and *G. aureomaculata* vs *G. ruizi*, paired sister species) to 12.7% (*G. zeugocystis* vs *G. elicioi*). Between paired sister species, the sequence divergence reached 3.3% (*G. elicioi* vs *G. monticola* and *G. aguaruna* and *G. elicioi*). Within species that were represented by samples from different localities, sequence divergence reached 0.2% within specimens of *G. pseustes* 1, *G. monticola*, and *G. turnerorum* (Table 2).

Systematics. Duellman & Hillis (1987) described *Gastrotheca litonedis* as a medium-sized species having distinctive features from various localities in the Cuenca Basin in Ecuador. The original description included 9 males and 15 females, of which only one was included as type specimen (the holotype). Subsequently many specimens collected from Cuenca and its surroundings have been identified as *G. litonedis* (e.g., Arbeláez Ortiz & Vega Toral 2008; Valencia *et al.* 2008). However, in 2008 a series of specimens was collected at San Fernando, a locality approximately 2.5 km (by road) from the type locality of *G. litonedis*; these specimens did not fit the original description of *G. litonedis* or that of any known Andean species of *Gastrotheca*. We examined 101 adults that had been identified as *G. litonedis*, including non-type specimens that were used in the original description and specimens that were collected in the vicinity of the type locality. We found two different groups that can be

TABLE 2. Proportional genetic distances between specimens of *Gastrotheca* used in the phylogenetic analyses. Pairwise comparisons were made using 438 bp of the16S ribosomal RNA gene from 49 specimens.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	*G. cuencana* CJ 1396														
2	*G. cuencana* QCAZ 42831	0.000													
3	*G. aguaruna* KU 212026	0.094	0.094												
4	*G. albolineata* MNRJ 54401	0.144	0.144	0.146											
5	*G. antoniiochoai* MUSM 27944	0.060	0.060	0.076	0.147										
6	*G. argenteovirens* KU18194	0.077	0.077	0.084	0.129	0.078									
7	*G. ariata* KU 212056	0.078	0.078	0.057	0.141	0.056	0.081								
8	*G. atympana* MHNSM 18692	0.091	0.091	0.099	0.139	0.073	0.091	0.081							
9	*G. aureomaculata* KU 181194	0.077	0.077	0.083	0.140	0.078	0.028	0.078	0.086						
10	*G. christiani* FML 2881	0.058	0.058	0.065	0.142	0.060	0.053	0.058	0.070	0.053					
11	*G. chrysosticta* LM 58	0.062	0.062	0.058	0.142	0.050	0.048	0.050	0.065	0.048	0.009				
12	*G. dendronastes* KU 181203	0.148	0.148	0.148	0.171	0.148	0.153	0.136	0.157	0.151	0.142	0.140			
13	*G. dunni* ICNMNH 10059	0.078	0.078	0.097	0.147	0.076	0.038	0.086	0.084	0.035	0.068	0.063	0.160		
14	*G. elicioi* QCAZ 21213	0.063	0.063	0.119	0.160	0.102	0.093	0.108	0.095	0.091	0.075	0.086	0.168	0.083	
15	*G. elicioi* CJ 1398	0.063	0.063	0.119	0.160	0.102	0.093	0.108	0.095	0.091	0.075	0.086	0.168	0.083	0.000
16	*G.* sp. (aff. *excubitor*) KU 173171	0.048	0.048	0.068	0.139	0.038	0.067	0.058	0.045	0.067	0.050	0.047	0.136	0.068	0.083
17	*G. fulvorufa* CTMZ 07467	0.104	0.104	0.116	0.165	0.104	0.091	0.113	0.096	0.099	0.094	0.089	0.176	0.104	0.110
18	*G. galeata* KU 181700	0.078	0.078	0.100	0.140	0.078	0.085	0.091	0.089	0.078	0.078	0.076	0.151	0.083	0.094
19	*G. guentheri* KU 173112	0.115	0.115	0.097	0.159	0.105	0.110	0.095	0.124	0.107	0.100	0.092	0.117	0.124	0.132
20	*G. pseustes* 1 QCAZ 45113	0.073	0.073	0.058	0.151	0.056	0.083	0.038	0.078	0.078	0.060	0.053	0.135	0.086	0.111
21	*G. pseustes* 1 CJ 1403	0.073	0.073	0.058	0.151	0.056	0.083	0.038	0.078	0.078	0.060	0.053	0.135	0.086	0.111
22	*G. pseustes* 1 CJ 1492	0.076	0.076	0.055	0.153	0.058	0.086	0.040	0.080	0.080	0.062	0.055	0.132	0.089	0.113
23	*G. litonedis* CJ 1405	0.012	0.012	0.089	0.147	0.055	0.077	0.073	0.086	0.072	0.057	0.062	0.148	0.070	0.060
24	*G. litonedis* QCAZ 49973	0.012	0.012	0.089	0.147	0.055	0.077	0.073	0.086	0.072	0.057	0.062	0.148	0.070	0.060
25	*G. litonedis* KU 202690	0.012	0.012	0.089	0.147	0.055	0.077	0.073	0.086	0.072	0.057	0.062	0.148	0.070	0.060
26	*G. lojana* QCAZ 42854	0.028	0.028	0.089	0.143	0.057	0.062	0.073	0.076	0.057	0.055	0.045	0.139	0.060	0.057
27	*G. lojana* CJ 1944	0.028	0.028	0.089	0.143	0.057	0.062	0.073	0.076	0.057	0.055	0.045	0.139	0.060	0.057
28	*G. lojana* CJ 1943	0.028	0.028	0.089	0.143	0.057	0.062	0.073	0.076	0.057	0.055	0.045	0.139	0.060	0.057
29	*G. marsupiata* MVZ 269022	0.072	0.072	0.063	0.141	0.050	0.062	0.045	0.062	0.060	0.040	0.033	0.145	0.060	0.096
30	*G. microdiscus* CFBH T3069	0.107	0.107	0.125	0.172	0.100	0.102	0.116	0.094	0.107	0.105	0.100	0.174	0.108	0.116
31	*G. monticola* KU 212035	0.065	0.065	0.113	0.156	0.086	0.091	0.108	0.081	0.091	0.086	0.091	0.151	0.083	0.030
32	*G. monticola* KU 219767	0.067	0.067	0.116	0.153	0.089	0.093	0.110	0.084	0.093	0.088	0.093	0.149	0.085	0.033
33	*G. nebulanastes* MUSM 27943	0.080	0.080	0.085	0.138	0.065	0.086	0.082	0.043	0.080	0.067	0.060	0.148	0.086	0.099
34	*G. nicefori* KU 181071	0.096	0.096	0.115	0.138	0.093	0.074	0.099	0.091	0.064	0.083	0.088	0.149	0.067	0.104
35	*G. ochoai* KU 173499	0.063	0.063	0.075	0.145	0.055	0.078	0.067	0.047	0.078	0.050	0.047	0.142	0.073	0.089

TABLE 2. (Continued)

		1	2	3	4	5	6	7	8	9	10	11	12	13	14
36	*G. orophylax* KU 178568	0.060	0.060	0.087	0.132	0.067	0.082	0.073	0.070	0.077	0.062	0.060	0.133	0.077	0.078
37	*G. pachachacae* MUSM 28492	0.070	0.070	0.075	0.158	0.052	0.065	0.070	0.055	0.060	0.057	0.050	0.128	0.065	0.104
38	*G. peruana* KU 181740	0.068	0.068	0.070	0.136	0.048	0.078	0.012	0.073	0.070	0.050	0.040	0.140	0.078	0.099
39	*G. plumbea* KU 178499	0.055	0.055	0.089	0.141	0.070	0.075	0.081	0.089	0.070	0.058	0.053	0.138	0.080	0.068
40	*G. turnerorum* CJ 415	0.092	0.092	0.028	0.146	0.079	0.084	0.060	0.094	0.086	0.068	0.063	0.148	0.102	0.114
41	*G. turnerorum* QCAZ 47299	0.092	0.092	0.030	0.147	0.079	0.086	0.060	0.094	0.089	0.068	0.063	0.149	0.099	0.111
42	*G. pseustes* 2 QCAZ 42862	0.070	0.070	0.055	0.151	0.053	0.078	0.033	0.075	0.075	0.055	0.048	0.131	0.084	0.105
43	*G. rebeccae* CORBIDIO 8006	0.060	0.060	0.070	0.147	0.043	0.055	0.060	0.047	0.055	0.047	0.040	0.134	0.060	0.094
44	*G. riobambae* KU 178468	0.073	0.073	0.092	0.151	0.081	0.042	0.078	0.084	0.042	0.060	0.060	0.157	0.045	0.086
45	*G. ruizi* KU 200002	0.072	0.072	0.078	0.134	0.073	0.028	0.073	0.080	0.005	0.053	0.048	0.148	0.031	0.086
46	*G. stictopleura* MTD 45230	0.070	0.070	0.078	0.133	0.057	0.080	0.055	0.067	0.070	0.057	0.050	0.131	0.073	0.098
47	*G. testudinea* QCAZ 16444	0.083	0.083	0.102	0.139	0.070	0.096	0.086	0.023	0.091	0.072	0.070	0.160	0.086	0.094
48	*G. trachyceps* KU 181189	0.077	0.077	0.084	0.129	0.078	0.000	0.081	0.091	0.028	0.053	0.048	0.153	0.038	0.093
49	*G. zeugocystis* MUSM 18675	0.094	0.094	0.103	0.140	0.092	0.102	0.095	0.116	0.097	0.084	0.079	0.130	0.105	0.127
50	*G. yacuri* QCAZ 21105	0.079	0.079	0.033	0.146	0.071	0.086	0.063	0.094	0.089	0.063	0.058	0.146	0.092	0.100

TABLE 2. (Continued)

		15	16	17	18	19	20	21	22	23	24	25	26	27	28
16	*G.* sp. (*excubitor*) KU 173171	0.083													
17	*G. fulvorufa* CTMZ 07467	0.110	0.083												
18	*G. galeata* KU 181700	0.094	0.062	0.113											
19	*G. guentheri* KU 173112	0.132	0.099	0.135	0.118										
20	*G. pseustes* 1 QCAZ 45113	0.111	0.058	0.121	0.084	0.100									
21	*G. pseustes* 1 CJ 1403	0.111	0.058	0.121	0.084	0.100	0.000								
22	*G. pseustes* 1 CJ 1492	0.113	0.060	0.124	0.086	0.103	0.002	0.002							
23	*G. litonedis* CJ 1405	0.060	0.043	0.104	0.075	0.115	0.068	0.068	0.071						
24	*G. litonedis* QCAZ 49973	0.060	0.043	0.104	0.075	0.115	0.068	0.068	0.071	0.000					
25	*G. litonedis* KU 202690	0.060	0.043	0.104	0.075	0.115	0.068	0.068	0.071	0.000	0.000				
26	*G. lojana* QCAZ 42854	0.057	0.052	0.094	0.065	0.096	0.073	0.073	0.076	0.025	0.025	0.025			
27	*G. lojana* CJ 1944	0.057	0.052	0.094	0.065	0.096	0.073	0.073	0.076	0.025	0.025	0.025	0.000		
28	*G. lojana* CJ 1943	0.057	0.052	0.094	0.065	0.096	0.073	0.073	0.076	0.025	0.025	0.025	0.000	0.000	
29	*G. marsupiata* MVZ 269022	0.096	0.045	0.094	0.078	0.094	0.055	0.055	0.057	0.067	0.067	0.067	0.057	0.057	0.057
30	*G. microdiscus* CFBH T3069	0.116	0.081	0.012	0.118	0.144	0.119	0.119	0.122	0.102	0.102	0.102	0.097	0.097	0.097

TABLE 2. (Continued)

		15	16	17	18	19	20	21	22	23	24	25	26	27	28
31	*G. monticola* KU 212035	0.030	0.076	0.107	0.089	0.129	0.105	0.105	0.108	0.060	0.060	0.060	0.062	0.062	0.062
32	*G. monticola* KU 219767	0.033	0.078	0.110	0.091	0.132	0.108	0.108	0.111	0.062	0.062	0.062	0.065	0.065	0.065
33	*G. nebulanastes* MUSM 27943	0.099	0.042	0.107	0.083	0.107	0.075	0.075	0.077	0.075	0.075	0.075	0.070	0.070	0.070
34	*G. nicefori* KU 181071	0.104	0.093	0.136	0.083	0.125	0.091	0.091	0.094	0.088	0.088	0.088	0.083	0.083	0.083
35	*G. ochoai* KU 173499	0.089	0.023	0.093	0.070	0.099	0.065	0.065	0.067	0.055	0.055	0.055	0.060	0.060	0.060
36	*G. orophylax* KU 178568	0.078	0.062	0.111	0.068	0.107	0.078	0.078	0.081	0.052	0.052	0.052	0.045	0.045	0.045
37	*G. pachachacae* MUSM 28492	0.104	0.033	0.093	0.077	0.107	0.070	0.070	0.067	0.065	0.065	0.065	0.055	0.055	0.055
38	*G. peruana* KU 181740	0.099	0.050	0.110	0.083	0.100	0.040	0.040	0.043	0.063	0.063	0.063	0.060	0.060	0.060
39	*G. plumbea* KU 178499	0.068	0.070	0.101	0.068	0.107	0.081	0.081	0.084	0.052	0.052	0.052	0.038	0.038	0.038
40	*G. turnerorum* CJ 415	0.114	0.070	0.113	0.102	0.092	0.065	0.065	0.068	0.091	0.091	0.091	0.081	0.081	0.081
41	*G. turnerorum* QCAZ 47299	0.111	0.071	0.113	0.105	0.093	0.065	0.065	0.068	0.092	0.092	0.092	0.081	0.081	0.081
42	*G. pseustes* 2 QCAZ 42862	0.105	0.055	0.113	0.081	0.092	0.009	0.009	0.011	0.066	0.066	0.066	0.070	0.070	0.070
43	*G. rebeccae* CORBIDIO 8006	0.094	0.026	0.091	0.067	0.097	0.060	0.060	0.062	0.055	0.055	0.055	0.045	0.045	0.045
44	*G. riobambae* KU 178468	0.086	0.063	0.099	0.086	0.112	0.089	0.089	0.091	0.068	0.068	0.068	0.058	0.058	0.058
45	*G. ruizi* KU 200002	0.086	0.062	0.094	0.073	0.104	0.073	0.073	0.075	0.072	0.072	0.072	0.057	0.057	0.057
46	*G. stictopleura* MTD 45230	0.098	0.050	0.109	0.080	0.091	0.055	0.055	0.057	0.062	0.062	0.062	0.057	0.057	0.057
47	*G. testudinea* QCAZ 16444	0.094	0.038	0.096	0.083	0.129	0.083	0.083	0.085	0.075	0.075	0.075	0.070	0.070	0.070
48	*G. trachyceps* KU 181189	0.093	0.067	0.091	0.085	0.110	0.083	0.083	0.086	0.077	0.077	0.077	0.062	0.062	0.062
49	*G. zeugocystis* MUSM 18675	0.127	0.078	0.118	0.105	0.116	0.090	0.090	0.092	0.089	0.089	0.089	0.089	0.089	0.089
50	*G. yacuri* QCAZ 21105	0.100	0.068	0.119	0.100	0.100	0.058	0.058	0.061	0.071	0.071	0.071	0.073	0.073	0.073

TABLE 2. (Continued)

		29	30	31	32	33	34	35	36	37	38	39	40
30	*G. microdiscus* CFBH T3069	0.097											
31	*G. monticola* KU 212035	0.096	0.105										
32	*G. monticola* KU 219767	0.099	0.108	0.002									
33	*G. nebulanastes* MUSM 27943	0.067	0.105	0.086	0.089								
34	*G. nicefori* KU 181071	0.090	0.139	0.109	0.106	0.101							
35	*G. ochoai* KU 173499	0.050	0.091	0.083	0.086	0.050	0.098						
36	*G. orophylax* KU 178568	0.072	0.115	0.088	0.090	0.080	0.083	0.065					
37	*G. pachachacae* MUSM 28492	0.047	0.091	0.081	0.083	0.057	0.100	0.045	0.085				
38	*G. peruana* KU 181740	0.043	0.108	0.097	0.099	0.075	0.096	0.060	0.065	0.062			
39	*G. plumbea* KU 178499	0.075	0.109	0.085	0.088	0.093	0.085	0.075	0.021	0.082	0.073		
40	*G. turnerorum* CJ 415	0.068	0.122	0.113	0.116	0.085	0.112	0.080	0.083	0.083	0.073	0.086	

TABLE 2. (Continued)

		29	30	31	32	33	34	35	36	37	38	39	40
41	*G. turnerorum* QCAZ 47299	0.068	0.122	0.111	0.113	0.085	0.115	0.081	0.084	0.083	0.073	0.087	0.002
42	*G. pseustes* 2 QCAZ 42862	0.047	0.116	0.102	0.105	0.072	0.088	0.062	0.076	0.067	0.040	0.078	0.063
43	*G. rebeccae* CORBIDIO 8006	0.037	0.089	0.081	0.083	0.042	0.090	0.030	0.070	0.018	0.052	0.072	0.073
44	*G. riobambae* KU 178468	0.063	0.105	0.086	0.088	0.091	0.072	0.078	0.080	0.060	0.073	0.078	0.097
45	*G. ruizi* KU 200002	0.055	0.102	0.085	0.088	0.075	0.059	0.073	0.072	0.060	0.065	0.070	0.081
46	*G. stictopleura* MTD 45230	0.047	0.107	0.101	0.098	0.067	0.070	0.059	0.065	0.062	0.050	0.067	0.075
47	*G. testudinea* QCAZ 16444	0.067	0.094	0.089	0.086	0.038	0.085	0.045	0.070	0.055	0.078	0.083	0.099
48	*G. trachyceps* KU 181189	0.062	0.102	0.091	0.093	0.086	0.074	0.078	0.082	0.065	0.078	0.075	0.084
49	*G. zeugocystis* MUSM 18675	0.092	0.124	0.123	0.126	0.105	0.116	0.086	0.071	0.102	0.086	0.081	0.112
50	*G. yacuri* QCAZ 21105	0.066	0.123	0.097	0.099	0.083	0.110	0.073	0.076	0.083	0.068	0.079	0.043

TABLE 2. (Continued)

		41	42	43	44	45	46	47	48	49
42	*G. pseustes* 2 QCAZ 42862	0.063								
43	*G. rebeccae* CORBIDIO 8006	0.073	0.057							
44	*G. riobambae* KU 178468	0.100	0.083	0.055						
45	*G. ruizi* KU 200002	0.083	0.070	0.055	0.042					
46	*G. stictopleura* MTD 45230	0.075	0.052	0.052	0.075	0.065				
47	*G. testudinea* QCAZ 16444	0.099	0.080	0.047	0.089	0.086	0.057			
48	*G. trachyceps* KU 181189	0.086	0.078	0.055	0.042	0.028	0.080	0.096		
49	*G. zeugocystis* MUSM 18675	0.112	0.087	0.094	0.108	0.091	0.094	0.108	0.102	
50	*G. yacuri* QCAZ 21105	0.043	0.056	0.073	0.103	0.083	0.076	0.094	0.086	0.092

distinguished by morphological characters, call features, and molecular characters, and that appear to have non-overlapping distribution ranges. The holotype of *G. litonedis* corresponds to the group of specimens collected from San Fernando (additional comments about the holotype are given under the *G. litonedis* account); therefore, this group belongs to *G. litonedis* that is redescribed herein. The other group, which included most of the specimens used for the original description of *G. litonedis*, is described herein as a new species, *G. cuencana*. These two species that apparently have parapatric distributions are shown to be sister taxa in our phylogenetic analyses.

Gastrotheca lojana was described by Parker (1932) as a subspecies of *G. marsupiata* from Loja, Ecuador, but Parker suggested that it had intermediate characteristics between *G. marsupiata* and *G. monticola* and that there was little morphological difference with the latter. Duellman (1974) redefined *G. lojana* and *G. monticola*. The former was recognized as a distinct species distributed in southern Ecuador and northern Perú. In Duellman's (1974) redescription, specimens from Loja and Zamora provinces in Ecuador and from Amazonas, Cajamarca, and Piura departaments in Perú were used. In addition, the distribution range of *G. monticola* was extended to southern Ecuador and specimens from Saraguro (Loja Province) and Girón (Azuay Province) in Ecuador were referred to as *G. monticola*. Later, Duellman & Hillis (1987) placed *G. lojana* in the synonymy of *G. monticola* because no consistent differences (using allozyme and morphological characters) were found between the specimens from Peru grouped as *G. monticola* vs the specimens examined from the vicinity of Loja, Ecuador. We have examined 85 specimens including individuals collected from several localities in Azuay, Loja and El Oro Provinces; most of them previously had been identified as *G. monticola*. We also included specimens from Peru and type specimens used in the original description of *G. marsupiata lojana* (Parker 1932). We found two groups among Ecuadorian specimens that were morphologically distinguishable between them and from Peruvian specimens. One of these groups of specimens includes the type specimens of *G. marsupiata lojana*, which leads to the resurrection of *G. lojana*. The other Ecuadorian group is named and described here as *G. elicioi*. These results were supported by our phylogenetic analyses (see below; Fig. 1) and the phylogenetic hypothesis provided by Blackburn & Duellman (2013), Duellman *et al.* (2014), and Duellman (2015). In our phylogenetic hypothesis *G. lojana* is the sister taxon of *G. litonedis* + *G. cuencana*, whereas *G. elicioi* appears as the sister taxon of *G. monticola*.

In addition, we describe *Gastrotheca turnerorum* and *G. yacuri* from the southern part of the Cordillera Oriental in Loja Province. These species are morphologically and genetically distinct from other species in southern Ecuador and northern Perú. According to our phylogenetic hypothesis it appears that *G. turnerorum* is the sister taxa of a clade composed by *G. aguaruna* from Perú and *Gastrotheca yacuri* from Ecuador. Finally, we also provide information of specimens of *G. pseustes* from the Andes in Loja and El Oro provinces, but we choose to leave a more detailed taxonomic, and phylogeographic revision of *G. pseustes* (using morphometric, molecular, vocalization, and ecological characters) for a future report.

Even though *Gastrotheca psychrophila* occurs in the Andes of southern Ecuador, we did not include it in this study because, in spite of several searching efforts, we have failed to find this species.

Species accounts

***Gastrotheca cuencana* sp. nov.**
urn:lsid:zoobank.org:act:82F87E67-2940-424C-AC03-BC751224D5E4

Holotype. CJ 1391 (Fig. 2), an adult male, from the city of Cuenca, 2579 m (02° 53' 57.91" S, 79° 01' 52.79" W), Azuay Province, Ecuador, one of a series obtained on 8 June 2011 by Elicio E. Tapia, Sofía Carvajal-Endara and Henry Grefa.

Paratypes. (Total 48: 10 adult males, 21 adult females, 17 juveniles). Ecuador: Azuay: CJ 1392–7, collected with the holotype; KU 120676 (female), 120683–4, 120690, 120695 (4 juveniles), 120699 (male), 120705 (male), 120709–10 (males), 120713 (female), 120718–9 (female, male), 120721 (female), 120722 (male) from Cuenca, 2600 m, (02° 53' 57.91" S, 79° 01' 52.79" W), on 19 June 1968 by John D. Lynch; KU 138616 (female), 138619–21 (male, females) from 4 km E: Cuenca 2540 m (02° 52' 59.88" S, 78° 22' 0.11" W), on 10 June 1970 by Thomas H. Fritts; KU 141572 (female) from 2.1 km S Cutchil, 2720 m (03° 06' 00"S, 78° 47' 59.99"W), on 16 May 1971 by Richard R. Montanucci; KU 141579 (female) from 3.5 km S Cutchil, 2785 m (03° 04' 59.87" S, 78° 47' 59.99" W), on 14 May 1971 by Richard R. Montanucci; KU 141582 (juvenile) from 8 km NW Cuenca, 2803 m (02° 51' 47.88"

S, 78° 58' 59.88" W), on 16 May 1971 by Richard R. Montanucci; KU 141583 (female) from 8.8 km NW Cuenca, 3820 m (02° 52' 00.12" S, 79° 04' 00.12" W), on 15 May 1971 by Richard R. Montanucci; KU 203441 (male) from Laguna de Zurucuchu, 16 km NW Cuenca, 3200 m (02° 50' 23.99" S, 79° 07' 47.99" W), on 5 March 1984 by William E. Duellman; KU 129779–82 (4 females), 129783–91 (9 juveniles), 129793–94 (juveniles), 129795 (female), 129796 (juvenile) from Río Matadero, 12 km E Cuenca (02° 52' 59.88"S, 78° 58' 00.12" W), on 17 November 1968 by Craig E. Nelson. *Cañar*: KU 141571 (male) and KU 141573 (female) from Biblián, 2620 (02° 42' 00" S, 78° 52' 00.12" W), on 17 and 23 May 1971, respectively, by Richard R. Montanucci; KU 142620–24 (4 females, male), from Biblián, 2620 m (02° 42' 00" S, 78° 52' 00.12" W), on 25 July 1971 by William E. Duellman; KU 147113 (female) from Biblián, 2620 m (02° 42' 00" S, 78° 52' 00.12" W), on 15 January 1972 by John E. Simmons.

Referred specimens. (Total 36, 28 adult males, 8 adult females). Ecuador: *Azuay*: QCAZ 1239 (male), from Sigsig, 2480 m (03° 03' 08.4" S, 78° 48' 10.56" W), on 24 July 1989 by Luis A. Coloma and Luis E. López; QCAZ 26309 (female), from Cumbe, 2740 m (03° 05' 55.64" S, 79° 00' 28.73" W), on 8 August 2003 by Patricio Vargas; QCAZ 26348–50 (males), 26353 (female), 26357–64 (8 males), from Cumbe, 2740 m (03° 05' 55.64" S, 79° 00' 28.73" W), on 9 August 2003 by Luis A. Coloma, Ítalo G. Tapia, Andrés Merino Viteri, Erik Wild and Patricio Vargas Mena; QCAZ 26354 (female), from Cumbe, 2740 m (03° 05' 55.64" S, 79° 00' 28.73" W), on 9 August 2003 by Ítalo G. Tapia; QCAZ 26357–8 (males), from Cumbe, 2740 m (03° 05' 55.64" S, 79° 00' 28.73" W), on 9 August 2003 by Andrés Merino Viteri; QCAZ 31477 (male), from Sigsig, 2424 m (03° 03' 08.4" S, 78° 48' 10.56" W), on 8 March 2006 by Ítalo G. Tapia; QCAZ 31509, 31511 (males), from Sigsig, 2424 m (03° 03' 8.4" S, 78° 48' 10.56" W), on 9 March 2006 by Ítalo G. Tapia and Giovanni Onore; QCAZ 34131 (female), from Cuenca, 2579 m (02° 53' 57.91" S, 79° 01' 52.79" W), on 27 February 1979 by Fernando I. Ortiz; QCAZ 37375–6, 37379–81, QCAZ 37386 (6 males), from unknown locality, on 31 May 2007 by Zoológico Amaru; QCAZ 38232 (male), from Carmen del Guzho, 2666 m (02° 56' 00" S, 79° 03' 00" W), on 16 June 2007 by Hari González Maldonado; QCAZ 39384–5 (female, male), from Tarqui, Patapamba, 2600 m (03° 00' 38.16" S, 79° 01' 53.43" W), on 21 June 2007 by Ernesto Arbeláez Ortiz; QCAZ 42720–1 (males) from Cuenca, 2579 m (02° 53' 57.91" S, 79° 01' 52.79" W), on 3 October 2007 by Sofía Carvajal-Endara and Flavio Jaramillo; QCAZ 47106 (male), from Tarqui, 2741 m (03° 00' 57.17" S, 79° 02' 40.13" W), on 21 June 2007 by Ernesto Arbeláez Ortiz. *Cañar*: QCAZ 42826, 42835, 42841 (females), from Papaloma de la Nube, 3011 m (02° 40' 21.54" S, 78° 54' 21.28" W), on 12–14 August 2008 by Sofía Carvajal-Endara.

Diagnosis. Included in the genus *Gastrotheca* by having a closed brood pouch on dorsum of female. A moderately large species (49.0–61.6 mm SVL in females, n = 28; 45.2–53.7 mm SVL in males, n = 38), with tibia length 39−50% SVL, slightly shorter than length of foot; (2) interorbital distance slightly larger than width of upper eyelid; (3) skin on dorsum finely granular, not co-ossified with skull, lacking transverse ridges; (4) supraciliary processes absent; (5) heel lacking calcar or tubercle; (6) tympanic annulus weakly granular to smooth; (7) Fingers I and II about equal in length, width of discs greater than digits; (8) fingers unwebbed; (9) webbing between external toes extending to antepenultimate subarticular tubercle on Toe IV, to penultimate subarticular tubercle on Toe V; (10) in life, dorsum green, tan, brown, or reddish-brown with or without dark paravertebral marks; (11) head markings consisting of pale labial stripe and, in some individuals, an inconspicuous canthal stripe; (12) pale white or cream dorsolateral stripe present; (13) flanks tan, brown, or green with cream flecks or spots; groin and anterior and posterior surfaces of thighs translucent cream without marks and with a faint pale blue tinge in some; (14) venter uniform creamy white; (15) in females, brood pouch single, dorsal.

In comparison with similar species in Ecuador, *G. cuencana* is most like *G. litonedis*, *G. lojana*, *G. elicioi*, and *G. riobambae*. It differs from these species by having a uniform creamy white venter; whereas the venter is pale gray in *G. litonedis*, and cream with dark flecks, spots or mottling in *G. lojana*, *G. elicioi*, and *G. riobambae*. In *G. cuencana* the dorsal surfaces of fingers are cream, whereas in the other species dorsal surfaces of fingers are of the same color as the rest of the body (tan, brown, or green). *Gastrotheca cuencana* also differs from *G. litonedis*, *G. elicioi*, and *G. riobambae* by lacking a dark canthal stripe. Moreover, in *G. cuencana* the groin and anterior surfaces of thighs are mostly translucent cream without marks; whereas, in *G. litonedis* the groin and anterior surface of thighs are usually bronze-brown or tan with cream or darks flecks and spots. In *G. lojana* and *G. riobambae* the groin and anterior surfaces of the thighs are usually cream with black mottling; in *G. elicioi* the groin and anterior surfaces of thighs usually have dark and cream flecks and spots. In profile, the snout in *G. cuencana* is rounded above and inclined anteroventrally, whereas the snout in *G. elicioi*, *G. lojana*, and *G. litonedis* is bluntly rounded.

Furthermore, *G. cuencana* has a conspicuous, elevated row of dorsolateral warts whereas these are barely raised in *G. litonedi*s; a narrow, cream supracloacal stripe is present in *G. litonedis*, *G. lojana*, and *G. riobambae*; whereas the stripe is fragmented in *G. elicioi* and absent in most *G. cuencana*. *Gastrotheca lojana* and *G. riobambae* also differ from *G. cuencana* and *G. litonedis* by having a complex call, whereas the call in the latter two species is a simple call. Additionally, the call of *G. cuencana* has a lower note rate, shorter note duration, longer inter-note interval and a lower dominant and 90% bandwidth frequency compared with *G. litonedis*. Finally, *G. cuencana* differs from its sister species (*G. litonedis*) by having a genetic distance of 1.2% (in a DNA dataset of 438 bp, 16S gene).

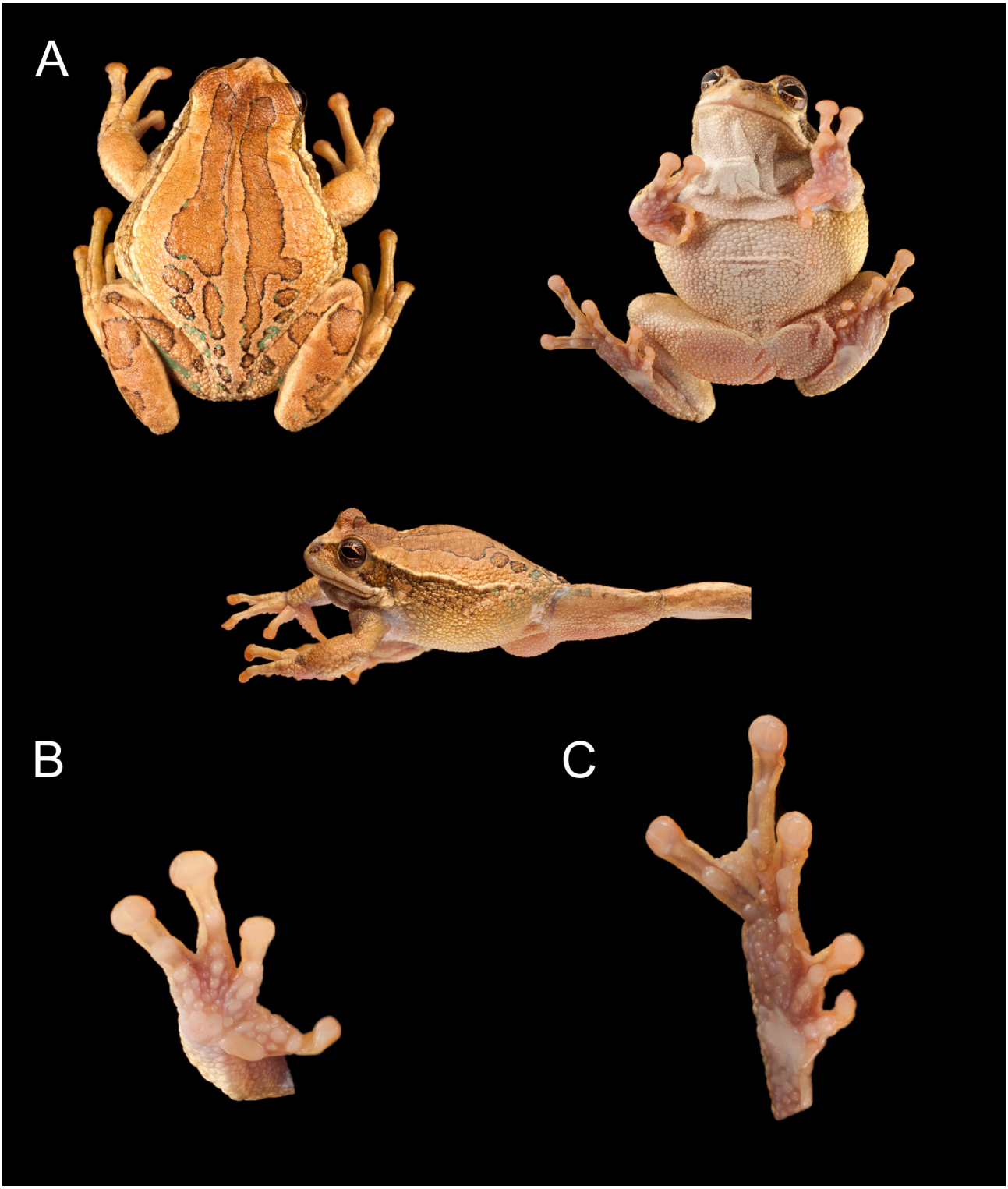

FIGURE 2. Live holotype of *Gastrotheca cuencana* (CJ 1391, male, SVL = 50.4 mm): A) dorsal, ventral and lateral views, (B) ventral view of left hand, enlarged 2.15X of A, and (C) ventral view of right foot, enlarged 2.4X of A. Photos by LAC.

Gastrotheca cuencana occurs in syntopy with *G. pseustes* (*sensu lato*) throughout most of its range. *Gastrotheca pseustes* differs from *G. cuencana* by having coarsely granular skin on the dorsum, in contrast to the usually finely granular dorsum in *G. cuencana*. In *G. cuencana* the venter is uniform creamy white, whereas it is cream or white with dark flecks or spots in *G. pseustes*; also the call of *G. cuencana* is simple, whereas in *G. pseustes* the call is complex.

Description of holotype. An adult male (Fig. 2); body moderately robust; SVL 50.6 mm; head wider that long; snout rounded in dorsal view, rounded and inclined anteroventrally in profile; canthus rostralis round in section; loreal region concave, lips rounded; top of head flat; interorbital distance 104% of width of upper eyelid; internarial area slightly elevated; nostrils not protuberant, directed anterolaterally, posterior to level of anterior margin of lower jaw; diameter of eye greater than its distance from nostril; tympanum round, separated from eye by distance about equal to diameter of tympanum; tympanic annulus and membrane weakly granular; supratympanic fold moderately weak, extending from behind the tympanum to the insertion of the forelimb. Dentigerous vomerine processes narrowly separated medially, each bearing four teeth.

Arm robust; ulnar tubercles absent; hand and fingers moderately large (TFL 35% of SVL), unwebbed, with distinct narrow lateral fringes; discs moderately large and rounded, width of disc of Finger III greater that diameter of tympanum; relative lengths of fingers I=II<IV<III; subarticular tubercles prominent, round, conical in lateral profile, non bifid; supernumerary tubercles, small, numerous, conical; palmar tubercle absent, prepollical tubercle elliptical. Hind limb robust; tibia length 46% SVL; foot length 49% SVL; calcar, tarsal tubercles, and inner tarsal fold absent; outer metatarsal tubercle absent; inner metatarsal tubercle large, elliptical; toes moderately long; relative length of toes I<II<III=V<IV; basal webbing between Toes I and II; webbing formula for other toes II1—2III1—2IV2—1V; subarticular tubercles moderately large, rounded; supernumerary tubercles, numerous, minute and rounded. Nuptial pad absent.

Skin on dorsum finely granular; skin on flanks coarsely granular; skin on throat, venter surfaces of thighs, and arms granular; skin on belly areolate; skin on venter surface of shanks smooth; numerous small tubercles lateral to cloacal opening. Vocal sac single, median, subgular. Vocal slits present at posterior lingual margins of mandibles. Tongue broad, suboval, not notched posteriorly, fully attached to mouth floor.

Coloration in life (Fig. 2). The dorsum is yellowish brown with two darker, black delineated, continuous, paravertebral markings. These markings extend to the sacrum where they bifurcate and become two rows of irregular blotches at each side of the vertebral axis. The dorsal surfaces of the limbs are yellowish brown with irregular gray blotches. Cream dorsolateral and labial stripes are present; the latter continues to the insertion of forelimb; a faint brown canthal stripe is present. The flanks are bronze-brown with small black spots. The venter, groin, and anterior surfaces of the thighs are uniform creamy white; the posterior surfaces of the thighs have a faint bluish coloration. The dorsal surfaces of the fingers are cream. The gular region is creamy gray laterally. The iris is reddish bronze with black reticulations.

Coloration in preservative. The dorsum is tan with two well-defined, gray paravertebral markings, which bifurcate at the level of sacrum to become two rows of irregular blotches on each side of the vertebral axis. A white dorsolateral stripe is present. The dorsal surfaces of limbs are tan with irregular gray blotches. A cream labial stripe continues to the insertion of the forelimb; a faint canthal is present. The flanks are gray; the venter, groin, and anterior surfaces of thighs are uniform creamy white; the posterior surfaces of thighs have a faint bluish coloration. The gular region is creamy gray.

Measurements (in mm). SVL: 50.4, TIBL: 21.9, FL: 24.9, HL: 16.9, HW: 19.1, IOD: 5.2, EW: 5.0 IND: 3.3, ED: 5.6, EN: 4.1, TD: 2.8, FFL: 10.0, TFL: 17.5, TFD: 3.4.

Variation. Morphometric variation of 28 females and 38 males is summarized in Table 3. Females are larger than males (54.2±2.9 mm; 49.6±2.4 mm). The skin on the dorsum is finely granular in most, but it varies in some specimens from weakly areolate to coarsely granular. All adults have a supratympanic fold that usually extends from the posterior part of the tympanum to point above the insertion of forelimb. The tympanic annulus is usually smooth, but some individuals (e.g., CJ 1395, 1940) have a slightly granular annulus (Fig. 3A, C). Each dentigerous vomerine process has 2–7 teeth (4.4±1.1, n = 39).

Color variation in preservative. Preserved specimens have bluish gray dorsum (tan and reddish-brown in CJ 1397). Faint paravertebral marks are present. A canthal stripe is absent in most specimens; the flanks and posterior surfaces of the thighs are dark gray with white spots evenly distributed in some specimens. In all specimens, a prominent white labial stripe extends from the posterior margin of the lip to the insertion of the forelimb. A narrow

white dorsolateral stripe is evident in most specimens. The groin and the anterior surfaces of the thighs are uniform creamy gray. The ventral surfaces are uniform creamy white. The posterior surfaces of thighs usually are creamy gray, but they are pale blue in some specimens. Some males have yellowish brown nuptial pads on the medial surface of the thumb.

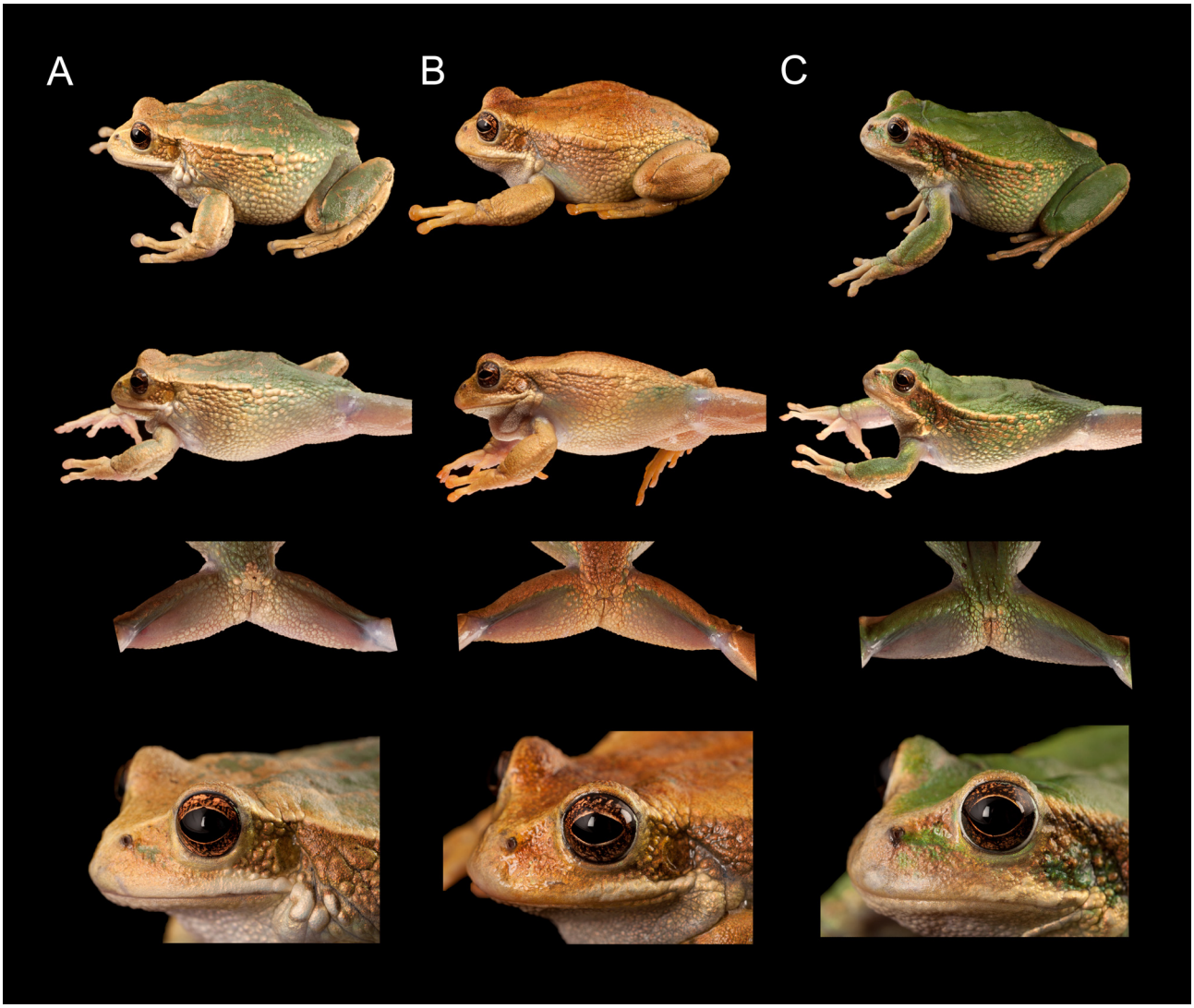

FIGURE 3. Live adults of *Gastrotheca cuencana* showing variation in dorsal and ventral color pattern: (A) CJ 1940, female, SVL = 50.2 mm, (B) CJ 1393, male, SVL = 46.7 mm, (C) CJ 1392, male, SVL = 49.8 mm, (D) CJ 1395, female, SVL = 61.6 mm, (E) CJ 1396, male, SVL = 52.2 mm, and (F) CJ 1397, female, SVL = 55.1 mm. Not to scale. Photos by LAC.

Color variation in life. (Figs. 3–4). The dorsum is uniform green (CJ 1393), reddish brown (CJ 1397), or tan (CJ 1392) with (CJ 1391) or without (CJ 1392) darker paravertebral marks. When present, the paravertebral markings usually are well defined; at the level of the sacrum they become two rows of irregular blotches at each side of the vertebral axis. The ventral surfaces are uniform creamy white. A cream labial stripe is extends from the posterior margin of the lip to the insertion of the forelimb; a dark brown canthal stripe is absent in most individuals. The tympanum is brown, tan, or olive green. The iris is reddish bronze with black reticulations. A creamy white dorsolateral stripe is evident in most individuals. The flanks are cream, bronze brown, or green. The groin and anterior surfaces of the thighs are translucent cream without dark markings (Fig. 3). The posterior surfaces of the thighs are translucent, cream, or pale blue or green. When present, supracloacal and heel stripes are cream or tan. The ventral surfaces of the shanks have a faint tinge of pale blue. The gular surface varies from white to creamy gray.

TABLE 3. Measurements (in mm) of adults of *Gastrotheca litonedis*, *G. lojana*, *G. cuencana*, *G. elicioi*, *G. turnerorum*, *G. pseustes* 1, *G. pseustes* 2, *G. psychrophila*, *G. monticola,* and *G. yacuri*. Mean±SD, and range are given. Abbreviations are: SVL (snout–vent length), TIBL (tibia length), FL (foot length), HL (head length), HW (head width), IOD (interorbital distance), EW (eyelid width), IND (internarial distance), ED (eye diameter), EN (eye–nostril distance), TD (tympanum diameter), FFL (thumb length), TFL (third finger length) and TFD (third finger disc width).

	Gastrotheca litonedis		*Gastrotheca lojana*		*Gastrotheca cuencana*	
	♀ n = 22	♂ n = 13	♀ n = 12	♂ n = 24	♀ n = 28	♂ n = 38
SVL	58.0±2.4	53.8±2.8	61.6±5.7	49.4±4.5	54.2±2.9	49.6±2.4
	53.5–62.4	48.9–57.4	54.1–76.1	40.2–61.0	49.0–61.6	45.2–53.7
TIBL	28.7±1.9	25.9±1.1	31.2±3.2	25.2±2.9	24.4±1.2	21.9±1.2
	23.3–31.6	23.5–27.4	27.4–36.5	19.8–31.1	21.7–26.7	19.5–26.0
FL	27.7±2.4	24.6±2.4	28.0±3.5	22.2±2.0	25.2±1.2	22.5±1.2
	19.0–30.4	17.9–27.2	22.8–35.5	17.9–26.6	22.2–28.0	20.5–25.6
HL	19.2±0.7	17.6±0.6	19.7±1.6	16.8±1.5	17.8±0.9	16.3±0.9
	18.1–20.5	16.5–19.0	17.9–22.8	13.9–19.2	16.0–19.6	14.2–17.7
HW	20.5±0.9	19.0±0.8	22.0±1.4	18.7±1.8	19.2±1.1	17.7±0.8
	18.7–22.2	17.6–20.1	19.4–24.2	15.4–22.1	17.1–21.1	15.6–19.4
IOD	7.7±0.4	6.8±0.4	8.2±1.1	6.7±0.9	5.6±0.6	5.4±0.6
	7.0–8.5	6.2–7.6	6.9–10.5	4.1–7.9	4.8–6.7	4.3–6.8
EW	4.8±0.4	4.6±0.4	4.4±0.4	4.3±0.5	4.1±0.5	4.3±0.5
	4.2–5.7	3.8–5.2	3.7–5.4	3.5–5.3	3.4–5.0	3.2–5.4
IND	3.5±0.3	3.2±0.3	3.7±0.2	3.0±0.4	3.2±0.2	3.0±0.4
	3.0–4.2	2.6–3.7	3.2–4.1	2.3–3.7	2.9–3.5	2.7–5.0
ED	5.4±0.3	5.1±0.4	5.6±0.3	4.9±0.5	5.0±0.4	4.8±0.6
	4.8–5.9	4.5–5.5	5.0–6.3	3.4–5.7	4.0–5.8	2.9–5.6
EN	5.4±0.3	4.9±0.2	5.6±0.5	4.9±0.4	4.2±0.3	4.1±0.4
	4.9–6.2	4.7–5.4	4.6–6.3	4.2–5.7	3.5–4.7	3.4–5.0
TD	3.8±0.3	3.5±0.3	3.5±0.6	3.4±0.4	2.9±0.5	3.1±0.5
	3.2–4.3	2.9–4.0	2.9–5.0	2.8–4.1	2.2–4.0	2.0–4.2
FFL	10.9±0.9	10.1±0.6	11.1±1.7	8.8±1.2	10.2±0.6	9.1±0.7
	8.9–12.2	9.2–11.0	9.1–14.5	6.3–10.9	8.9–11.6	8.0–11.3
TFL	19.3±1.1	17.1±0.7	18.7±3.6	15.4±1.8	17.3±1.0	15.5±0.9
	17.4–21.5	16.0–18.1	9.2–24.4	12.3–19.5	14.5–19.7	14.0–17.8
TFD	3.4±0.4	3.1±0.3	3.2±0.6	2.6±0.4	2.5±0.3	2.4±0.4
	2.7–4.1	2.5–3.5	2.4–4.2	2.0–3.8	1.8–3.2	1.8–3.4

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TABLE 3. (Continued)

	Gastrotheca elicioi		*Gastrotheca turnerorum*		*Gastrotheca pseustes* 1	
	♀ n = 1	♂ n = 13	♀ n = 3	♂ n = 4	♀ n = 14	♂ n = 4
SVL	67.5	56.0±8.1	55.9±2.1	52.7±2.5	59.2±3.3	58.8±2.9
		46.4–67.8	54.0–58.2	50.0–55.6	54–63.7	54.8–61.4
TIBL	34.1	26.4±5.0	22.4±1.7	22.3±3.5	27.2±2.0	25.4±1.2
		19.8–34.9	20.5–23.6	19.9–27.4	23.1–30.2	23.7–26.3
FL	30.8	24.6±3.7	25.5±0.8	23.3±2.6	28.7±2.2	23.1±5.8
		20.0–32.3	24.7–26.1	21.4–27.2	24.6–31.8	14.8–27.3
HL	21.1	17.5±2.6	17.9±0.6	17.2±1.5	18.4±1.1	18.1±0.8
		14.1–21.3	17.4–18.5	16.2–19.4	16.4–20	17.3–19.2
HW	23.9	19.1±2.8	19.9±0.6	19.0±1.4	20.5±1.4	20±0.7
		14.8–23.3	19.5–20.5	17.9–20.9	17.4–22.2	20±0.7
IOD	9.7	6.5±1.4	5.1±0.2	5.1±0.7	6.2±0.4	6.4±0.6
		4.8–9.2	4.9–5.2	4.6–6.0	5.5–6.9	5.7–7.0
EW	4.4	4.7±0.7	4.8±1.0	4.8±0.3	4.4±0.4	4.8±0.4
		3.8–6.2	3.7–5.6	4.6–5.2	3.9–5.1	4.4–5.2
IND	4.0	3.7±0.8	3.5±0.2	3.5±0.5	3.7±0.3	3.8±0.1
		2.8–5.4	3.3–3.7	2.8–4.0	3.1–4.2	3.7–3.9
ED	6.0	5.3±0.6	5.9±0.2	5.8±0.5	5.4±0.2	5.0±0.4
		4.4–6.5	5.7–6.1	5.4–6.3	5.0–5.8	4.8–5.6
EN	6.3	4.9±0.6	4.4±0.1	4.4±0.3	4.8±0.3	4.8±0.4
		4.1–6.2	4.3–4.5	4.1–4.8	4.4–5.2	4.4–5.2
TD	3.7	3.5±1.0	2.7±0.5	2.9±0.4	2.9±0.4	3.8±0.2
		2.3–5.0	2.3–3.2	2.5–3.4	2.4–3.8	3.5–4.0
FFL	12.9	10.3±2.1	10.3±0.7	8.9±0.9	10.8±0.8	9.9±0.6
		7.9–13.5	9.9–11.1	8.2–10.1	9.5–12.7	9.4–10.7
TFL	22.4	17.7±2.8	18.6±0.1	16.8±1.6	20.0±1.4	18.6±1.3
		14.6–23.0	18.5–18.7	15.5–19.1	17.5–21.8	16.9–19.9
TFD	3.0	3.1±0.4	3.7±0.3	2.8±0.5	3.0±0.3	2.6±0.2
		2.2–3.8	3.4–4.0	2.1–3.3	2.7–3.5	2.4–2.9

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TABLE 3. (Continued).

	Gastrotheca pseustes 2		*Gastrotheca psychrophila*	*Gastrotheca monticola*		*Gastrotheca yacuri*
	♀ n = 43	♂ n = 62	♀ n = 3	♂ n = 2	♀ n = 12	♂ n = 7
SVL	52.7±4.3	48.1±3.8	60.7±2.5	58.1	59.4±3.8	53.0±1.6
	45.1–62.0	37.9–56.3	58.7–63.5	57.4–58.9	54.3–66.3	51.3–55.7
TIBL	23.6±1.7	21.4±1.7	30.4±0.3	27.9	30.2±1.6	27.6±1.2
	20.3–27.6	17.9–25.6	30.2–30.7	27.2–28.6	28.0–33.0	26.2–29.7
FL	25.2±2.8	23.1±2.0	31.0±1.1	26.5	25.9±1.8	23.4±1.1
	13.2–30.1	18.1–28.9	29.8–31.8	24.8–28.3	23.0–28.6	21.7–24.7
HL	16.7±1.2	15.8±1.2	20.0±0.4	17.5	18.9±1.0	16.9±0.6
	14.5–19.5	12.6–20.0	19.8–20.5	17.1–17.9	17.4–20.4	16.2–18.0
HW	18.8±1.5	17.5±1.3	22.4±0.4	19.6	21.7±1.2	19.7±1.0
	16.3–23.2	15.1–20.4	22.0–22.8	19.2–20.1	19.6–23.2	18.0–21.0
IOD	5.5±0.6	5.2±0.5	7.1±0.2	6.8	7.8±0.6	6.9±0.5
	4.6–6.9	4.0–6.9	7.0–7.3	6.7–6.9	7.1–9.0	6.3–7.7
EW	4.6±0.6	4.4±0.5	3.9±0.1	4.8	4.5±0.4	4.2±0.4
	3.2–6.0	2.7–5.5	3.8–4.0	4.3–5.2	3.8–5.1	3.8–4.6
IND	3.3±0.4	3.0± 0.4	3.3±0.2	2.8	3.9±0.2	3.6±0.1
	2.5–4.3	2.0–3.9	3.2–3.5	2.8–2.8	3.3–4.1	3.5–3.8
ED	5.2±0.5	5.0±0.5	4.7±0.2	5.8	5.6±0.3	5.3±0.3
	3.8–6.4	3.2–5.8	4.5–4.8	5.6–6.0	5.3–6.2	4.9–5.7
EN	4.1±0.4	4.0±0.3	4.9±0.5	4.0	5.3±0.3	4.9±0.3
	3.4–5.1	3.2–4.7	4.4–5.4	3.0–5.0	4.6–5.7	4.4–5.4
TD	3.1±0.5	2.9±0.3	3.0±0.2	3.15	3.1±0.3	2.9±0.4
	2.4–3.9	2.3–3.5	2.8–3.2	3.0–3.3	2.7–3.4	2.5–3.6
FFL	9.7±1.1	8.9±1.1	11.5±0.1	9.5	10.8±1.0	9.4±0.5
	7.2–13.0	6.4–12.8	11.4–11.5	8.2–10.8	9.0–12.2	8.9–10.3
TFL	17.1±1.5	15.6±1.3	20.2±1.2	17.6	18.9±1.4	16.9±0.7
	14.2–20.4	12.1–18.3	18.9–21.0	16.2–19.0	16.4–20.8	16.0–17.9
TFD	2.1±0.3	1.9±0.3	3.4±0.1	2.8	3.1±0.4	2.8±0.2
	1.6–2.8	1.1–2.4	3.3–3.5	2.7–2.8	2.5–3.8	2.3–3.0

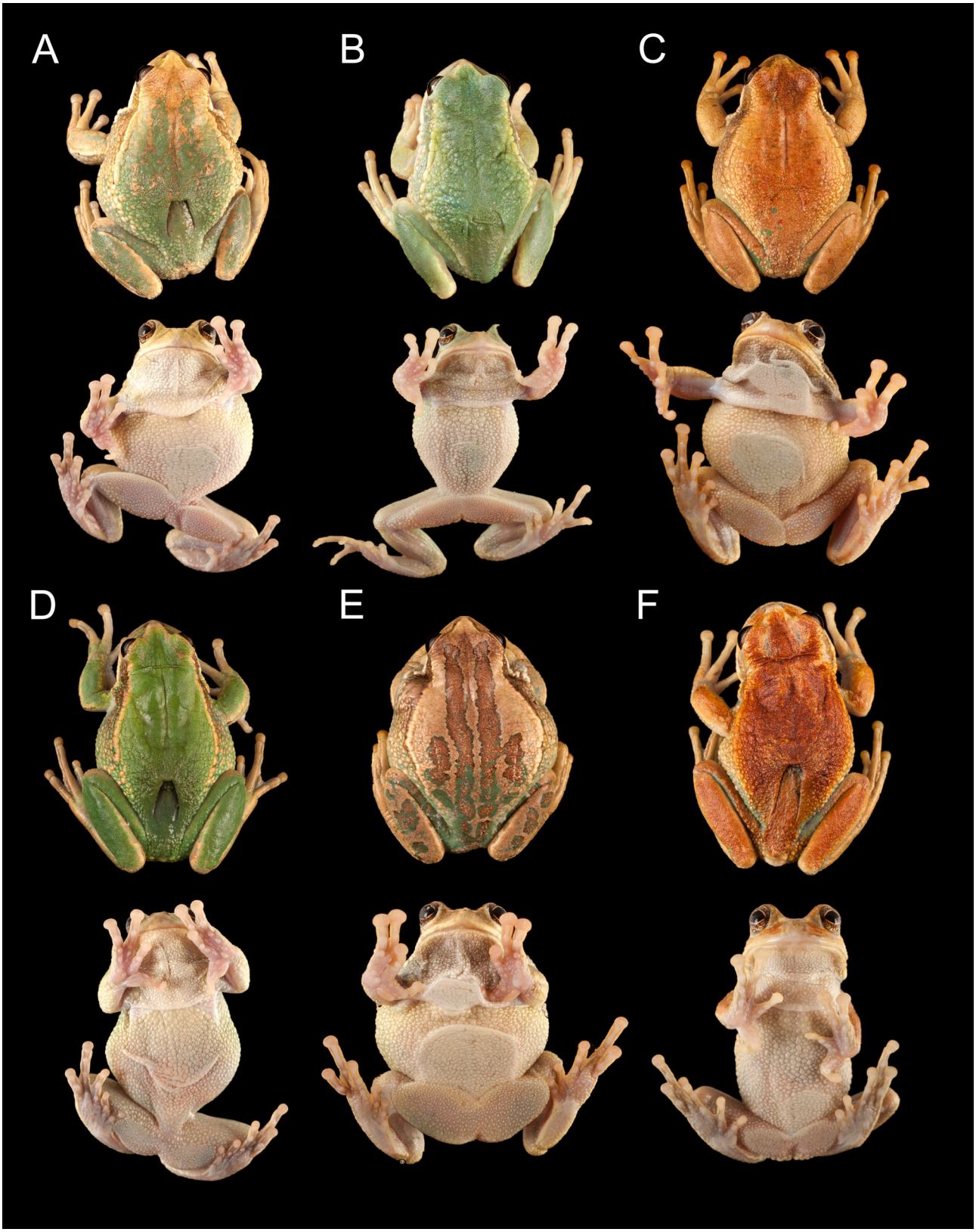

FIGURE 4. Live adults of *Gastrotheca cuencana* showing variation in lateral, groin, thighs and eye color pattern: (A) CJ 1940, female, SVL = 50.2 mm, (B) CJ 1392, male, SVL = 49.2 mm, and (C) CJ 1395, female, SVL = 62.7 mm. Not to scale. Photos by LAC.

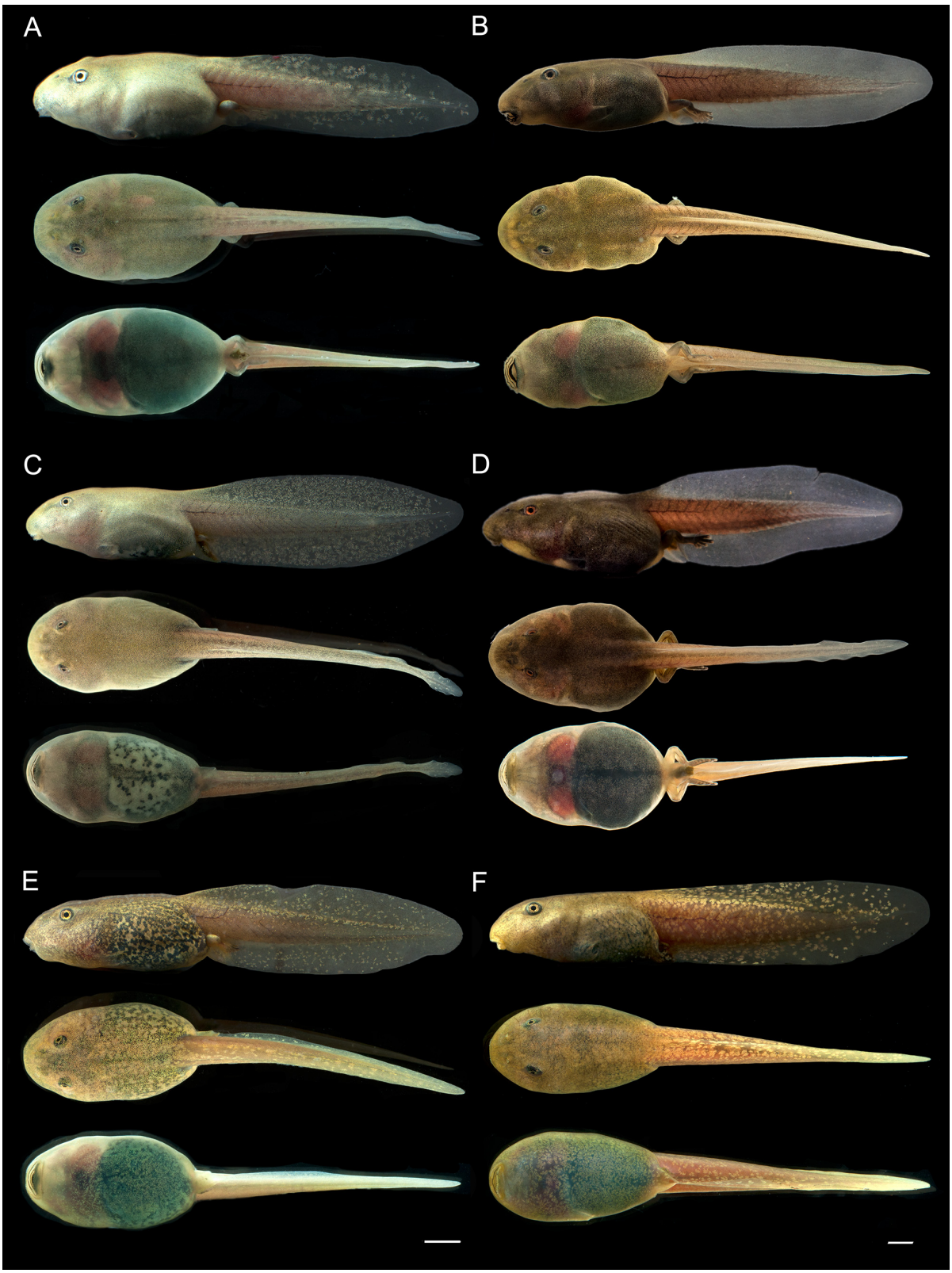

FIGURE 5. Live tadpoles of: (A) *Gastrotheca cuencana* (CJ 1945, Stage 37), from Cuenca, Azuay Province, (B) *Gastrotheca litonedis* (CJ 6813, Stage 37), from Laguna de Busa, San Fernando, Azuay Province, (C) *Gastrotheca lojana* (CJ 1948, Stage 35), from Oña, Azuay Province, (D) *Gastrotheca elicioi* (CJ 4312a, Stage 37), from Loja, Loja Province, (E) *Gastrotheca turnerorum* (CJ 1957, Stage 36), from Laguna Negra de Jimbura, Parque Nacional Yacuri, Loja Province, and (F) *Gastrotheca pseustes* 1 (CJ 1949, Stage 37), from Chillacocha, El Oro Province. Scales = 3 mm (A–D, F) (E). Photos by LAC (A, C, E) and MAM (B, D).

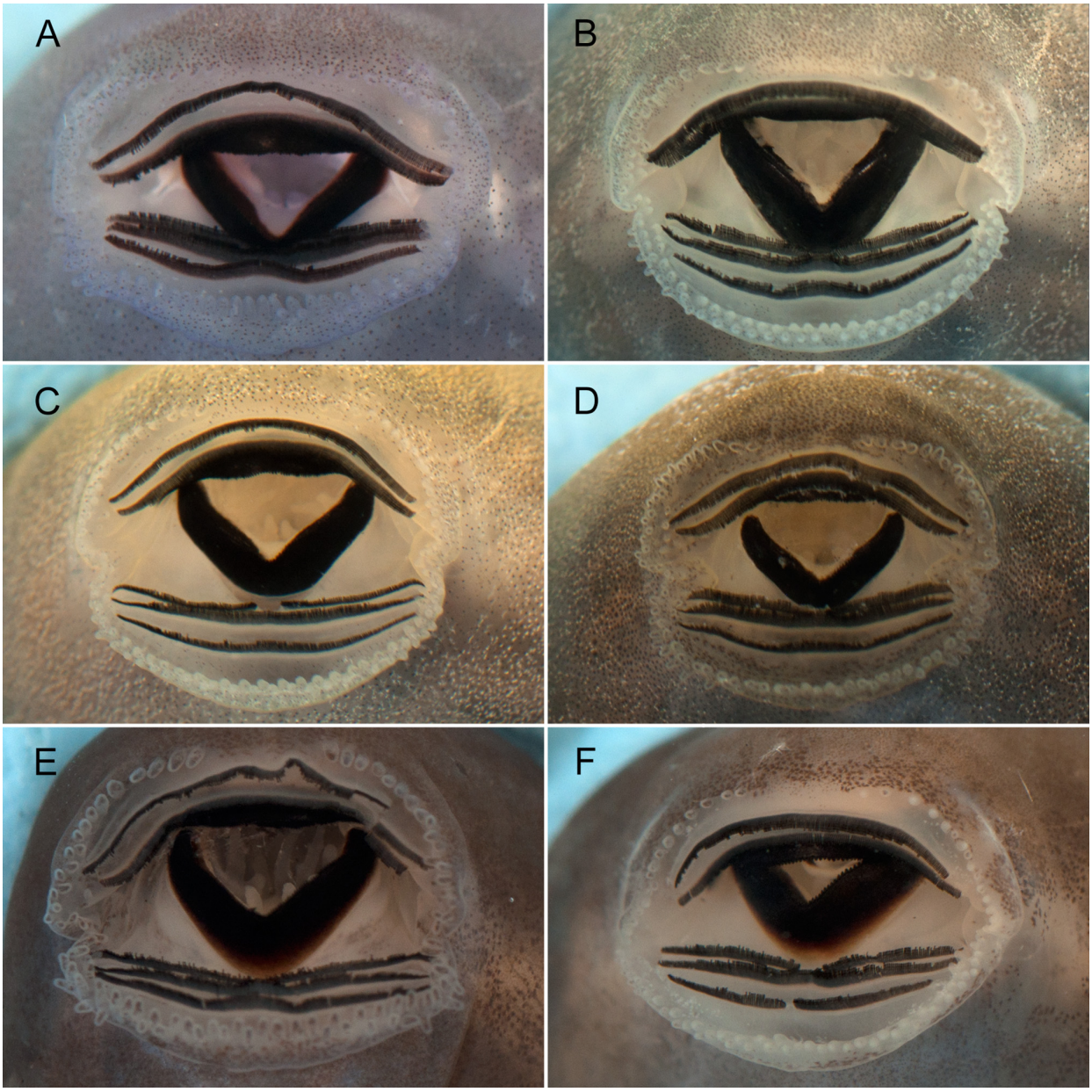

FIGURE 6. Oral discs of: (A) *Gastrotheca cuencana* (CJ 1945, Stage 38), from Cuenca (south control), Azuay Province, (B) *Gastrotheca litonedis* (CJ 5292, Stage 35), from from Laguna de Busa, San Fernando, Azuay Province, (C) *Gastrotheca lojana* (CJ 4309, Stage 37), from El Tablón, Loja Province, (D) *Gastrotheca elicioi* (CJ 4311, Stage 36), from Barrio Puntzará Grande, Loja, Loja Province, (E) *Gastrotheca turnerorum* (CJ 1959, Stage 39), from Laguna Negra de Jimbura, Parque Nacional Yacuri, Loja Province, and (F) *Gastrotheca pseustes* (CJ 1949, Stage 37), from Chillacocha, El Oro Province. Not to scale. Photos by LAC.

Tadpoles. Tadpoles belong to Type IV tadpole of Orton (1953), and the exotroph, benthic ecomorphological guild. All measurements are expressed in millimeters. The following description is based on a specimen in Stage 38 (CJ 1945a), from a series of eight tadpoles (CJ 1945) obtained from a pond at south Cuenca, 2579 m, Azuay Province, Ecuador, by Elicio E. Tapia, Sofía Carvajal-Endara, and Henry Grefa on 8 June 2011 (Fig. 5A). Total length 44.6; body length 17.3 (39% of total length). Body ovoid in dorsal and lateral views, slightly depressed; throat slightly concave in lateral profile, sloping from tip of snout to belly; body width at the level of spiracle 11.5, and height at same position 9.3, head width at level of eyes 8.5. Lateral line system present but barely visible, supraorbital and infraorbital lines both rising at level of tip of snout, extending parallel to the eye and making contact immediately behind eye; angular line descending vertically just porterior of eye to throat, it dorsally contacts with post infraorbital line; anterior oral line descending vertically from oral disc level and behind nares

level to throat; it makes a curve that parallels infraorbital line, forming a circuit continuous with angular and loreal lines; dorsal body and middle body lines not visible. Nostril medium sized (in proportion to body length), ovoid, protruding, having a fleshy annulus, its opening directed anterolaterally. Snout–nostril distance 2.3; internarial distance 2.4. Eye directed dorsally; eye length 1.8, eye width 1.8; interorbital distance 4.3. Spiracle sinistral, located at midbody level, spiracular opening oriented posteriorly; distance from tip of snout to spiracular opening 11.0; end of spiracular tube rounded, attached to body wall, inner wall of spiracular tube not evident; tube length 3.1, tube transverse width 2.0. Vent tube dextral, opening oriented posteriorly, tube length 1.7, tube transverse width 1.8. Tail length 27.2; caudal musculature slender, narrowing gradually until tail terminus; caudal muscle height 3.7, width 3,2; caudal fins well developed and proportional, arising near tail-body junction, forming a low hump; dorsal fin height 3.0, ventral fin height 2.8; maximum height of tail 9.3; tail terminus rounded, caudal musculature not reaching fin terminus.

Oral disc small, ventral, located near tip of snout, not protruding laterally beyond body; transverse width 4.7. It is surrounded by a uniserial row of marginal papillae, interrupted medially on upper lip; lower lip papillae alternate in orientation, giving appearance of two rows; upper lip with 29 papillae on right side and 27 papillae on left side; lower lip bearing 62 marginal papillae; upper jaw sheath medium-sized, forming a smooth arch and finely serrated, height 0.36, transverse width 2.8 (60% of width of oral width); lower jaw sheath V-shaped, open and finely serrated, width 1.92, height 0.7. Labial tooth row formula 2/3(1); tooth rows lengths: A1: 3.6, A2: 3.5, P1 right row 1.5, P1 left row 1.6, P1 gap 0.2, P2: 3.4, P3: 3.0. (Fig. 6B).

Color in preservative. Dorsum dull gray with darker areas on flanks, above eye, and on throat; body contour and snout translucent. Caudal musculature and fins with scattered cream dots, with higher suffusion near tail base, otherwise translucent. Venter pale, translucent in belly region, guts exposed; eyes lavender gray; oral apparatus translucent.

Color in life. In dorsal view, body olive-cream; snout and flanks paler olive-cream. In ventral view, guts dark gray in belly area; reddish gills visible throughout throat. Caudal musculature covered by a nearly continuous line of cream marks, proximal half of musculature reddish cream with myomeres and medial line well defined, distal half translucent; dorsal and ventral fins translucent, with scattered cream dots, heavily suffused near tail-body junction. Spiracle, oral apparatus, and legs olive-cream. Iris gold.

Variation. Variation of 28 meristic characters of tadpoles in Stages 37–39 (CJ 1945) are shown in Table 4. Total length varies between 42.3 (Stage 37) and 48.7 (Stage 39) and tail length proportion remains about 61%; labial tooth row formula is 2/3(1). The number of marginal papillae varies among specimens and Gosner stages, variation in number of ventral papillae at lower lip is high (39–64).

TABLE 4. Variation of 26 meristic characters of tadpoles in Stages 37–39 of *Gastrotheca cuencana* (CJ 1945). Values are given in mm, mean±standard deviations (first row) and ranges (second row), number of specimens in parentheses. See Materials and methods for character abreviations.

	Stage 37 (n=2)	Stage 38 (n=1)	Stage 39 (n=5)
TL	42.34–43.2	44.62	44.6±2.33
			42.83–48.65
BL	16.3–17.08	17.44	17.14±0.77
			16.49–18.66
BW	10.16–10.38	11.53	11.14±0.81
			10.44–12.53
BH	8.57–8.62	9.27	9.34±0.23
			8.94–9.49
HWEL	7.99–8.49	8.5	8.81±0.57
			8.28–9.73
TAL	26.04–26.12	27.18	27.45±1.56
			25.93–29.99

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TABLE 4. (Continued)

	Stage 37 (n=2)	Stage 38 (n=1)	Stage 39 (n=5)
TLP (%)	60.46–61.5	60.91	61.56±0.77
			60.54–62.56
MTH	7.79–8.06	9.33	8.49±0.36
			8.01–9.02
TMW	2.99–3.07	3.16	3.19±0.17
			3.01–3.37
TMH	3.32–3.77	3.7	3.65±0.4
			3.16–4.26
SND	1.93–2.3	2.3	2.32±0.24
			2–2.6
IND	2.33–2.4	2.4	2.33±0.08
			2.2–2.4
END	1.67–1.7	1.7	1.76±0.05
			1.7–1.8
EL	1.7–1.8	1.8	1.86±0.05
			1.8–1.9
EW	1.7–1.73	1.8	1.86±0.05
			1.8–1.9
IOD	4.13–4.33	4.33	4.43±0.19
			4.27–4.73
VP	60–64	62	49±11.38
			39–67
DP right	22–26	29	23.8±1.48
			22–27
DP left	26–27	27	24.6±1.95
			22–26
WOD	4.67–4.67	4.73	4.73±0.12
			4.6–4.87
WUJ	2.67–2.67	2.8	2.72±0.16
			2.53–2.93
UJP (%)	57.14–57.14	59.15	57.46±2.9
			55.07–61.11
SL	1.8–1.8	3.1	2.25±0.6
			1.5–3
SW (%)	1.93–2	2	2.25±0.42
			1.6–2.67
VTL	1.33–2.25	1.7	2.81±0.23
			2.5–3.13
VTW	1.2–1.63	1.8	1.9±0.32
			1.6–2.33

We documented changes in coloration during ontogenetic development of one, mostly brown individual (CJ 1945) (Fig. 7). At Stage 41, the dorsum and flanks are diffuse brown with a well-defined pattern of brown-gray paravertebral stripes and a couple of blotches at posterior dorsolateral body. A dark, gray-black stripe borders the canthal and dorsolateral body extending to level of midbody, bordered dorsally by a creamy-white stripe that becomes wider at the distal end. The iris has a red suffusion. By Stage 46, markings on the dorsum and flanks are better defined and the black-gray stripe of flanks becomes a nearly black stripe; fingers are yellowish cream. Scattered green pigments are present in the anterior portion of the paravertebral stripes.

Comparisons. Tadpoles of *Gastrotheca cuencana* may occur in sympatry with the ones of *G. pseustes* 2. *Gastrotheca cuencana* differs from it by having less pigmentation on dorsum and venter, by lacking a reticulated pattern on flanks and by having a flesh colored tail musculature.

FIGURE 7. Ontogenetic changes in live *Gastrotheca cuencana* (CJ 1945) from Cuenca, Azuay Province, Ecuador. Stages of Gosner: (A) Stage 41, and (B) Stage 46. Scale = 3 mm. Photos by LAC.

Vocalization. Eight individuals of *Gastrotheca cuencana* were recorded from two locations in Azuay Province (3 individuals from Cuenca and 3 from Río Mazán) and from one location in Cañar Province (2 individuals from Papaloma de la Nube) (Appendix III). Descriptive statistics of the acoustic variables are provided in Table 5. The advertisement call of *G. cuencana* is a *simple call*, composed of a series of short, single-pulsed notes, emitted at regular intervals (Fig. 8A–D). In our recordings the calls have between 3 and 19 notes per call. The notes had a mean duration of 0.016 s (SD = 0.007) and a mean inter-note interval of 2.783 s (SD = 1.004). The mean dominant frequency of the call was 1147.9 Hz (SD = 99.536), with a mean 90% bandwidth of 1018.6–1269.4 Hz. The fundamental frequency and harmonics are not clearly recognizable.

TABLE 5. Quantitative description of the advertisement calls (mean±SD, range) of the *Gastrotheca* species from Southern Ecuador. See text for details.

	Gastrotheca litonedis	***Gastrotheca cuencana***	***Gastrotheca lojana***	***Gastrotheca elicioi***	***Gastrotheca yacuri***	***Gastrotheca pseustes***	***Gastrotheca testudinea***
Call structure	simple	simple	complex	complex	complex	complex	complex
Number of calls (number of individuals)	23 (9)	9 (8)	41 (5)	16 (7)	15 (4)	9 (4)	17 (6)
Call duration (s)	8.758±11.029 (0.036–34.579) n = 23	26.279±18.899 (5.813–65.629) n = 9	1.078±0.288 (0.567–1.375) n = 41	3.697±1.286 (1.543–5.878) n = 16	2.552±0.606 (1.636–3.658) n = 15	5.498±2.513 (3.682–11.779) n = 9	1.561±0.719 (0.459–2.622) n = 17
Inter-call interval (s)	8.026±8.996 (3.077–38.860) n = 14	25.354	5.319±1.883 (3.466–11.610) n = 36	21.866±11.511 (5.501–46.398) n = 8	5.656±3.185 (1.455–10.844) n = 16	19.008±23.379 (5.047–53.913) n = 4	4.382±2.729 (2.093–11.399) n = 10
Call rate (calls/min)	6.34±3.245 (0.93–8.64) n = 5	1.65	10.33±1.804 (7.55–12.18) n = 5	2.53±0.313 (2.16–3.03) n = 5	7.37±1.761 (6.14–9.39) n = 3	3.52±2.233 (1.03–5.34) n = 3	10.51±4.302 (4.37–14.26) n = 5
Long notes/call	–	–	1	1–7	1–3	1–5	1
Short notes/call	1–21	3–19	0–2	0–6	0–3	0–6	0–3
Long note rate (notes/s)	–	–	–	1.66±0.414 (1.00–2.86) n = 15	0.66±0.098 (0.48–0.79) n = 11	0.47±0.122 (0.37–0.65) n = 5	–
Short note rate (notes/s)	0.53±0.049 (0.43–0.58) n = 11	0.41±0.138 (0.20–0.58) n = 9	2.34±0.113 (2.17–2.51) n = 15	2.21±0.451 (1.58–2.86) n = 15	1.73±0.350 (1.22–2.11) n = 10	1.55±0.193 (1.28–1.81) n = 6	1.92±0.166 (1.60–2.06) n = 10
Long notes duration (s)	–	–	0.562±0.125 (0.246–0.764) n = 41	0.188±0.150 (0.030–1.112) n = 65	0.634±0.091 (0.518–0.892) n = 35	0.878±0.188 (0.440–1.227) n = 18	0.746±0.154 (0.459–1.040) n = 17

……*continued on the next page*

TABLE 5. (Continued)

	Gastrotheca litonedis	***Gastrotheca cuencana***	***Gastrotheca lojana***	***Gastrotheca elicioi***	***Gastrotheca yacuri***	***Gastrotheca pseustes***	***Gastrotheca testudinea***
Short notes duration (s)	0.075±0.025 (0.036–0.142) n = 133	0.016±0.007 (0.008–0.046) n = 92	0.064±0.027 (0.025–0.119) n = 50	0.027±0.014 (0.005–0.077) n = 47	0.072±0.020 (0.040–0.100) n = 33	0.080±0.046 (0.014–0.169) n = 30	0.080±0.040 (0.033–0.188) n = 26
Inter-note interval (s)	1.768±0.286 (1.264–2.772) n = 113	2.783±1.004 (1.552–5.907) n = 82	0.356±0.107 (0.247–0.593) n = 48	0.452±0.125 (0.264–0.784) n = 95	0.549±0.214 (0.284–1.041) n = 38	0.795±0.502 (0.420–2.433) n = 40	0.452±0.069 (0.344–0.608) n = 25
Number of pulses	–	–	17.59±2.418 (9–21) n = 41	3.47±1.695 (2–8) n = 72	32.24±7.504 (22–49) n = 33	32.72±6.867 (23–54) n = 18	18.88±2.870 (13–24) n = 17
Pulse rate (pulses/s)	–	–	33.78±6.023 (23.71–40.50) n = 41	53.33±8.007 (32.26–90.90) n = 70	54.48±7.965 (45.74–64.81) n = 33	40.11±5.605 (32.95–53.79) n = 18	25.85±2.778 (19.89–29.90) n = 17
Dominant frequency (Hz)	1224.0±66.415 (1119.7–1312.5) n = 58	1147.9±99.536 (937.5–1292.0) n = 47	1118.1±126.872 (947.5–1378.1) n = 29	1249.4±169.862 (861.3–1550.4) n = 89	1496.7±38.643 (1464.3–1550.4) n = 23	1359.0±37.981 (1292.0–1378.1) n = 9	1069.1±86.448 (861.3–1205.9) n = 17
Frequency 5% (Hz)	1114.7±106.277 (861.3–1218.8) n = 58	1018.6±123.218 (750.0–1205.9) n = 47	986.1±127.326 (861.3–1205.9) n = 29	807.1±121.382 (602.9–1119.7) n = 89	1366.7±25.433 (1312.5–1378.1) n = 23	1043.2±245.3 (689.1–1205.9) n = 9	800.5±79.203 (602.9–947.5) n = 17
Frequency 95% (Hz)	1308.1±67.707 (1205.9–1406.3) n = 59	1269.4±78.136 (1125.0–1378.1) n = 47	1348.4±86.977 (1205.9–1464.3) n = 29	1416.8±159.568 (1205.9–1636.5) n = 89	1637.9±33.837 (1550.4–1687.5) n = 23	1483.4±57.422 (1378.1–1550.4) n = 9	1205.9±105.5 (947.5–1378.1) n = 17

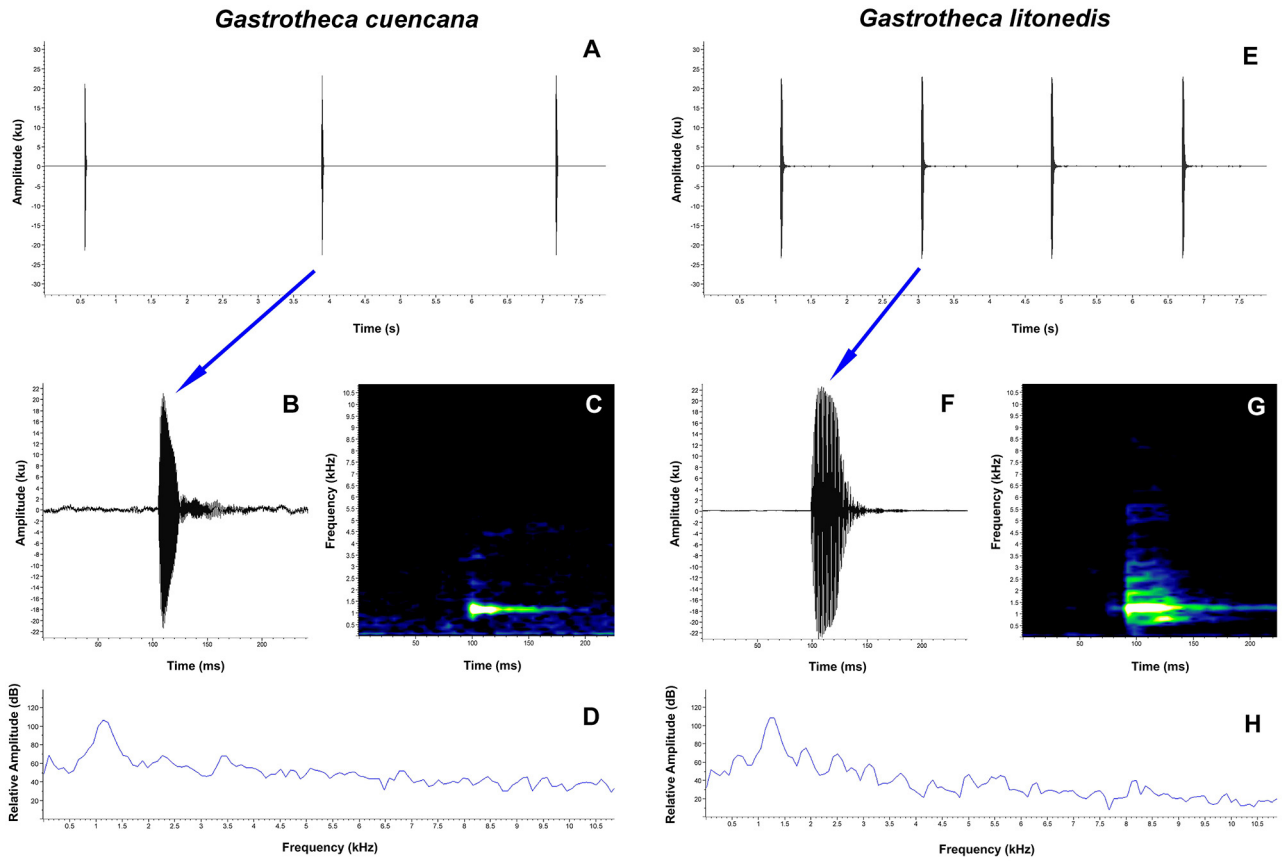

FIGURE 8. Advertisement calls of *Gastrotheca cuencana* (A–D) and *G. litonedis* (E–H): (A) oscillogram of a three notes section of the call, (B) oscillogram of a single note, (C) spectrogram of a single note, (D) power spectrum of a single note, (E) oscillogram of a four notes section of the call, (F) oscillogram of a single note, (G) spectrogram of a single note, (H) power spectrum of a single note. All spectrograms at Hanning window function, 512 bands resolution. See text for details.

Comparisons. The advertisement call of *Gastrotheca cuencana* is similar to that of *G. litonedis*, all the other species of *Gastrotheca* in the southern Ecuadorian Andes have complex calls. However, the call of *G. cuencana* has a lower note rate, shorter note duration, longer inter-note interval and a lower dominant and 90% bandwidth frequency compared with *G. litonedis* (Table 5).

Distribution and ecology. *Gastrotheca cuencana* is known from the Paute Basin, which includes the eastern and western Cordilleras (Fig. 9). Its elevational range is 2407–3172 m in an area of extent of occurrence of about 1168 km^2.

This nocturnal, semiarboreal species inhabits mostly disturbed areas and a few forests in the Evergreen High Montane Forest of the Cordillera Occidental of the Andes (Ministerio de Ambiente del Ecuador 2012), where the average annual rainfall is 660–1122 mm and the average annual temperature is 9.6–15.2 ºC (Fick & Hijmans 2017). This species is found in pasture lands and urban grasslands where lentic water is available for tadpoles; thus, the frogs occur close to irrigation ditches, water reservoirs, temporary ponds or wetlands. The holotype and eight other individuals were collected in grassland in an urban area (Cuenca). Males were calling from small shrubs at approximately 80–100 cm above the ground. Females were perched on branches of shrubs at approximately 40 cm above the ground and also among the grass. A brooding female is depicted in Figure 10K. Eight tadpoles were found in a small temporary pond. *Gastrotheca cuencana* is syntopic with *G. pseustes* (*sensu lato*) throughout most of its range.

Conservation status. We suggest that *Gastrotheca cuencana* should be considered as Endangered according to criteria B1ab(i,ii,iii,iv) of the IUCN Red List. Its small area of known occurrence (1168 km^2) is fragmented, and its habitats are in heavily human populated areas. For example, the city of Cuenca is rapidly growing and occupying previous rural areas (Fig. 11B) where swampy areas are being drained. One population inhabits Cajas National Park, which affords protection from habitat destruction. Some efforts (*in situ* and *ex situ*) to protect this

species are underway by parties of the Cajas National Park, by Amaru Zoo (Amphibian Ark 2013), and the city council of Cuenca (Siavichay-Pesántez *et al.* 2016). However, these efforts urgently need to be reinforced.

Etymology. The specific name *cuencana* is an adjective referring to people born in Cuenca, the capital city of the province of Azuay, where this species occurs. We also use this name to highlight the pioneer efforts taking place in Cuenca, throughout the project Conservation of the Urban Biodiversity of the Municipality. The project is directed to protect the urban and suburban species of frogs through biorestauration and protection of watersheds, river banks, wetlands, and frog ponds (Arbeláez Ortiz & Vega Toral 2008, Siavichay-Pesántez *et al.* 2016).

Comments. *Gastrotheca cuencana* was confused with *G. litonedis* in the past. Our recognition of both species emphasizes the discrete morphological and acoustic differences between them. *Gastrotheca cuencana* belongs to the subgenus *Duellmania* (*sensu* Duellman 2015).

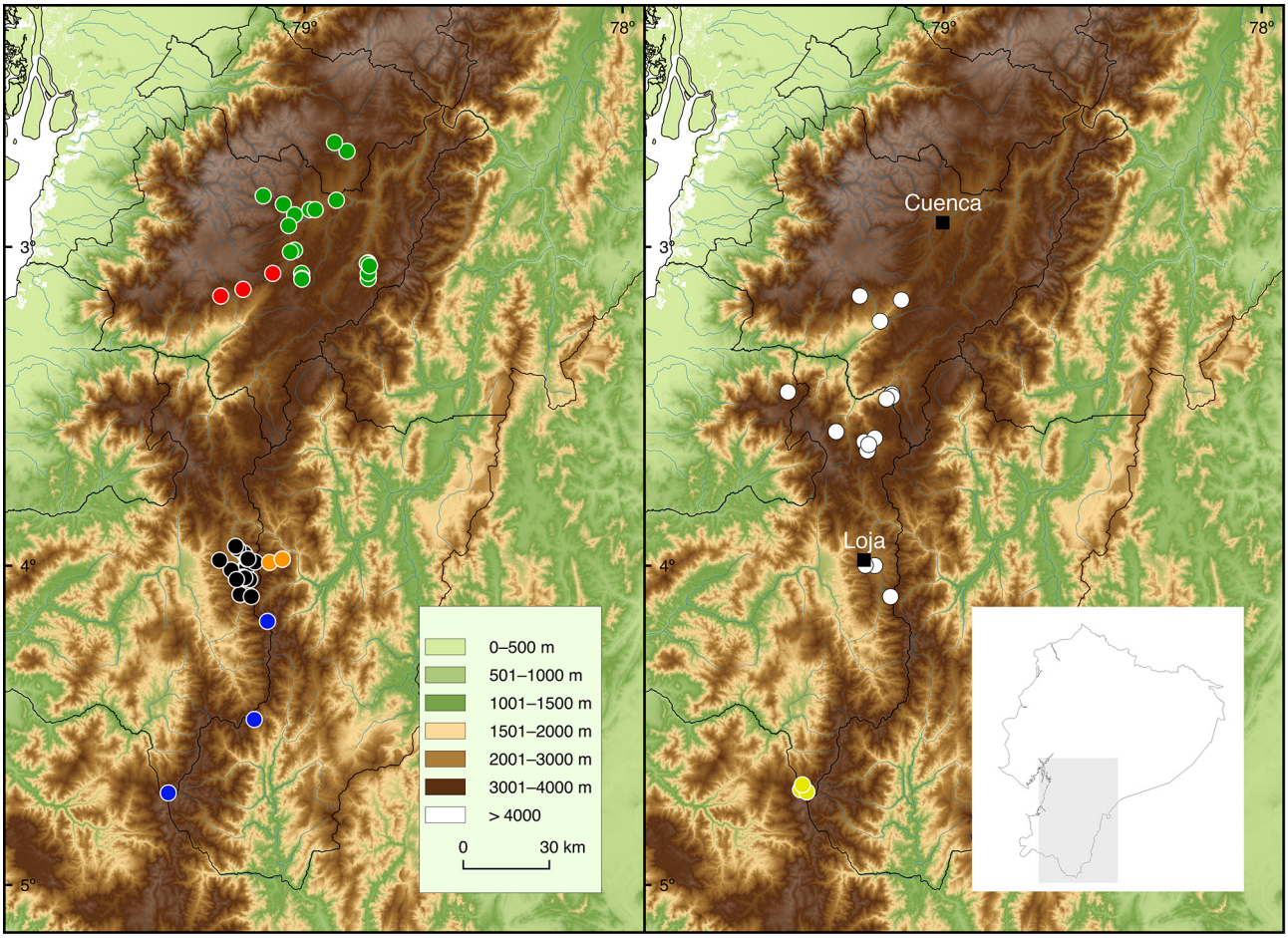

FIGURE 9. Localities of known occurrence of *Gastrotheca cuencana* (green), *G. litonedis* (red), *G. elicioi* (black), *G. psychrophila* (orange), *G. turnerorum* (blue), *G. lojana* (white), and *G. yacuri* (yellow). See Appendix II for detailed locality data. Some nearby localities are represented by a single symbol. Inset map indicates location of southern Ecuador (box) in Ecuador.

***Gastrotheca elicioi* sp. nov.**

urn:lsid:zoobank.org:act:3D26B088-B527-4362-94E8-647FF26C8419

Holotype. CJ 1402 (Fig. 12), an adult male (collected as tadpole in the field and captive raised), from Cajanuma, entrance to Parque Nacional Podocarpus in the Loja-Vilcabamba road, 2456 m (04° 05' 25.51" S, 79° 12' 09.97" W), Loja Province, Ecuador, one of a series obtained on 14 June 2011 by Elicio E. Tapia, Sofía Carvajal-Endara, and Henry Grefa.

Paratypes. (Total 18: 11 males, 3 females, 4 juveniles). Ecuador: Loja: CJ 413–4 (juvenile, male), 1398–401 (four males), 1941 (male) collected with the holotype; KU 142603–5 (female, subadults), from 5.5 km W Loja,

2330 m (04° 00' 48.99" S, 79° 13' 50.99" W), on 17 July 1971 by William E. Duellman and Linda Trueb; KU 142607–8 (subadult, female), 148549–51 (males, female), from 5.5 Km W Loja, 2330 m (04° 00' 48.99" S, 79° 13' 50.99" W), on 23 July 1971 by William E. Duellman and Linda Trueb; KU 202688 (male), from 5.2 km W Loja, 2310 m (03° 58' 58.73" S, 79° 16' 02.21" W), on 10 March 1984 by William E. Duellman; KU 217511–2 (males), from 6.8 km E Loja ca. Loja-Zamora line (03° 59' 19" S, 79° 09' 21.99" W), on 9 January 1990 by David Kizirian, John J. Wiens, and Luis A. Coloma.

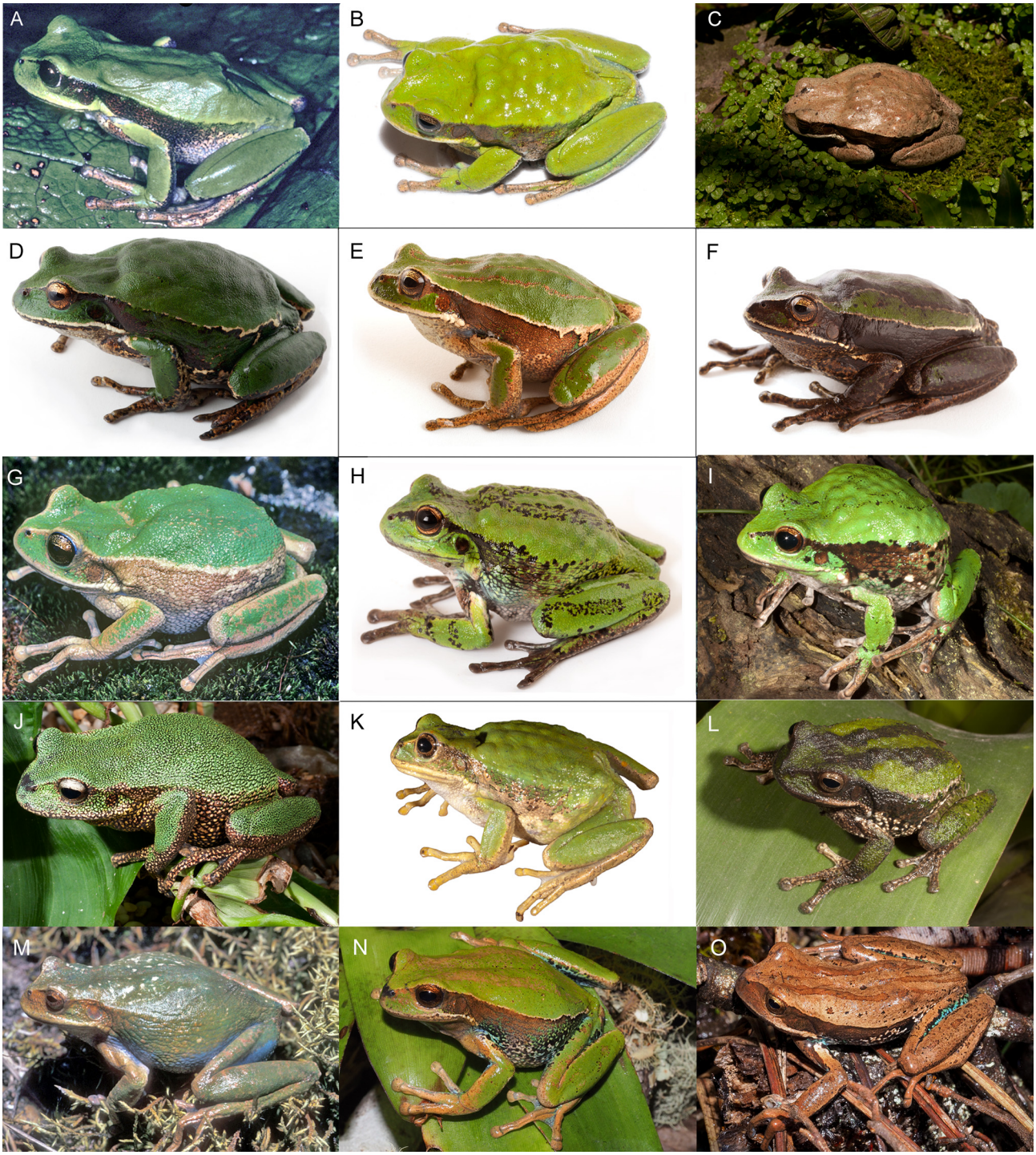

FIGURE 10. Live adults and brooding females of (A) holotype of *Gastrotheca litonedis* (KU 202690, SVL = 62.4 mm), of (B–C) *G. litonedis* (D–G) *G. pseustes*, G is the holotype (KU 203443, SVL = 55.2 mm) from 7.1 km N San Lucas, 2940 m, (H–I) *G. elicioi*, (J) *G. turnerorum*, (K) *G. cuencana*, (L) *G. lojana*, (M) female *G. psycrophila* (KU 164233, SVL = 63.5 mm) from 15 km E of Loja, 2850 m, and (N–O) *G. yacuri*, N is the holotype (CJ 5822, SVL = 57.4 mm). Not to scale. Photos A, G, M by WED; B–F, H–L by LAC, and N–O by PS.

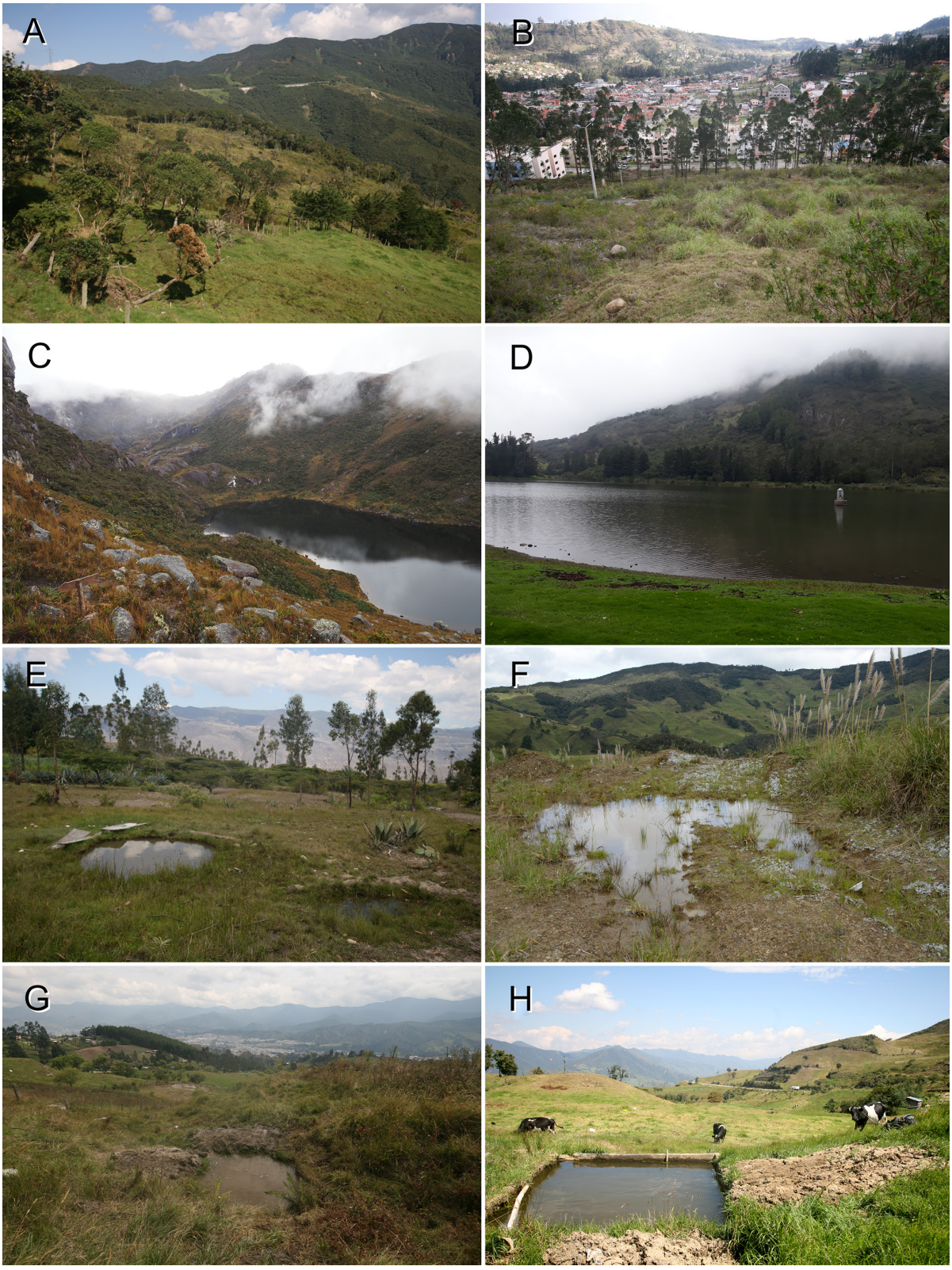

FIGURE 11. (A) Habitat of *Gastrotheca elicioi*, *G. lojana*, *G. pseustes*, *G. psychrophila*, and *G. turnerorum* at the Abra de Zamora, Loja Province, (B) habitat at the type locality of *G. cuencana* in Cuenca, Azuay Province, (C) habitat of *G. turnerorum* and *G. yacuri* at Lagunas Negras, Parque Nacional Yacuri, Loja Province, (D) habitat of *G. litonedis, G. lojana,* and *G. pseustes* at Laguna de Busa, Azuay Province, (E) habitat of *Gastrotheca lojana* at El Tablón, Loja Province, (F) habitat of *G. pseustes* and (G–H) habitats of *G. elicioi* at Loja and 15 Km N of Loja, Loja Province. Photos A–B, E, G, H by LAC, C by PS, D by MMM, and F by Jan Verkade.

FIGURE 12. Live holotype of *Gastrotheca elicioi* (CJ 1402, male, SVL = 46.4 cm): A) dorsal, ventral and lateral views, (B) ventral view of left hand, enlarged 1.8X of A, and (C) ventral view of left foot, enlarged 2.1X of A. Photos by LAC.

Referred specimens. Ecuador: Loja: QCAZ 22370 (male), from Zamora Huayco, Loja, 3018 m (04°0 5' 49.98" S, 79° 10' 02.5" W), on 2 December 2002 by Diego Almeida-Reinoso; QCAZ 46319–20 (males), from Zamora Huayco, Loja, 3018 m (04° 05' 49.98" S, 79° 10' 02.5" W), on 5 December 2009 by Diego Almeida-Reinoso and Samael D. Padilla; CJ 1841–902 (62 juveniles), from Loja, Barrio La Palmera, Parroquia Sucre, on 22–25 April 2013 by Elicio E. Tapia.

Diagnosis. Included in the genus *Gastrotheca* by having a closed brood pouch on dorsum of female. A moderately large species (up to 67.5 mm SVL in female, 46.4–67.8 mm SVL in males, n = 13) with tibia length

42−50% SVL, slightly longer than foot; (2) interorbital distance larger than the width of upper eyelid; (3) skin on dorsum finely granular, not co-ossified with skull, lacking transverse ridges; (4) supraciliary processes absent; (5) heel lacking calcar or tubercle; (6) tympanic annulus smooth to slightly granular; (7) Fingers I and II about equal in length, width of discs about twice width of the digits proximal to discs; (8) fingers unwebbed; (9) webbing between external toes extending nearly to antepenultimate subarticular tubercle on Toe IV and proximal to penultimate subarticular tubercle on Toe V; (10) in life, dorsum green, tan, brown, or reddish-brown with or without dark paravertebral marks; (11) head markings consisting of a pale labial stripe on the posterior margin of the lip, a black canthal stripe and a dark triangular interorbital mark in some individuals; (12) a fragmented, narrow, pale dorsolateral stripe present; (13) flanks bronze-brown, tan, or green with or without small pale spots; groin and anterior and posterior surfaces of thighs lightly mottled with tinges of green or blue; (14) venter cream with small brown flecks or spots; (15) brood pouch single, dorsal.

In comparison with similar species *Gastrotheca elicioi* is most like *G. lojana*, *G. cuencana*, *G. litonedis*, *G. turnerorum*, and *G. pseustes* in Ecuador and *G. monticola* in Peru. *Gastrotheca elicioi* differs from *G. lojana*, *G. cuencana*, and *G. litonedis* in color pattern as follows (compare these species in Fig. 10). *Gastrotheca elicioi* and *G. litonedis* have distinct dark canthal stripes, which are absent in *G. lojana* and inconspicuous or absent in *G. cuencana*. The groin and anterior and posterior surfaces of the thighs are slightly mottled in *G. elicioi*, whereas in *G. lojana* they are heavily mottled; these surface are translucent cream without marks in *G. cuencana* and usually brown in *G. litonedis*. If any marks are present on the dorsum in *G. elicioi*, they usually consist of a triangular interorbital mark, which is connected or not with two narrow and curved paravertebral marks. In contrast, in *G. lojana* the interorbital mark is a transverse bar usually connected with two broad paravertebral marks; in *G. cuencana* and *G. litonedis* an interorbital mark is absent. *Gastrotheca lojana* and *G. cuencana* have a conspicuous, elevated row of dorsolateral warts, whereas they are barely raised in *G. elicioi* and *G. litonedis*. Additionally, in *G. elicioi* the dark bars on the limbs, when present, are shorter, thinner and less defined than in *G. lojana*, whereas in *G. cuencana* and in some *G. litonedis* the bars are replaced by irregular blotches. *Gastrotheca elicioi* has a cream venter with dark flecks or marks, whereas the venter is uniform creamy white in *G. cuencana* and pale brownish gray in *G. litonedis*. *Gastrotheca cuencana* also differs from *G. elicioi* by having cream dorsal surfaces of the fingers, whereas they are brown, green, or tan in *G. elicoi*. *Gastrotheca turnerorum* and *G. pseustes* differ from *G. elicioi* (compare these species in Fig. 10) by having the skin on dorsum areolate and weakly areolate respectively, whereas in *G. elicioi* the skin on dorsum is finely granular. Also, they differ by lacking an interorbital mark, and bars on limbs, which can be present *G. elicioi*. *Gastrotheca pseustes* is sympatric with *G. elicioi*, from which it differs notably by having smaller digital discs (larger in *G. elicioi*) and lacking a pale dorsolateral and supracloacal stripes, which are fragmented in *G. elicioi*. *Gastrotheca monticola* is the sister species of *G. elicioi* and their minimum genetic divergence is 3.0% (in a DNA dataset of 438 bp, 16S gene). *Gastrotheca monticola* differs from *G. elicioi* by having the axilla and groin, concealed surfaces of the thighs, and the dorsal surfaces of the feet green with well-defined black spots on a green or tan background, whereas in *G. elicioi* the groin and anterior and posterior surfaces of thighs are lightly mottled with tinges of green or blue. Finally, the advertisement call of *G. elicioi* is unique amongst the calls of *Gastrotheca* in southern Ecuador, in that the long, pulsed notes are produced after the short ones, whereas the other species tend to produce the long, pulsated notes before the short ones.

Description of the holotype. An adult male (Fig. 12) collected as a tadpole and raised in the laboratory; body moderately robust; SVL 46.4 mm; head wider that long; snout rounded in dorsal view, bluntly rounded in profile; canthus rostralis round in section; loreal region concave, lips rounded; top of head flat; interorbital distance 142% of width of upper eyelid; internarial area elevated; nostrils not protuberant, directed anterolaterally, posterior to level of anterior margin of lower jaw; diameter of eye greater than its distance from nostril; tympanum round, separated from the eye in a distance approximately one and a half the diameter of tympanum; tympanic annulus and membrane smooth; supratympanic fold moderately weak, extending from corner of eye to tympanum and on to insertion of forelimb. Dentigerous vomerine processes narrowly separated medially, each bearing three teeth.

Arm robust; ulnar tubercles absent; hand and fingers moderately large (TFL 31% of SVL), unwebbed, with distinct narrow lateral fringes; discs much wider than digits, slightly truncated, width of disc on Finger III greater that diameter of tympanum; relative lengths of fingers I=II<IV<III; subarticular tubercles prominent, round, none bifid; supernumerary tubercles, small, numerous, rounded; palmar tubercle bifid, prepollical tubercle elliptical. Hind limb robust; tibia length 43% SVL; foot length 43% SVL; calcar and tarsal tubercles absent, inner tarsal fold on distal half of tarsus; outer metatarsal tubercle absent; inner metatarsal tubercle large, elliptical; toes moderately

long; relative length of toes I<II<III<V<IV; basal webbing between Toes I and II; webbing formula for other toes II1—2III1—2IV2—1V; subarticlular tubercles moderately small, rounded; supernumerary tubercles, numerous, rounded, present on proximal segments of digits. Nuptial pad absent.

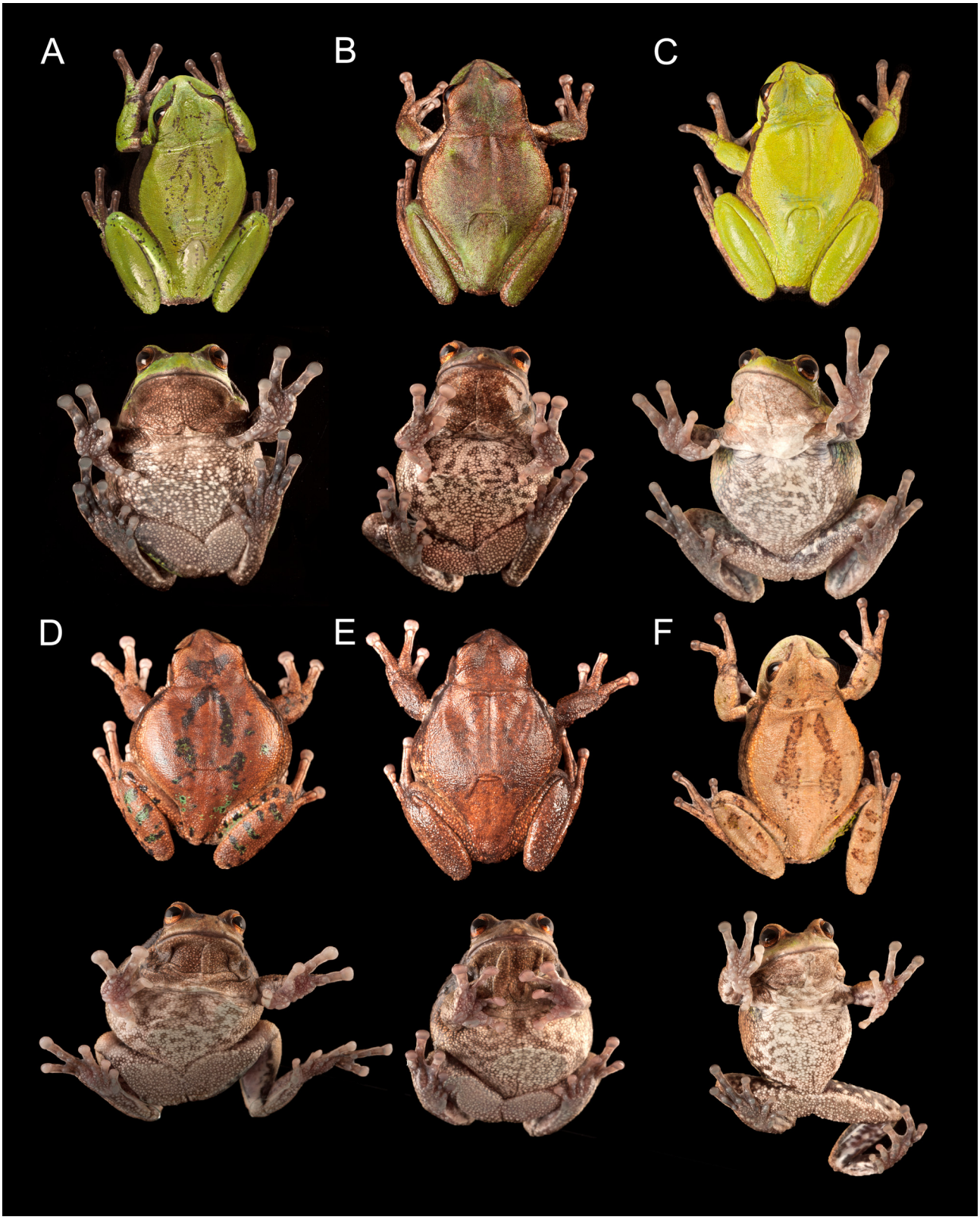

FIGURE 13. Live adults and subadults of *Gastrotheca elicioi* showing variation in dorsal and ventral color pattern: (A) CJ 1841, subadult female, SVL = 33.9 mm, (B) CJ 1399, male, SVL = 48.9 mm, (C) CJ 1843, subadult female, SVL = 40.1 mm, (D) CJ 1400, male, SVL = 52.0 mm, (E) CJ 1941, male, SVL = not taken, and (F) CJ 1842, subadult female, SVL = 33.7 mm. Not to scale. Photos by LAC.

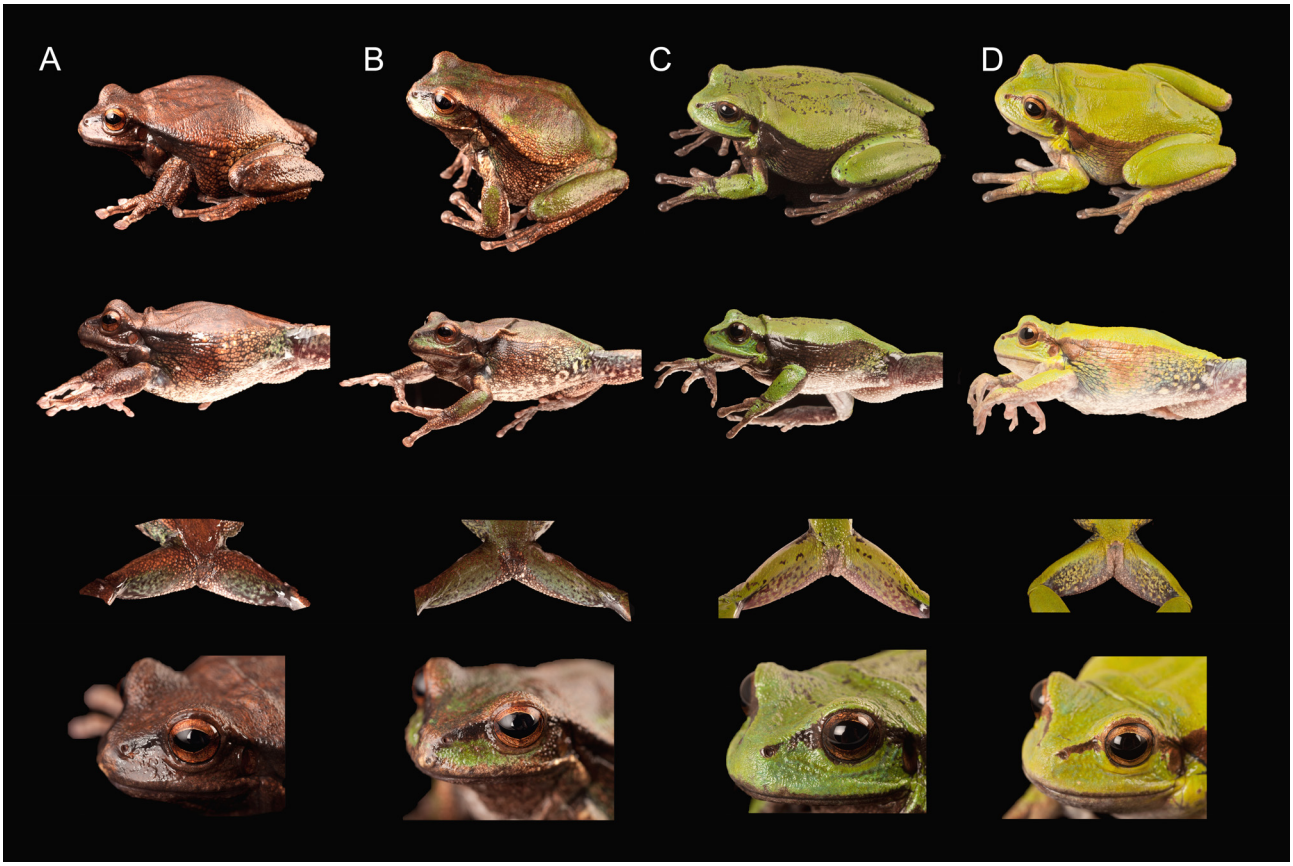

FIGURE 14. Live adults of *Gastrotheca elicioi* showing variation in lateral, groin, thighs and eye color pattern: (A) CJ 1941, male, SVL = not taken, (B) CJ 1399, male, SVL = 48.9 mm, (C) CJ 1841, subadult female, SVL = 33.9 mm, and (D) CJ 1843, subadult female, SVL = 40.1 mm. Not to scale. Photos by LAC.

Skin on dorsum finely granular; skin on flanks coarsely granular; skin on throat, venter surfaces of thighs, and arms granular; skin on belly areolate; skin on venter surfaces of shanks smooth; numerous small tubercles lateral to cloacal opening. Vocal sac single, median, subgular. Vocal slits present at posterior lingual margins of mandibles. Tongue broad, suboval, notched posteriorly, fully attached to mouth floor.

Coloration in life (See also under Comments). The dorsum is uniform brown becoming yellowish brown on the flanks. The dorsal surfaces of limbs have an olive-green tinge. A bronze labial stripe is present at the margin of the lip and continues to the insertion of the forelimb. A bronze inconspicuous and highly fragmented dorsolateral stripe is present; a black canthal stripe is present. The flanks are bronze-brown; the groin and anterior and posterior surfaces of the thighs are pale green with white and black spots. The venter is brownish gray with black and white marks; the gular region is gray dark. The iris is copper colored with a few black reticulations.

Coloration in preservative. The dorsum is gray without markings. A narrow pale, fragmented dorsolateral stripe is present. The dorsal surfaces of the limbs are tan with irregular gray blotches. A short pale labial stripe extends from the margin of the lip to the level of the insertion of forelimb; a dark canthal stripe is present. The flanks are dark gray anteriorly and pale gray posteriorly; the groin and anterior and posterior surfaces of the thighs are pale gray with black marks. The venter is cream with dark gray spots; the gular region is gray.

Measurements (in mm). SVL: 46.4, TIBL: 19.8, FL: 20.0, HL: 14.1, HW: 16.2, IOD: 4.9, EW: 4.6 IND: 3.3, ED: 5.6, EN: 4.1, TD: 2.2, FFL: 7.9, TFL: 14.6, TFD: 2.6.

Variation. Morphometric variation of one female and 13 males is summarized in Table 2. The female is larger than most males (67.5 mm; 56.0±8.1 mm). The skin on the dorsum is finely granular. The tympanic annulus usually is smooth but is slightly granular in some individuals. Each dentigerous vomerine process has 6–8 teeth (6.3±1.5, n = 3).

Color variation in preservative. Preserved specimens have a bluish gray, pale gray, or brownish gray dorsum. Interorbital and paravertebral marks usually are present but the paravertebral marks may be absent. The dark gray

interorbital mark, when present, is triangular in most specimens, but it is divided into two blotches in some specimens. A dark canthal stripe is present in all specimens. A short, pale labial stripe is inconspicuous in most specimens. The flanks are gray, darkest anteriorly, with or without white and dark flecks. The groin and anterior surfaces of thighs are pale gray with slight mottling in some; the posterior surfaces of the thighs are pale gray with black flecks and marks usually only distally. In some specimens, the dorsal surfaces of arms and limbs present short dark gray bars. The venter is white with evenly, or densely distributed dark marks.

Color variation in life. (Figs. 10H, 10I, 13–14). In living individuals the dorsum is uniform green (CJ 1843), reddish-brown (CJ 1400), or tan (CJ 1842), with or without contrasting dark gray paravertebral marks. When present, these paravertebral marks usually are narrow, curved, and fragmented; these marks are adherent at the scapular level and may be connected with the interorbital mark. A short cream labial stripe is present on the margin of the lip; the stripe continues posteriorly to the insertion of the forelimb. A dark brown canthal stripe is always present, but it is inconspicuous in some individuals with a dark ground color. The tympanum is brown, tan, or olive green. The iris is usually copper almost without black reticulations. A bronze highly fragmented dorsolateral stripe is present in most individuals. The flanks are brown, bronze-brown, or green. The groin has bluish coloration with slight mottling. The posterior surfaces of the thighs usually are pale green with black flecks and some specimens show black fringes. When present, supracloacal and heel stripes are cream and fragmented. The ventral surfaces usually are cream with dark marks, but some specimens lack dark marks. The gular surface varies from brownish gray to white with black spots. Duellman (1974) provided detailed descriptions of coloration in life of four adult males (KU 148549–51 and 142603, under the name *Gastrotheca lojana*).

Tadpoles. Tadpoles belong to Type IV tadpole of Orton (1953), and the exotroph, benthic ecomorphological guild. All measurements are expressed in millimeters. The following description is based on a specimen in Stage 36 (CJ 4311), from a series of 50 tadpoles (CJ 4311) obtained from a pond at Puntzará Alto, near Loja city, 2311 m, Province of Loja, Ecuador, by Luis A. Coloma, Manuel A. Morales-Mite, and Elicio E. Tapia on 28 January 2016. Total length 51.4; body length 19.4 (38% of total length). Body ovoid in dorsal and lateral views, slightly depressed; throat slightly concave in lateral profile, sloping from tip of snout to belly; body width at the level of spiracle 11.9, and height at same position 9.9; head width at level of eyes 11.1. Lateral line system present but barely visible, supraorbital and not evident at level of snout, infraorbital line present at level of the eye, touching the inferior portion of the orbit, and making contact with supraorbital line immediately behind the eye. Inferior oral line visible at the eye level, where it contacts angular line, which descends from eye level. Supraorbital line represented for scattered stiches, which does not make contact with the orbit. Posorbital line forming a circle of stitches, just behind the eye. Anterior oral line and loreal lines not visible; dorsal body and middle bodylines not visible.

Nostril medium sized (in proportion to body length), ovoid, protruding, having a fleshy annulus, its opening directed anterolaterally. Snout–nostril distance 3.5; internarial distance 2.9. Eye directed dorsally; eye length 2, eye width 1.8; interorbital distance 5. Spiracle sinistral, located at midbody level, spiracular opening oriented posteriorly; distance from tip of snout to spiracular opening 13.0; end of spiracular tube rounded, attached to body wall, inner wall of spiracular tube not evident; spiracle length 2.9, tube transverse width 2.9. Vent tube dextral, opening oriented posteriorly, tube length 3.4, vent tube transverse width 3. Tail length 32.4; caudal musculature slender, narrowing gradually until tail terminus; caudal muscle height 4.4, width 3.4; caudal fins well developed and proportional, arising abruptly near tail-body junction and forming a notorious hump, which makes and arc in the body plane. Dorsal fin height 4.18, ventral fin height 3.7; maximum height of tail 11.9; tail terminus rounded, caudal musculature not reaching fin terminus.

Oral disc small, ventral, located near tip of snout, not protruding laterally beyond body; transverse width 4.9. It is surrounded by an uniserial row of marginal papillae, interrupted medially on upper lip; lower lip papillae alternate in orientation, giving appearance of two rows. Upper lip with 23 papillae on right side and 20 papillae on left side; lower lip bearing 52 marginal papillae; upper jaw sheath medium-sized, forming a smooth arch and finely serrated, transverse width 2.6 (53% of oral disc width) height 0.4; lower jaw sheath V-shaped, open and finely serrated, width 4.1, height 1.3. Labial tooth row formula 2/3(1); tooth rows lengths: A1: 4.15, A2: 4.0, P1 right row 1.75, P1 left row 1.75, P1 gap 0.1, P2: 3.75, P3: 3.70. (Fig. 6D).

Color in life. Based on a specimen (CJ 4312a) in Stage 37 from a series (CJ 4312) obtained at Loja (neigborhood Puntzará Grande), Loja Province, Ecuador, by Luis A. Coloma, Manuel A. Morales-Mite, and Elicio E. Tapia on 28 January 2016 (Fig. 5D). In dorsal and ventral views, body dark brown. Snout and flanks dark brown;

guts gray; red gills visible through the throat. Venter gray. Caudal musculature reddish brown with brown stippling, distal portion lacking pigments; dorsal and ventral fins gray with minute cream stippling. Vent tube translucent. Iris reddish-gold.

Variation. Variation of 28 meristic characters of tadpoles in Stages 31–40 (CJ 4306, 4310–13) are shown in Table 6. Total length varies between 15.8 (Stage 31) and 73.2 (Stage 39) and tail length proportion varies from 57% to 70% until Stage 38. Number of marginal papillae varies among specimens and Gosner stages; variation in number of ventral papillae at lower lip is high (43–64).

Based on specimens CJ 1950–2 from a series obtained at Loja (neigborhoods La Palmera and Puntzará Grande), Loja Province, Ecuador, by Elicio E. Tapia on 22–25 April 2013 (Fig. 15). We documented changes in coloration during ontogenetic development of one, mostly brown individual (CJ 1950) (Figs. 15A–B). At Stage 40, the dorsum and flanks were cream and brown with a diffuse pattern of brown-gray paravertebral marks and a dark gray stripe bordering the canthus and body dorsolaterally, extending to about level of midbody, bordered dorsally by a diffuse cream area. The caudal musculature is pink proximally, with a gray suffusion distally. The caudal fins are pale gray. The iris is pale red. By Stage 46, the markings on the dorsum of body and limbs are diffuse gray and green on a dark brown background; the fingers and toes are yellowish cream dorsally. The flanks have a wide, brown-gray band. There are well-defined creamy white dorsolateral and labial stripes and supracloacal white marks. Color variation in six additional metamorphs (CJ 1951–2, CJ 4313) from Loja and Loja–Abra de Zamora, in Stage 46 is depicted in Figure 16. They vary from plain dark brown to plain green, and have a complete supracloacal stripe.

FIGURE 15. Ontogenetic changes in live *Gastrotheca elicioi*. Stages of Gosner: (A) Stage 40 (CJ 1950), (B) Stage 46 (CJ 1950). From Loja, Loja Province, Ecuador. Scale = 5 mm. Photos by LAC.

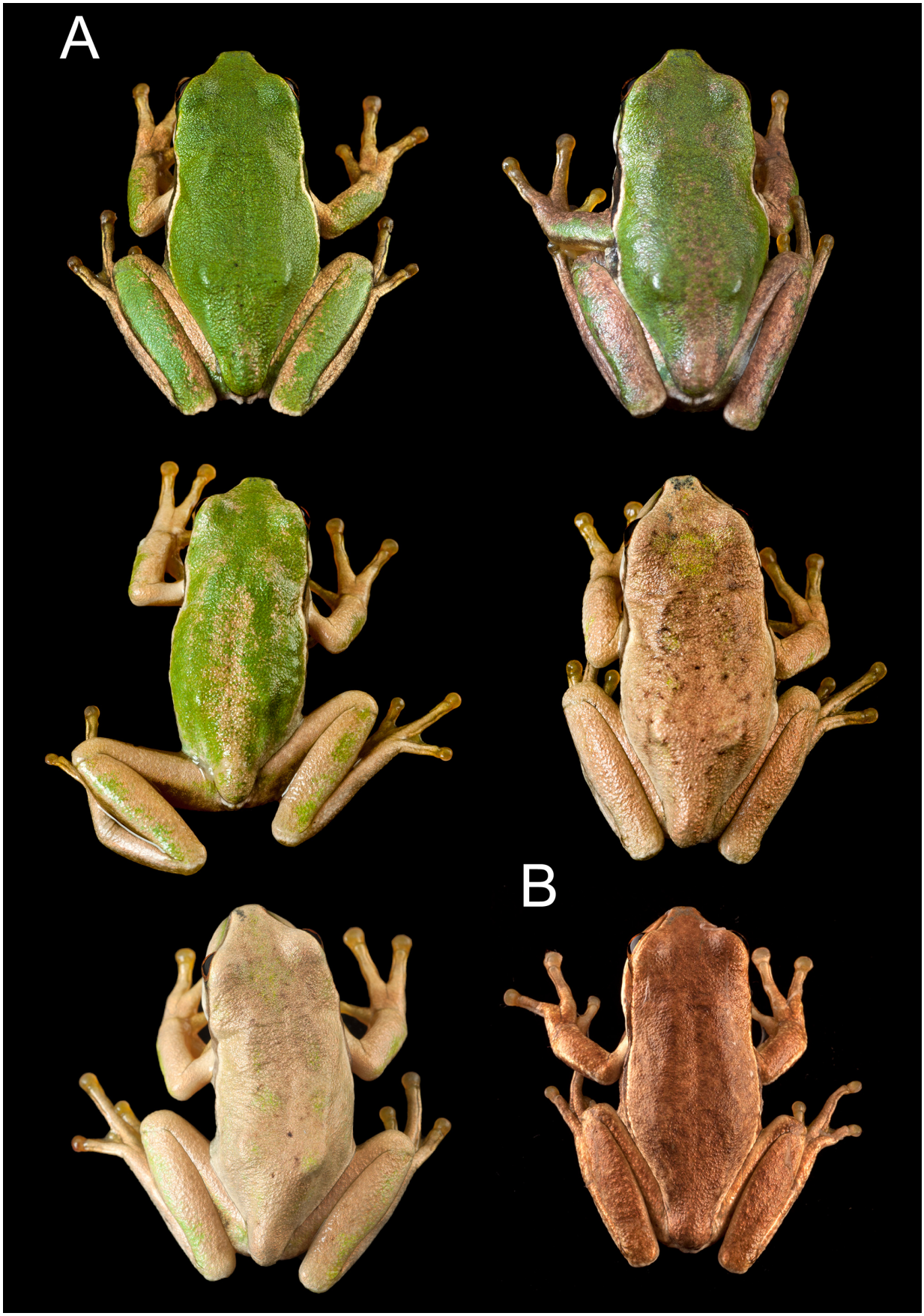

FIGURE 16. Metamorph variation in live *Gastrotheca elicioi* in Stage 46 of Gosner: (A) CJ 4313 from Loja-Abra de Zamora, and (B) CJ 1950 from Loja, Loja Province, Ecuador. Photos by LAC.

TABLE 6. Variation of 28 meristic characters of tadpoles in stages 31–40 of *Gastrotheca elicioi* (CJ 4306, 4310–13). Values are given in mm, mean±standard deviations (first row) and ranges (second row), number of specimens in parentheses. See Materials and methods for character abreviations.

	Stage 31 (n=3)	**Stage 32** (n=3)	**Stage 33** (n=6)	**Stage 34** (n=3)	**Stage 35** (n=4)	**Stage 36** (n=2)	**Stage 37** (n=1)	**Stage 38** (n=1)	**Stage 39** (n=2)	**Stage 40** (n=2)
TL	16.28±0.65	30.80±0.74	34.54±0.77	35.61±0.31	39.99±0.33					
	15.78–17.01	30.22–31.63	33.29–35.27	35.26–35.85	39.58–40.29	50.55–51.39	49.37	68.51	68.43–73.20	70.60–70.87
BL	6.65±0.22	11.83±0.26	12.96±0.48	13.25±0.24	15.36±0.78					
	6.51–6.90	11.62–12.12	12.19–13.41	12.97–13.41	14.22–15.87	17.17–18.97	17.70	20.48	22.14–23.42	21.61–25.31
BW	4.23±0.02	7.81±0.58	8.84±0.31	9.17±0.60	10.63±0.62					
	4.22–4.25	7.33–8.45	8.37–9.22	8.71–9.85	9.92–11.18	11.88–12.51	11.50	16.36	16.11–16.29	17.26–17.45
BH	3.17±0.03	6.44±0.37	7.04±0.41	7.67±0.61	8.62±1.13					
	3.14–3.19	6.21–6.86	6.48–7.49	6.97–8.09	7.00–9.40	9.91–10.20	10.37	13.22	13.03–13.19	13.13–13.31
HWEL	3.66±0.19	7.07±0.18	7.95±0.57	8.37±0.23	9.46±0.60					
	3.47–3.84	6.90–7.25	7.15–8.38	8.16–8.62	8.72–10.12	10.56–11.07	10.44	14.40	13.97–14.30	14.80–15.20
TAL	9.63±0.73	18.97±0.79	21.59±0.67	22.36±0.08	24.63±0.70					
	9.14–10.47	18.43–19.88	20.65–22.35	22.29–22.44	24.10–25.66	32.42–33.38	31.67	48.03	46.29–49.78	45.29–49.26
TLP%	59.09±2.30	61.58±1.26	62.49±1.20	62.79±0.37	61.59±1.84					
	56.98–61.55	60.33–62.85	61.36–64.51	62.56–63.22	60.53–64.34	63.09–66.03	64.15	70.11	67.65–68.01	64.15–69.51
MTH	3.77±0.15	7.48±0.44	8.66±0.54	8.94±0.49	9.77±0.65					
	3.60–3.88	7.00–7.85	8.06–9.39	8.37–9.25	8.85–10.37	11.85–12.26	12.24	15.07	16.60–16.63	15.82–16.72
TMW	0.79±0.05	2.03±0.06	2.20±0.28	2.48±0.17	2.68±0.17					
	0.74–0.83	1.96–2.07	1.85–2.50	2.34–2.67	2.49–2.87	3.44–3.62	3.47	5.45	5.78–6.39	6.19–6.48

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TABLE 6. (Continued)

	Stage 31 (n=3)	**Stage 32** (n=3)	**Stage 33** (n=6)	**Stage 34** (n=3)	**Stage 35** (n=4)	**Stage 36** (n=2)	**Stage 37** (n=1)	**Stage 38** (n=1)	**Stage 39** (n=2)	**Stage 40** (n=2)
TMH	1.13±0.08	2.38±0.17	2.79±0.26	2.91±0.14	3.23±0.24					
	1.05–1.21	2.22–2.56	2.43–3.09	2.75–3.00	2.88–3.45	4.19–4.35	3.96	6.44	6.98–7.69	7.16–8.10
SND	0.97±0.06	1.83±0.06	2.10±0.14	2.17±0.12	2.40±0.29					
	0.90–1.00	1.80–1.90	1.90–2.30	2.10–2.30	2.10–2.70	3.00–3.50	2.60	3.20	3.40–3.50	3.70–4.20
IND	1.13±0.03	1.93±0.15	2.13±0.05	2.20±0.00	2.40±0.08					
	1.10–1.15	1.80–2.10	2.10–2.20		2.30–2.50	2.80–2.90	2.70	3.00	2.70	2.70
END	0.73±0.06	1.37±0.12	1.66±0.13	1.62±0.08						
	0.70–0.80	1.30–1.50	1.50–1.80	1.55–1.70	1.70	2.10	1.90	2.20	2.40–2.50	2.40–2.50
EL	0.70±0.00	1.13±0.06	1.20±0.09	1.30±0.10	1.43±0.05					
		1.10–1.20	1.10–1.30	1.20–1.40	1.40–1.50	2.00	2.00	2.40	2.30	2.20–2.30
EW	0.67±0.06	1.13±0.06	1.17±0.08	1.23±0.12	1.38±0.05					
	0.60–0.70	1.10–1.20	1.10–1.30	1.10–1.30	1.30–1.40	1.80	1.90	2.30	2.10–2.30	2.00
IOD	1.87±0.12	3.53±0.32	3.77±0.19	4.00±0.30	4.25±0.06					
	1.80–2.00	3.30–3.90	3.40–3.90	3.70–4.30	4.20–4.30	4.80–5.00	5.30	6.20	6.20–6.40	6.40–6.80
VP	48.33±4.62	56.00±4.36	54.17±5.12	56.33±1.15	52.00±6.58					
	43.00–51.00	53.00–61.00	48.00–62.00	55.00–57.00	45.00–59.00	52.00–53.00	59.00	24.00	54.00–64.00	57.00–63.00
DP right	21.67±1.15	22.00±2.65	23.17±2.23	22.00±3.00	21.75±6.85					
	21–23	2–25	21–27	19–25	12–28	23	21	11	23–27	23–24

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TABLE 6. (Continued)

	Stage 31 (n=3)	**Stage 32** (n=3)	**Stage 33** (n=6)	**Stage 34** (n=3)	**Stage 35** (n=4)	**Stage 36** (n=2)	**Stage 37** (n=1)	**Stage 38** (n=1)	**Stage 39** (n=2)	**Stage 40** (n=2)
MP right		3.00±1.00	4.33±1.03	3.33±1.53	3.25±4.50					
	–	2–4	3–5	2–5	1–1	2–3	4	0	5–6	0–3
DP left	22.00±1.00	23.67±1.15	22.67±3.39	22.00±2.65	21.75±3.20					
	21–23	23–25	19–28	19–24	17–24	2–21	21	15	2–24	22–26
MP left		3.00±1.00	4.00±1.55	3.33±0.58	3.25±2.63					
	–	2–4	1–5	3–4	1–7	3	4	0	4	2–3
WOD	2.10±0.10	3.70±0.10	3.80±0.28	4.03±0.38	4.40±0.41					
	2.00–2.20	3.60–3.80	3.40–4.10	3.60–4.30	3.80–4.70	4.90–5.10	4.80	6.00	5.80–6.30	6.20–6.30
WUJ	1.00±0.20	1.90±0.17	1.95±0.14	2.07±0.15	2.33±0.10					
	0.80–1.20	1.80–2.10	1.80–2.10	1.90–2.20	2.20–2.40	2.60–2.70	2.60	3.30	3.30–3.50	3.40
UJP%	47.85±11.15	51.30±3.49	51.34±1.23	51.73±8.32	53.07±3.50					
	38.10–6	48.65–55.26	5–52.94	45.24–61.11	5–57.89	52.94–53.06	54.17	55.00	55.56–56.90	53.97–54.84
SL	0.92±0.10	1.70±0.10	2.27±0.18	2.47±0.42	2.58±0.71					
	0.80–1.00	1.60–1.80	2.10–2.60	2.00–2.80	2.10–3.60	2.20–2.90	2.70	4.60	4.60–6.10	4.50–5.00
SW	1.10±0.26	1.73±0.15	2.23±0.18	2.80±0.26	2.88±0.66					
	0.90–1.40	1.60–1.90	1.90–2.40	2.60–3.10	2.40–3.80	2.90	2.50	4.20	4.50–6.70	4.10–4.30
VTL	1.07±0.21	1.50±0.17	1.97±0.23	2.05±0.23	2.00±0.16					
	0.90–1.30	1.30–1.60	1.70–2.20	1.85–2.30	1.80–2.20	3.40	2.50	3.70	4.80	4.30–4.80
VTW	0.77±0.15	1.63±0.23	1.77±0.18	1.80±0.26	1.93±0.33					
	0.60–0.90	1.50–1.90	1.50–1.90	1.50–2.00	1.50–2.30	3.00–3.10	2.70	2.90	4.50	3.70

Comparisons. Tadpoles of *Gastrotheca elicioi* may occur in sympatry with those of *G. lojana*, *G. psychrophila*, *G. pseustes*, and *G. turnerorum* in the Loja-Abra de Zamora region. *Gastrotheca elicioi* differs from all of them by having a dorsal gray-pigmented fin that abruptly arises from the body, whereas is nearly translucent and arises gradually in the other species (compare in Fig 5). The tadpole described as *G. psychrophila* by Duellman (2015) is *G. elicioi.* It has a similar dorsal fin and fit well our description of *G. elicioi* tadpoles. Nonetheless, until tadpoles of *G. psychrophila* are described and unequivocally assigned to its species, some doubts will remain.

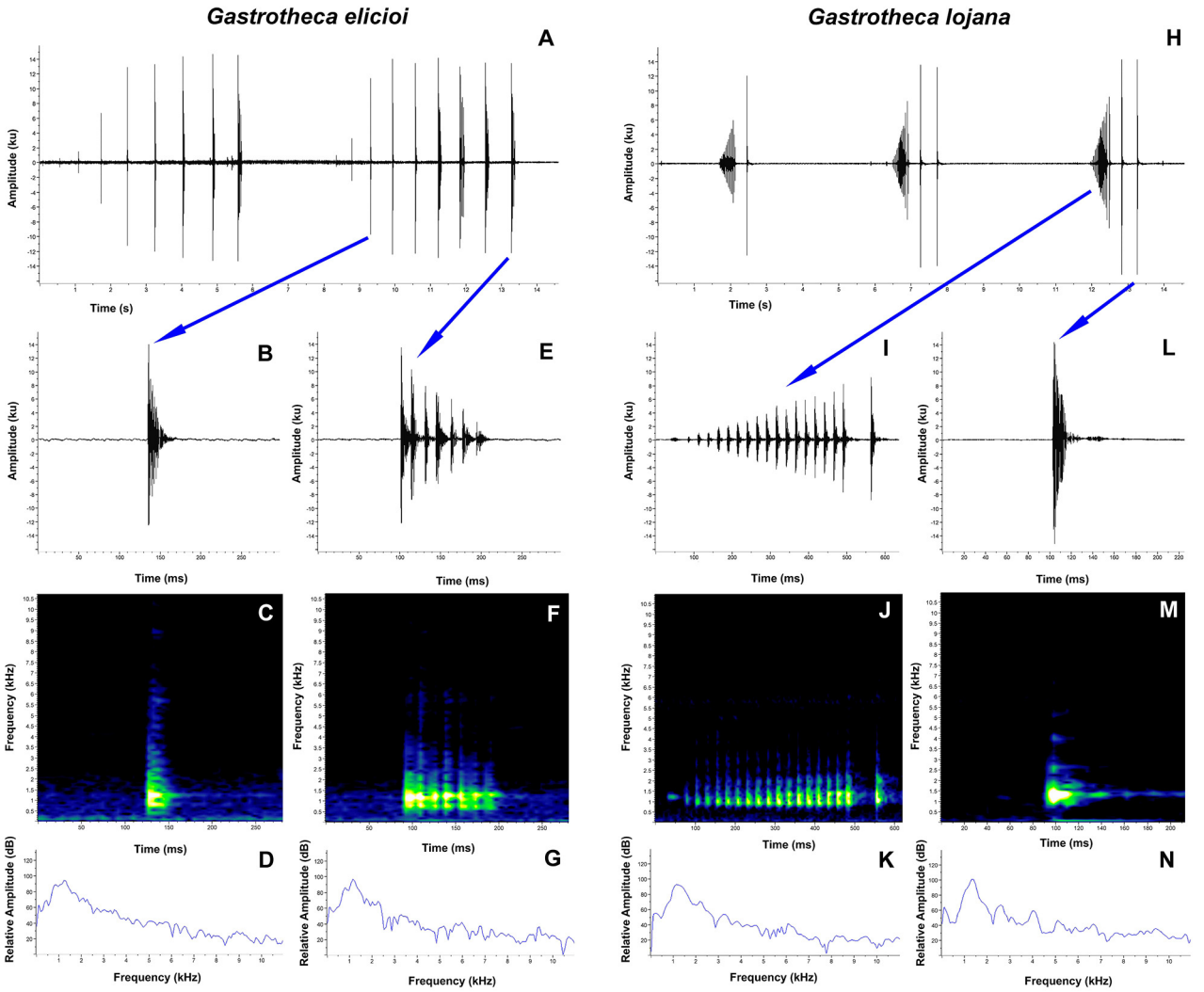

FIGURE 17. Advertisement calls of *Gastrotheca elicioi* (A–G) and *G. lojana* (H–N): (A) oscillogram of two consecutive calls with the first call composed of five short and three long notes and the next call composed of five short and four long notes, (B) oscillogram of a single short note, (C) spectrogram of a single short note, (D) power spectrum of a single short note, (E) oscillogram of a single long note, (F) spectrogram of a single long note, (G) power spectrum of a single long note, (H) oscillogram of three consecutive calls, with the first call composed of one long and one short notes and the next two calls composed of one long and two short notes, (I) oscillogram of a single long note, (J) spectrogram of a single long note, (K) power spectrum of a single long note, (L) oscillogram of a single short note, (M) spectrogram of a single short note, (N) power spectrum of a single short note. All spectrograms at Hanning window function, 512 bands resolution. See text for details.

Vocalization. Seven individuals of *Gastrotheca elicioi* were recorded from three locations in Loja Province (one individual from the old Loja-Catamayo road, three from Loja, Parque Universitario de Educación Ambiental y Recreación (PUEAR) and one from Loja, Quebrada El Salado) and two individuals in the facilities of Centro Jambatu in San Rafael, Quito, Ecuador (Appendix III), inside outdoor enclosures. Descriptive statistics of the acoustic variables are provided in Table 5. The advertisement call of *G. elicioi* is a complex call, composed of up to 6, short, single-pulsed notes, and followed by up to 7 longer pulsed notes (Fig. 17A–G). It can be characterized as a series of short notes, which become gradually longer, pulsated notes by the end of the call. The long notes have a mean

duration of 0.188 s (SD = 0.150) and consists on average of 3.47 (SD = 1.695) distinct pulses, partly fused, without silent intervals (amplitude modulation close but less than 100%). The amplitude of the long note decreases gradually towards the end. The short notes have a mean duration of 0.027 s (SD = 0.014) and the inter-note interval is on average of 0.452 s (SD = 0.125). The mean dominant frequency of the call is 1249.4 Hz (SD = 169.862), with a mean 90% bandwidth of 807.1–1416.8 Hz. The fundamental frequency and harmonics are not clearly recognizable.

Comparisons. The advertisement call of *Gastrotheca elicioi* is unique amongst the calls of the Southern Ecuadorian species of *Gastrotheca* in that the long, pulsed notes are produced after the short ones, whereas the other species tend to produce the long, pulsed notes before the short ones. Also, the duration of the long notes of *G. elicioi* is significantly shorter and there are fewer pulses per long note, compared to all other species with complex calls from southern Ecuador (Table 5).

Distribution and ecology. *Gastrotheca elicioi* is known only from the vicinity of the city of Loja, Loja Province, in the Loja Basin and slopes of the adjacent cordilleras (Fig. 9). Its elevational range is 2026–3018 m in an area of extent of occurrence of about 102.7 km^2.

This nocturnal, semiarboreal species inhabits mostly disturbed areas and a few forests in the Evergreen Montane Forest from the south of the Cordillera Oriental of the Andes (Ministerio de Ambiente del Ecuador 2012), where the average annual rainfall is 764–1128 mm and the average annual temperature is 12.6–17.4 ºC (Fick & Hijmans 2017).

At the locality 5.5 km W of Loja, many *Gastrotheca elicioi* were found in a roadside agave fence-row, where they were sitting on the agave leaves (WED field notes, 17 July 1971). At the locality 5.2 km W of Loja, an individual of *G. elicioi* (KU 202688) was under an overhanging bank at the edge of small pond in a pasture by day (WED field notes, 10 March 1984). At Zamora Huayco, in the vicinity of Loja, two individuals were sitting on branches of shrubs at approximately 4–5 m above the ground; they were about 7 m from a river within moderately dense mountain forest (Diego Almeida-Reinoso field notes, 5 December 2009). Brooding females under captive conditions are depicted in Figures 10H–I. The holotype was one of a series of 16 tadpoles that were at the edge of a pond. At the type locality, *G. elicioi* is syntopic with *G. pseustes*; *G. elicioi* is also syntopic with *G. lojana*. On 5 December 2017 a pregnant female *G. elicioi* was caught (Quebrada Shucos, Loja, Loja Province) by Diego Armijos-Ojeda and brought to the laboratory. After 20 days, the female deposited 434 tadpoles, in Gosner Stage 34 (CJ 7874). To the best of our knowledge, this is the largest number of tadpoles deposited by a female *Gastrotheca*. The female (SVL = 71.7 mm) weighed 43.06 g when caught and 24.38 g after she deposited the tadpoles.

Conservation status. We suggest that *Gastrotheca elicioi* should be considered as Endangered according to criteria B1ab(i,ii,iii,iv) of the IUCN Red List. We suggest this conservation status because of its small known area of occurrence (102.7 km^2) that is extremely fragmented. Its habitats are in heavily human populated areas. Loja and environs have been deforested and modified for human activities (Fig. 11G–H). None of its populations is within the National System of Protected Areas (SNAP), but there is a population in the private Madrigal del Podocarpus Natural Reserve.

Etymology. The specific name *elicioi* is a patronym of Elicio E. Tapia, an Ecuadorian biologist and member of the Tapia family, whom have contributed substantially to the growth of biodiversity collections in Ecuador (Pollet 2003, Páez-Vacas *et al.* 2010). We highlight Elicio´s intense field collecting efforts and enormous contribution to the museums that hold Ecuadorian amphibians, including many tissues, call recordings, ecological data, and specimens of *Gastrotheca* reported here.

Comments. In the past, *Gastrotheca elicioi* was confused with *G. lojana* and *G. monticola*. It belongs to the subgenus *Duellmania* and is reported as species B in Duellman (2015: Fig 11.1). Specimens in captivity were not as brightly colored as specimens from the wild; however, the color in life of the holotype does not show remarkable differences from wild-collected specimens.

***Gastrotheca turnerorum* sp. nov.**

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Holotype. CJ 393 (Fig. 18), an adult female (collected as tadpole and raised in captivity), from Laguna Negra de Jimbura, Parque Nacional Yacuri, Amaluza, 3406 m (04° 42' 44.24" S, 79° 25' 42.38" W), Loja Province, Ecuador, one of a series collected on 12 June 2011 by Elicio E. Tapia, Sofía Carvajal-Endara and Henry Grefa.

Paratypes. (Total 9: 6 males, 2 females, 1 juvenile). Ecuador: *Loja:* CJ 394–5 (female, male), 415–7 (males, juvenile), 1386 (female), and KU 335390 (male), collected with the holotype. CJ 7823 (male, collected as tadpole and captive raised), from Parque Nacional Yacuri, Amaluza, 3331 m (04° 43' 25.22" S, 79° 26' 15.47" W), Loja Province, Ecuador, one of a series collected on 7 July 2016 by Dan Cogălniceanu, Diana Székely and Paul Székely. *Zamora Chinchipe:* MUTPL 221, male from Reserva Tapichalaca, 3073 m (04° 28' 55.58" S, 79° 09' 29.76" W), collected on 9 December 2014 by Diego Armijos-Ojeda.

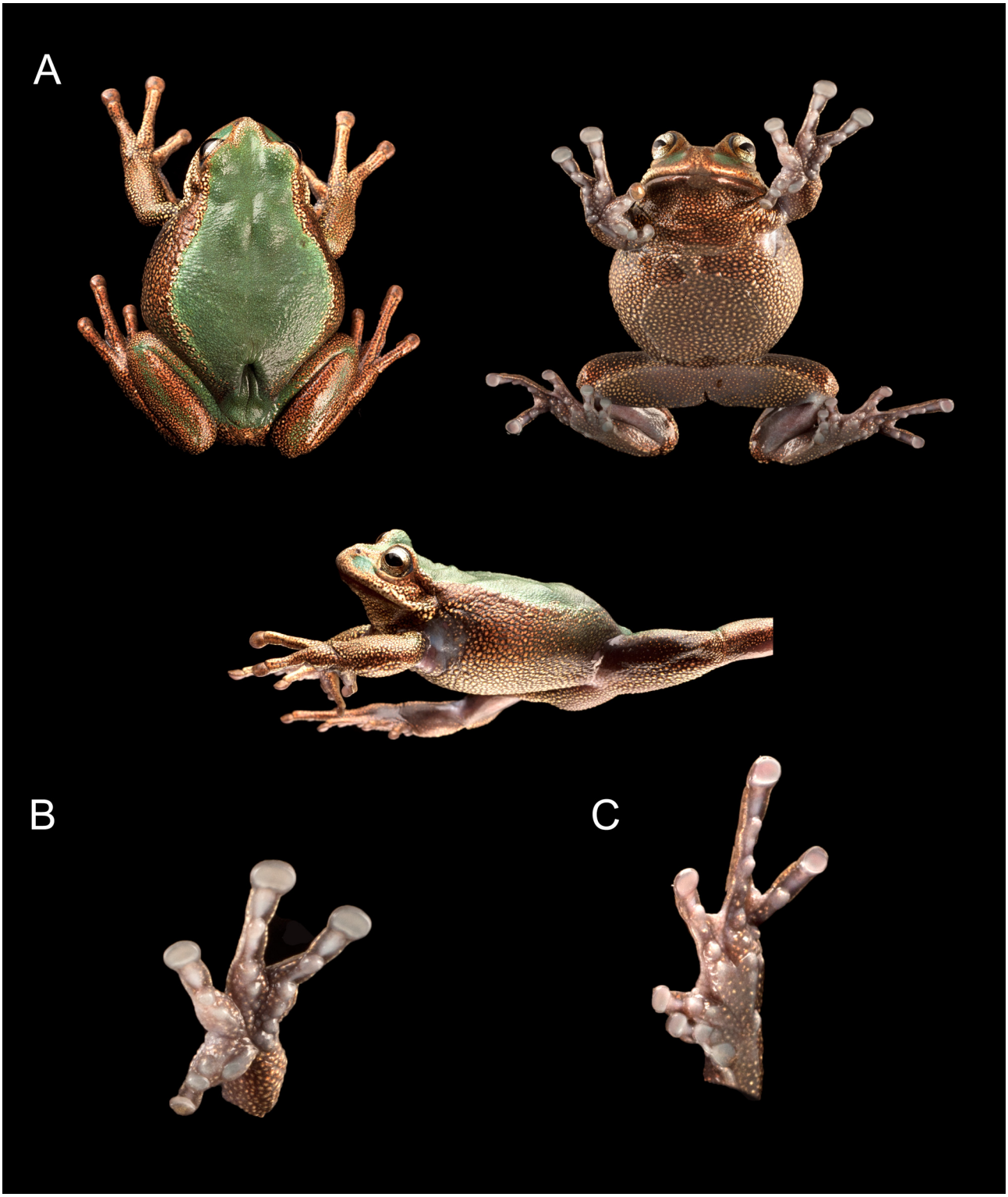

FIGURE 18. Live holotype of *Gastrotheca turnerorum* (CJ 393, female, SVL = 54.0): A) dorsal, ventral and lateral views, (B) ventral view of left hand, enlarged 1.9X of A, and (C) ventral view of left foot, enlarged 2.1X of A. Photos by LAC.

Referred specimens. Ecuador: *Zamora Chinchipe*: QCAZ 9575 (captive raised tadpoles and juveniles) from Parque Nacional Podocarpus, Lagunas del Compadre, 3205 m (04° 10' 29.24" S, 79° 06' 59.54" W), on 1 December 1994 by Jenny Rudston; QCAZ 47299 (tadpole), QCAZ (sc 29154) (female) from Parque Nacional Podocarpus, Lagunas del Compadre, 3205 m (04° 10' 29.24" S, 79° 06' 59.54" W), on 20 October 2009 by Elicio E. Tapia.

Diagnosis. Included in the genus *Gastrotheca* by having a closed brood pouch on dorsum of female. A moderately large species (54.0– 58.2 mm SVL in females, n = 3; 50.0–55.6 mm SVL in males, n = 4), with tibia length 37−42% SVL, shorter than foot; (2) interorbital distance slightly greater than width of upper eyelid; (3) skin on dorsum areolate, not co-ossified with skull, lacking transverse ridges; (4) supraciliary processes absent; (5) heel lacking calcar or tubercle; (6) tympanic annulus smooth; (7) Finger I slightly shorter than Finger II, width of discs much wider than digits; (8) fingers unwebbed; (9) foot webbing between external toes extending to antepenultimate subarticular tubercle on Toe IV, to penultimate subarticular tubercle on Toe V; (10) in life, dorsum uniform green without dark paravertebral marks; (11) head markings consisting of pale labial and canthal stripes formed by a series of small bronze dotes; (12) dorsolateral stripe present, also consisting in a series of small bronze dotes; (13) flanks brown and groin green both with or without a few cream spots; anterior surfaces of thighs dark brown, posterior surfaces of thighs bluish brown with numerous cream tubercles proximal to the vent; (14) venter dark brown with uniformly distributed cream spots; gular region dark brown; (15) brood pouch single, dorsal.

Gastrotheca turnerorum most closely resembles three other species in southern Ecuador, *G. pseustes*, *G. elicioi*, and *G. litonedis*. *Gastrotheca turnerorum* differs from all of them by having a different skin texture on the dorsum, and a distinctive color pattern (compare Figs. 10J, 19–20 vs 10A–I, K, L). The dorsal skin is areolate in *G. turnerorum*, whereas it is weakly areolate or smooth in *G. pseustes*, finely granular in *G. elicioi*, and smooth in *G. litonedis*. In *G. turnerorum* the venter is dark brown with uniformly distributed cream spots, whereas it is cream with dark marks in *G. pseustes* and *G. elicioi* and pale brown-gray in *G. litonedis*. The labial stripe consists of a series of small bronze dots in *G. turnerorum*, and mostly uniform cream in *G. pseustes*, *G. elicioi*, and *G. litonedis. Gastrotheca pseustes* and *G. elicioi* have a dark brown canthal stripe, whereas *G. turnerorum* has a canthal stripe formed by a series of small bronze dots.

Gastrotheca turnerorum is the sister species of *G. aguaruna* + *G. yacuri*, with a genetic distance of at least 2.85 % (in a DNA dataset of 438 bp, 16S gene). The Peruvian *G. aguaruna* differs from *G. turnerorum* by having a weakly granular to smooth dorsal skin (areolate in *G. turnerorum*), Fingers I and II equal in length (Finger I shorter in *G. turnerorum*), and a cream venter with dark fleck or spots (venter dark brown with uniformly distributed cream spots in *G. turnerorum*).

Description of the holotype. An adult female (Fig. 18) that was collected as a tadpole and raised in the laboratory; body moderately robust; SVL 54.0 mm; head wider that long; snout rounded in dorsal view, bluntly rounded in profile; canthus rostralis round in section; loreal region concave; lips rounded; top of head flat; interorbital distance 89% of width of upper eyelid; internarial area flat; nostrils not protuberant, directed anterolaterally, posterior to level of anterior margin of lower jaw; diameter of eye greater than its distance from nostril; tympanum round, separated from the eye by distance about equal to diameter of tympanum; tympanic annulus barely evident;, supratympanic fold moderately weak, extending from behind the tympanum to the insertion of the forelimb. Dentigerous vomerine processes narrowly separated medially, each bearing five teeth.

Arm robust; ulnar tubercles absent; hand and fingers moderately large (TFL 34% of SVL); fingers unwebbed; discs large and rounded, width of disc of Finger III greater that diameter of tympanum; relative lengths of fingers I<II<IV<III; subarticular tubercles prominent, round, conical in profile, none bifid; supernumerary tubercles, conical; palmar tubercle bifid, prepollical tubercle large, elliptical. Hind limb robust; tibia length 38% of SVL; foot length 46% of SVL; calcar and tarsal tubercles absent; inner tarsal fold approximately ¼ the length of the tarsus; outer metatarsal tubercle rounded; inner metatarsal tubercle elliptical elevated; toes moderately long; relative length of toes I<II<III<V<IV; basal webbing between Toes I and II; webbing formula for other toes II1—2III1—2.5IV2—1V; subarticular tubercles moderately large, rounded; supernumerary tubercles, numerous, and rounded.

Skin on dorsum weakly areolate; skin on flanks coarsely areolate; skin on throat, venter surfaces of thighs, and arms heavily areolate; skin on belly areolate; skin on venter surface of shanks smooth; numerous white tubercles ventrolateral to cloacal opening. Tongue broad, suboval, not notched posteriorly, fully attached to mouth floor. Pouch opening V-shaped with anterior border at level of posterior edge of sacrum.

FIGURE 19. Live adults of *Gastrotheca turnerorum* showing variation in dorsaleral lateral, dorsal, ventral, groin, thighs and eye color pattern: (A) CJ 1386, female, SVL = 58.2 mm, and (B) CJ 7823, male, SVL = 46.7 mm. Not to scale. Photos by LAC.

Coloration in life. The dorsal surfaces of the head, body, and limbs are green; the inner and outer surfaces of the forearm, thighs, and shanks are brown (Fig. 18). Head markings are canthal and labial stripes that consist of a series of small bronze dots. The labial stripe continues to the insertion of the forelimb. The dorsolateral stripe also consists of a series of small bronze dots. The flanks are bronze-brown with some small white stippling; the groin is green. The anterior surfaces of the thighs are dark brown with some cream stippling; the posterior surfaces of the thighs are dark brown with cream tubercles lateral and below the vent. The ventral surfaces are dark brown with uniformly distributed cream spots. The iris is yellow-cream with brown reticulations and a brown horizontal bar across the eye.

Coloration in preservative. The dorsum is uniform bluish-gray. The pale labial, canthal, and dorsolateral stripes formed by a series of small bluish gray dots. The labial stripe continues to the insertion of the forelimb. The flanks, groin, and anterior surfaces of thighs are uniform dull gray; the posterior surfaces of thighs are dark gray with numerous white tubercles lateral to, and below, the cloacal opening. The ventral surfaces are uniform dark bluish-gray.

Measurements (in mm). SVL: 54.0, TIBL: 20.5, FL: 24.7, HL: 17.8, HW: 20.5, IOD: 4.9, EW: 5.6 IND: 3.4, ED: 5.6, EN: 4.3, TD: 2.3, FFL: 9.9, TFL: 18.5, TFD: 3.4.

Variation. Morphometric variation of three females and three males is summarized in Table 3. Females are larger than males (55.9±2.1 mm; 52.7.±2.5 mm). The skin on the dorsum varies from weakly to coarsely areolate. All adults have a supratympanic fold, which usually extends from the posterior edge of the tympanum to a point above the insertion of the forelimb.

Color variation in preservative. All preserved specimens have a uniformly bluish gray dorsum; labial, canthal, and dorsolateral stripes are formed by a series of small brown dots. The dorsal surfaces of hands and feet also have brown dots. The flanks, groin, and anterior surfaces of the thighs are uniform dull gray, but in some specimens the flanks are covered by small dark gray dots. The posterior surfaces of the thighs are dark gray with numerous white tubercles lateral to, and below the cloacal opening; a short, fragmented supracloacal stripe is present in some individuals. The ventral surfaces are uniform dark bluish-gray.

Color variation in life. (Figs. 10J, 18–19). The dorsum is uniform green (e.g., CJ 1386) or brown (e.g., CJ 7823). In CJ 1386, the dorsal surfaces of limbs are green, whereas the inner and outer surfaces of the forearms, thighs, and shanks are brown. Dorsal surfaces of hands and feet have a pattern of brown dots over a lighter background. Head markings are like those of the holotype; a dorsolateral stripe is present in all specimens. The flanks are bronze-brown with or without white stippling; the axillae and groin are green, with a bluish suffusion in some specimens. The anterior surfaces of thighs are dark brown with or without cream stippling and, and the posterior surfaces of thighs are dark brown with cream tubercles lateral to, and below, the vent. The ventral surfaces are dark brown with uniformly distributed cream dots, but some specimens have larger cream spots, thereby resulting in a paler venter.

Tadpoles. Tadpoles belong to Type IV tadpole of Orton (1953), and the exotroph, benthic ecomorphological guild. All measurements are expressed in millimeters. The following description is based on a specimen in Stage 39, from a series (CJ 1959) obtained from a pond at Laguna Negra de Jimbura, Parque Nacional Yacuri, 3406 m, Loja Province, Ecuador, by Elicio E. Tapia, Sofía Carvajal-Endara, and Henry Grefa on 12 June 2011 (Fig. 5F). Total length 61.3, body length 23.5 (38% of total length). Body robust, ovoid in dorsal and lateral views, slightly depressed; throat slightly concave in lateral profile; body width at level of spiracle 14.7, and height at same position 11.9; head width at level of eyes 12.9. Lateral-line system not evident. Nostril medium sized (in proportion to body length), ovoid, protruding, with a fleshy annulus, its opening directed anterolaterally. Snout–nostril distance 3.7. Eyes positioned and directed dorsally, eye length 2.4, eye width 2.2. Spiracle sinistral, located at midbody level; spiracular opening oriented posteriorly; distance from tip of snout to spiracle opening 15.9; spiracle end rounded, not free, attached to body wall, inner wall of spiracle not evident; tube length 3.4, tube transverse width 1.4. Vent tube dextral, the opening oriented posteriorly, tube length 4.0, tube transverse width 2.6. Tail length 38.8, caudal musculature robust in the two-thirds proximal to body, narrowing gradually until tail terminus; tail muscle height 5.4, tail muscle width 4.8; caudal fins thin at proximal half of tail, getting higher on distal half and raising near tail–body junction, dorsal fin height 3.5, ventral fin height 3.7; maximum height of tail 12.7; tail tip rounded, tail musculature not reaching fin terminus.

Oral disc small, ventral, located near tip of snout, not protruding laterally beyond body, not visible dorsally; transverse width 5.6. It is surrounded by an uniserial row of marginal papillae, interrupted medially in upper lip;

lower lip papillae alternating in and out, giving the appearance of two series; upper lip with 18 papillae on right side and 17 papillae on left side; lower lip with 42 marginal papillae; upper jaw sheath medium-sized, forming a finely serrated, smooth arch, height 0.4, transverse width 3.3 (59% of oral disc width); lower jaw sheath V-shaped, open and finely serrated, width 2.4, height 0.7. Labial tooth row formula 2/3(1), tooth rows lengths: A1: 4.7, A2: 4.0, P1 right row 1.9, P1 left row 2.1, P1 gap 0.1, P2: 3.6, P3: 3.5. (Fig. 6E).

Color in preservative. Dorsum dull gray, with darker areas on flanks, above the eyes and on the throat; body contour and snout translucent. Caudal musculature and fins with scattered, white spots, densely arranged near tail-body junction; fins otherwise translucent. Venter dark gray; eyes lavender gray, oral apparatus translucent.

Color in life. (CJ 1957, Stage 36). Fig. 5F. In dorsal and lateral views, body tan, speckled with black; areas around the snout are lighter. Venter cream with black markings, semi-translucent; guts visible as a darker area; throat translucent with small cream flecks; gills evident as a red hue. Caudal musculature reddish-pink in proximal half, decreasing its intensity towards distal half; myomeres and nerves barely visible; caudal musculature and fins with cream marks, clustered in dorsal line of caudal musculature, otherwise caudal fins translucent. Legs cream. Oral apparatus light cream. Iris copper-yellow, with small black reticulations.

Variation. Variation of 26 meristic characters of tadpoles in Stages 35–39 (CJ 1959) are shown in Table 7. Total length varies between 61.3 (Stage 39) and 75.0 (Stage 35); tail length proportion varied from 63.2 to 67.0 until Stage 39; labial tooth row formula was 2/3(1). Number of marginal papillae varied among specimens and Gosner stages, variation in lower lip papillae is high (42–57).

TABLE 7. Variation of 26 meristic characters of tadpoles in stages 35–39 of *Gastrotheca turnerorum* (CJ 1959). Values are given in mm, mean±standard deviations (first row) and ranges (second row), number of specimens in parentheses. See Materials and methods for character abreviations.

	Stage (n=1)	Stage (n=2)	Stage (n=4)	Stage (n=1)
TL	75.01	61.2–64.14	64.19±1.83	61.3
			62.12–66.55	
BL	24.73	21.69–22.63	23.12±0.31	22.54
			21.68–25.37	
BW	17.44	12.5–13.67	14.81±3.15	14.71
			12.82–19.51	
BH	15.62	9.56–11.16	11.7±1.92	11.93
			9.76–14.35	
HWEL	15.34	10.98–11.45	12.22±1.4	12.87
			11.19–14.28	
TAL	50.28	39.51–41.51	41.06±1.52	38.76
			38.88–42.11	
TLP (%)	67.03	64.56–64.72	63.98±2.06	63.23
			61.88–66	
MTH	17.64	12.18–12.41	13.64±1.89	12.71
			12.21–16.41	
TMW	6.88	5.01–5.04	5.38±0.8	4.83
			4.57–6.47	
TMH	8.92	5.45–5.55	6.58±1.29	5.35
			5.18–8.3	
SND	2.6	2.54–2.6	2.66±0.29	3.7
			2.33–2.9	
IND	4	3.3–3.5	3.63±0.21	–
			3.4–3.8	

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TABLE 7. (Continued)

	Stage (n=1)	Stage (n=2)	Stage (n=4)	Stage (n=1)
END	2.6	2.5–2.5	2.63±0.14 2.5–2.8	2.7
EL	2.5	2.1–2.4	2.3±0.27 2.1–2.7	2.4
EW	2.2	2.1–2.1	2.13±0.31 1.93–2.6	2.2
IOD	8.6	7.6–7.7	7.43±0.33 7.1–7.8	–
VP	57	43–53	54.25±5.19 47–58	42
DP right	24	18–18	19.75±2.75 17–23	18
DP left	17	19–20	19.5±3 17–23	17
WOD	6.5	5.5–5.7	5.9±0.27 5.7–6.3	5.6
WUJ	4	3.2–3.3	3.43±0.15 3.3–3.6	3.3
UJP (%)	61.54	56.14–60	58.05±1.58 56.9–60.34	58.93
SL	4	3.2–4.2	3.49±0.57 2.8–4.18	3.4
SW	1.9	0.9–1.6	1.76±0.2 1.5–1.94	1.4
VTL	2.8	2.6–3.6	2.8±0.13 2.7–2.99	4
VTW	3.7	2–2.5	2.77±1.15 2.1–4.48	2.6

We documented changes in coloration during ontogenetic development of CJ 1958–9 (Fig. 20). At Stage 36, the dorsum and flanks are pale brown with dark brown areas on posterior body and flanks. By Stage 42, dorsal surfaces of body and limbs are uniform green; fine, cream, dorsolateral stripes are present, extending to midbody. Cream stripes border the outer dorsal margins of the limbs. At Stage 46, dorsal surfaces of body and limbs have more well-defined cream stripes, and a cream labial stripe; the canthus rostralis is green, and remaining flanks are mostly dark brown with an upper diffuse black-stripe. Dorsal surfaces of fingers and toes are brown except on finger and toe discs, which are yellowish-cream. The iris is copper-yellow, lacking the brown horizontal band that is observed in adults.

Comparisons. Tadpoles of *Gastrotheca turnerorum* may occur in sympatry with those of *G. elicioi*, *G. lojana*, *G. psychrophila*, and *G. pseustes*, in the Loja-Abra de Zamora region. *Gastrotheca turnerorum* differs from *G. elicioi* by lacking a dorsal gray-pigmented fin that abruptly arises from the body; from *G. lojana* by having a more rounded tail terminus and having bold cream marks in a dorsal line of caudal musculature, and from *G. pseustes* by having a more rounded tail terminus (compare in Fig. 5). For *G. psychrophila*, see remarks under *G. elicioi* tadpole account.

Distribution and ecology. *Gastrotheca turnerorum* only is known from three localities in the Cordillera Oriental of the Andes in southern Ecuador. These localities are in Parque Nacional Yacuri, Parque Nacional

Podocarpus, and Reserva Tapichalaca in Zamora Chinchipe and Loja provinces. Its elevational range is 3073–3406 m in an area of extent of occurrence of about 450 km^2.

This mostly nocturnal, semiarboreal species inhabits mainly paramos and a few forests in the Evergreen Shrub and Herbazal of Paramo, and the Evergreen Montane Forest of Catamayo-Alamor (Ministerio de Ambiente del Ecuador 2012), where the average annual rainfall is 895–1278 mm and the average annual temperature is 10.4–13.5 ºC (Fick & Hijmans 2017).

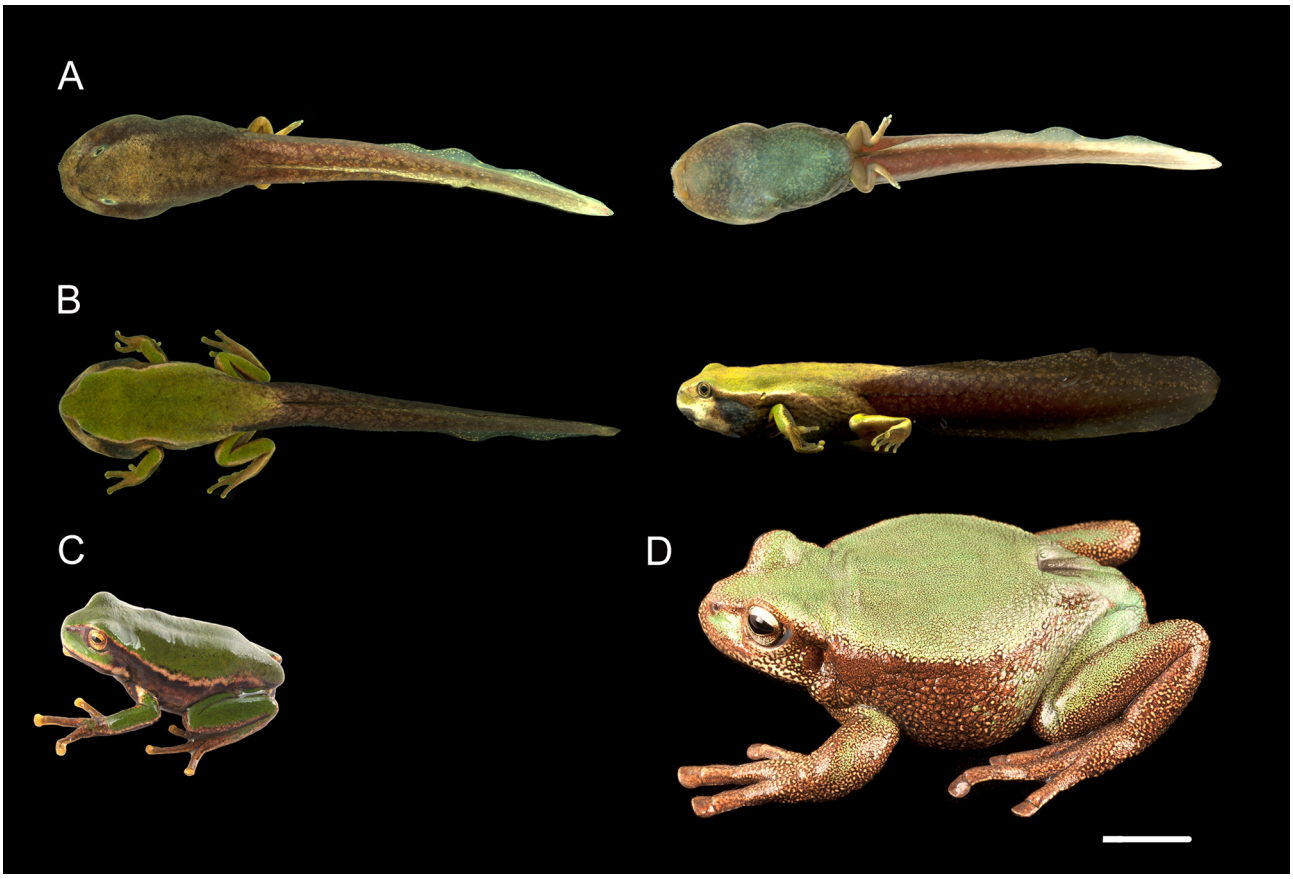

FIGURE 20. Ontogenetic changes in live *Gastrotheca turnerorum* (CJ 1958), from Laguna Negra de Jimbura, Loja Province, Ecuador. Stages of Gosner: (A) Stage 36, (B) Stage 42, (C) Stage 46 (CJ 1959), and (D) adult. Scale = 10 mm. Photos by LAC.

At the Lagunas del Compadre in the Parque Nacional Podocarpus, a gravid female was collected on 1 December 1994. It deposited tadpoles on 12 December in the laboratory, some of them were raised, and others were preserved. On 20 September 2009, another female with eggs in her pouch was found at the same locality. It was sitting on moss at approximately 2 m from the Río Sabanilla, which is about 1.5 km from Lagunas del Compadre. The holotype, from Laguna Negra de Jimbura in the Parque Nacional Yacuri (Fig. 11C), was found at the edge of a pond about 3 x 2 m at the edge of a lagoon, at 14:00 h. The water temperature was 16.4º C, and water pH was 5.3. Eighteen tadpoles were collected at this pond. Another group of tadpoles was found at 18:00 h; at the same locality in another lagoon, the water temperature was 7.4 ° C. Strong winds blow across the lagoon, and only a small patch of forest remained at one border (Elicio E. Tapia field notes, 12 June 2011). A brooding female is depicted in Figure 10J.

Conservation status. We suggest that *Gastrotheca turnerorum* should be considered as an Endangered species according to criteria B2ab(i,ii,iii) of the IUCN Red List. Although this species occurs at the Yacuri and Podocarpus National Parks, we suggest this conservation status because of its small known area of occurrence (159 km^2) that is vulnerable to improperly regulated tourism activities (Aguirre 2001), introduced species such as trout, climate change, and pathogens. Laguna Negra de Jimbura has suffered the synergistic effects of agriculture, cattle and sheep raising, fires, introduced species, pesticide use, and unregulated tourism activitites.

Etymology. The specific name *turnerorum* is a latinized word that honors the Turner family. As unique as this marsupial frog is to the amphibian world, the Turner family stands out in their exceptional, unwavering and ever-

growing commitment to conservation of the world natural resources. From Ted Turner's pioneering efforts to protect very large land areas and restore them to their original and natural states of clean water and abundant fauna and flora to granddaughter Elizabeth's awareness-raising book "Our friends the frogs," there are multiple generations of active conservationists with a true appreciation for the value of all of our natural resources. In 1991, Laura Turner Seydel (with father Ted) co-founded the Captain Planet Foundation and continues to work diligently to inspire the same appreciation for conservation and sustainable living in the next generation of young people who will surely be making big decisions that will affect the health of our planet for themselves and their own grandchildren. Through the camera's eye, Rhett Turner has managed to put conservation issues such as the pollinator perils and amphibian crisis in front of millions of people. Through the Turner Endangered Species Fund, there is hope for dozens of threatened species of plants and animals in the US and abroad that was not there before. Together, the Turner family has put their hearts, souls, and personal resources into helping make the planet a better place for the next generation.

Comments. *Gastrotheca turnerorum* belongs to the subgenus *Gastrotheca* as reported as species C in Duellman (2015: Fig 12.1).

***Gastrotheca yacuri* sp. nov.**

urn:lsid:zoobank.org:act:6261932E-02AB-4C9E-B2BD-BD213BBDC771

Holotype. CJ 7822 (Figs. 21–22), an adult male, from El Salado de Jimbura, at about 2.5 km (by road) west from the entrance in the Parque Nacional Yacuri, 2914 m (04° 42' 08.37" S, 79° 27' 00.09" W), Loja Province, Ecuador, collected on 9 April 2016 by Paul Székely and Diana Székely.

Paratype. Ecuador: Loja: QCAZ 21105, adult male, from El Salado de Jimbura, 2712 m, on 26 June 2002 by Fernando Nogales Sornoza.

Referred specimen. Ecuador: Loja: Not collected (Fig. 11O), subadult, 43 mm SVL, from nearby of Lagunas Negras, Parque Nacional Yacuri, 3492 m (04° 42' 31.81" S, 79° 25' 49.61" W).

Diagnosis. Included in the genus *Gastrotheca* by molecular evidence and general morphological similarity with species of *Gastrotheca.* Although females are unknown, we infer presence of dorsal brood pouch because all its closely related species have it. A moderately large species (57.4–58.9 mm SVL in males, n = 2) with tibia length 47−49% SVL, larger than foot; (2) interorbital distance greater than width of upper eyelid; (3) skin on dorsum weakly granular to smooth, co-ossified with skull, having a transverse ridge at occipital region; (4) supraciliary processes absent; (5) heel lacking calcar or tubercle; (6) tympanic annulus smooth; (7) Finger I shorter than Finger II, width of discs much wider than digits; (8) fingers unwebbed; (9) toes one-half webbed, webbing extending to antepenultimate subarticular tubercle on Toe IV, to penultimate subarticular tubercle on Toe V; (10) in life, dorsum uniform green or brown with brown paravertebral marks; (11) head markings consisting of brown labial stripe with cream glandular areas at posterior end, canthal and supraciliary stripe of black, brown, and bronze; (12) dorsolateral stripe absent or present, when present above consisting in a series of bronze and cream warts, bordered below with a black and brown line, (13) flanks brown and green with a blue and black reticulum towards the lower flanks, axillae, groin, anterior and posterior surfaces of thighs, shanks, and tarsus; brown pelvic patch; (14) venter cream with nearly uniformly distributed, small, dark brown marks or brown with cream marks; gular region dark brown in males.

Gastrotheca yacuri differs from all other species of *Gastrotheca* in southern Ecuador by having a blue and black reticulated pattern on flanks, axilla, groin, thighs, and shanks. It most closely resembles two other species, *G. pseustes* and *G. psychrophila* by having the blue colors, but they lack a blue and black reticulum (compare these species in Fig. 10). *Gastrotheca yacuri* differs from its sister species, *G. aguaruna,* from the Cordillera Central in northern Peru, by lacking blue colors, having the skin co-ossified with skull, and being smaller (SVL of males of *G. yacuri* 57.4–58.9 mm vs 41.6–46.8 mm in *G. aguaruna*). The genetic distance between them is of at least 2.8 % (in a DNA dataset of 438 bp, 16S gene).

Description of the holotype. An adult male (Figs. 21–22); body moderately robust; SVL 57.4 mm; head wider that long; snout slightly acuminate in dorsal view, bluntly rounded in profile; canthus rostralis angular in section; loreal region concave; lips rounded; top of head flat; interorbital distance 92% of width of upper eyelid; internarial area flat; nostrils not protuberant, directed anterolaterally, at about level of anterior margin of lower jaw; diameter of eye greater than its distance from nostril; tympanum round, separated from the eye by distance about equal to

FIGURE 21. Live holotype of *Gastrotheca yacuri.* CJ 7822, male, SVL = 57.4. Photos by Diego Acosta-López.

FIGURE 22. Live holotype of *Gastrotheca yacuri* showing details of color and texture in groin, thighs, shanks, eye, and tympanum. CJ 7822, male, SVL = 57.4. Photos on left side by Diego Acosta-López, on right side by PS.

diameter of tympanum; tympanic evident; supratympanic fold elevated, extending from behind the tympanum to the insertion of the forelimb. Dentigerous vomerine processes narrowly separated medially, each bearing four teeth.

Arm robust; ulnar tubercles absent; hand and fingers moderately large (TFL 28% of SVL); fingers unwebbed bearing fringes; discs large and rounded, width of disc of Finger III lesser that diameter of tympanum; relative lengths of fingers I<II<IV<III; subarticular tubercles prominent, round, in lateral profile, none bifid; supernumerary tubercles small and nearly indistinct; palmar tubercle bifid, prepollical tubercle large, elliptical. Hind limb robust; tibia length 47% of SVL; foot length 43% of SVL; calcar and tarsal tubercles absent; inner tarsal fold approximately ¼ the length of the tarsus; outer metatarsal tubercle rounded; inner metatarsal tubercle absent; toes moderately long; relative length of toes I<II<III<V<IV; webbing absent between Toes I and II, but bearing fringes; webbing formula for other toes II2—3III2—4IV3—2V; subarticular tubercles moderately large, rounded; supernumerary tubercles small, numerous, and rounded.

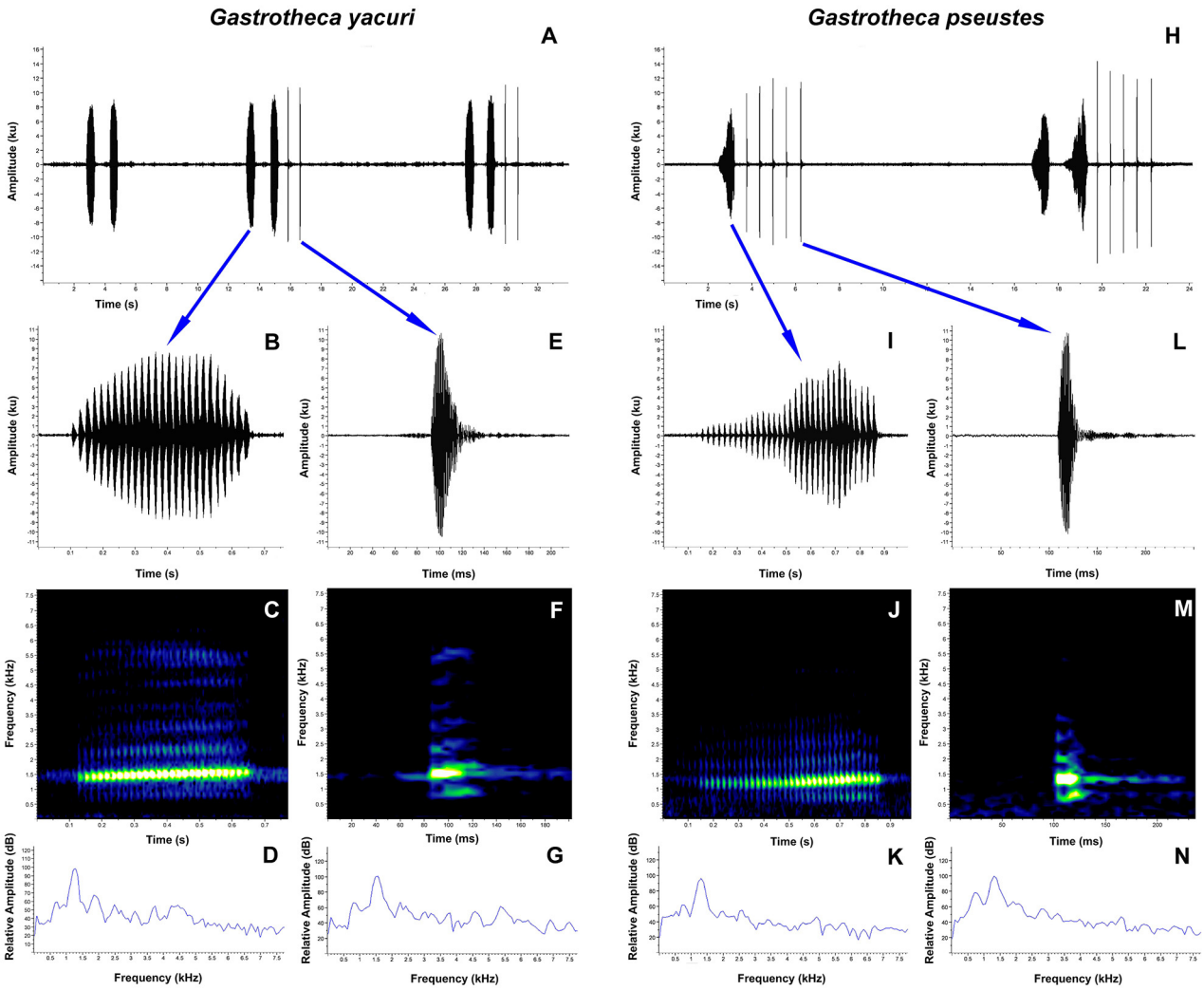

FIGURE 23. Advertisement calls of *Gastrotheca yacuri* (A–G) and *G. pseustes* (H–N): (A) oscillogram of three consecutive calls, with the first call composed of two long notes and the next two calls composed of two long and two short notes, (B) oscillogram of a single long note, (C) spectrogram of a single long note, (D) power spectrum of a single long note, (E) oscillogram of a single short note, (F) spectrogram of a single short note, (G) power spectrum of a single short note, (H) oscillogram of two consecutive calls, with the first call composed of one long and five short notes and the next call composed of two long and five short notes, (I) oscillogram of a single long note, (J) spectrogram of a single long note, (K) power spectrum of a single long note, (L) oscillogram of a single short note, (M) spectrogram of a single short note, (N) power spectrum of a single short note. All spectrograms at Hanning window function, 512 bands resolution. See text for details.

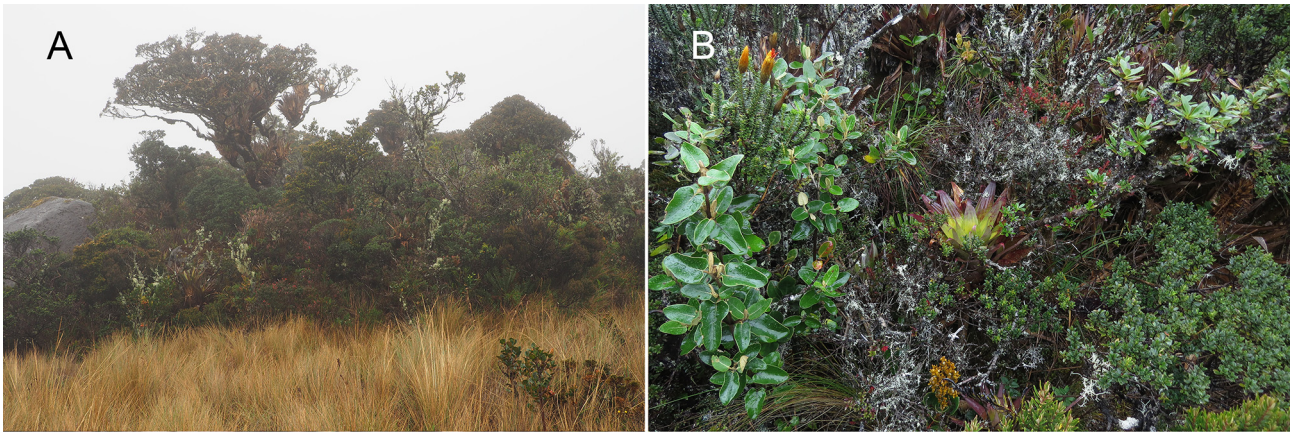

FIGURE 24. Macro and microhabitat of *Gastrotheca yacuri* in Parque Nacional Yacuri. Photos by PS.

Skin on dorsum smooth to shagreen; smooth occipital ridge present; U-shaped ridges (vestigial) in sacrum region; skin on flanks rugose and coarsely areolate; skin on throat loose bearing folds of smooth vocal sac; skin on ventral surfaces of thighs, arms, and belly heavely areolate; skin on venter surface of shanks smooth; rugose surfaces around cloacal opening. Tongue broad, suboval, not notched posteriorly, fully attached to mouth floor.

Coloration in life. The dorsal surfaces of the head, body, and limbs are green; the hidden surfaces of the forearm, thighs, and shanks are reticulated with black and blue markings (Figs. 21–22). Head markings are brown canthal and labial stripes. The canthal stripe is diffuse; the labial stripe varies from brown anteriorly to white posteriorly until the insertion of the forelimb. The dorsolateral stripe is thin and consists of a series of bronze and cream warts, bordered below with a black and brown line. The flanks are brown and green with a blue and black reticulum towards the lower flanks, axillae, groin, anterior and posterior surfaces of thighs, shanks, and tarsus; the pelvic patch is brown. The venter is cream with nearly uniformly distributed, small, dark brown marks; gular sac is nearly uniform grayish-brown with small dark brown marks. Palms and soles are pinkish gray; ventral fingers and toes are fleshy. The iris is copper with abundant black reticulations.

Coloration in preservative. Similar to coloration in life, but green and blue surfaces have begun to fade.

Measurements (in mm). SVL: 57.4, TIBL: 27.2, FL: 24.8, HL: 17.1, HW: 19.2, IOD: 6.9, EW: 5.2, IND: 2.8, ED: 6.0, EN: 3.0, TD: 3.3, FFL: 8.2, TFL: 16.2, TFD: 2.8.

Variation. Morphometric variation of the male paratype is as follows: SVL: 58.9, TIBL: 28.6, FL: 28.3, HL: 17.9, HW: 20.1, IOD: 6.7, EW: 4.3, IND: 2.8, ED: 5.6, EN: 5.0, TD: 3.0, FFL: 10.8, TFL: 19.0, TFD: 2.7.

The skin on the dorsum varies in the subadult by lacking a smooth tranverse occipital ridge.

Color variation in life. The referred subadult specimen varies from the holotype in that it is mostly brown; it has a light reddish-brown dorsum of body and limbs with darker, well-defined stripes, two paravertebral and one at the coccyx position; scattered black spots are present on dorsum towards the flanks (Fig. 10O). The loreal region is brown, and a thin dark brown canthal line is present; the labial stripe is dark brown and bordered along its upper margin by a thin pale stripe that varies from brown anteriorly to cream posteriorly until the insertion of the forelimb. There is no dorsolateral stripe but the reddish-brown dorsal color contrasts with a broad dark brown band on the flanks. The flanks are brown with black and cream marks (without blue colors). The venter is mostly brown with cream marks that are larger towards the chest; the gular region is slightly darker that the venter. The palms and soles are gray. The iris is cooper with black reticulations and has a shade of red in the lower half.

Vocalization. Four individuals of *Gastrotheca yacuri* were recorded at El Salado, Loja Province (Appendix III). Descriptive statistics of the acoustic variables are provided in Table 5. The advertisement call is a complex call, composed of one to three (usually two) long pulsed notes and followed (or not) by one to three (usually two) short, single-pulsed notes (Fig. 23A–G). The long note had a mean duration of 0.634 s (SD = 0.091) and consisted on average of 32.24 (SD = 7.504) distinct pulses, partly fused, without silent intervals (amplitude modulation close but less than 100%). The amplitude of the long note increases gradually towards the middle of the note after which it decreases gradually by the end. The short notes had a mean duration of 0.072 s (SD = 0.020) and the inter-note interval was on average of 0.549 s (SD = 0.214). The mean dominant frequency of the call was 1496.7 Hz (SD = 38.643), with a mean 90% bandwidth frequency of 1366.7–1637.9 Hz, having the highest values recorded among the analyzed species. The fundamental frequency is recognizable; when visible, 5 to 7 harmonics are distinguishable.

Comparisons. The advertisement call of *Gastrotheca yacuri* is most similar to that of *G. pseustes*, but *G. yacuri* has a much shorter call duration, shorter long notes duration, shorter inter-note interval, a higher dominant frequency, and a higher 90% bandwidth frequency compared with the call of *G. pseustes* (Table 5). Also, *G. yacuri* emits usually only two short notes compared with 4–6 short notes of *G. pseustes*. The call of *G. yacuri* can be easily distinguished form those of *G. lojana* and *G. testudinea* by the amplitude modulation of the longer note, longer call duration, lower short note rate, larger number of pulses, higher pulse rate, a much higher dominant frequency, and higher 90% bandwidth frequency. Also, *G. yacuri* emits up to three (usually two) long notes per call compared with the only one emitted by *G. lojana* and *G. testudinea* (Table 5).

Distribution and ecology. *Gastrotheca yacuri* is only known from three nearby localities 2.8 km apart (maximum distance) at elevations of 2712–3492 m in the Cordillera Oriental de los Andes in southern Ecuador. One locality is within Parque Nacional Yacuri and the others are in El Salado de Jimbura in Loja Province (Fig. 9). This nocturnal, semiarboreal species inhabits paramo and subparamo in the Evergreen Montane Forest of Catamayo-Alamor (Ministerio de Ambiente del Ecuador 2012), where the average annual rainfall is 895–1159 mm

and the average annual temperature is 10.4–14.6 ºC (Fick & Hijmans 2017). The male holotype was found near the road, calling from the branches of a bush, at about 3.5 m above ground. In this same location, choruses were heard from April to late July 2016; the males were calling usually from the vegetation nearby the road. An additional subadult was found during the day in a large terrrestrial bromeliad (Fig. 24A, B). Females and tadpoles are unknown. In this location, in Parque Nacional Yacuri, *Gastrotheca yacuri* is syntopic with *G. turnerorum*.

Conservation status. We suggest that *Gastrotheca yacuri* should be assigned to the Data Deficient category according to guidelines of the IUCN (2001), given the inadecuacy of the current information to establish its status. Further searches and definition of its distribution, area of occupancy, habitat use, and biological information are required. Currently its known area of occurrence is less than 10 km^2, thus it could qualify for a Critically Endangered category; however, we can reasonably predict that if further surveys are conducted within the protected Yacuri National Park, its area will increase to more than 100 km^2. In any case, Lagunas Negras de Jimbura have suffered the synergistic effects of agriculture, cattle and sheep raising, fires, introduced species such as trout, pesticide use, and unregulated tourism activitites. Areas in the Salado de Jimbura that are out of the Yacuri National Park already have been heavily modified by human actions.

Etymology. The specific name yacuri is a noun in apposition and refers to the Yacuri National Park, where this species has been found. According to Chamba-Troya (2017), Yacuri takes its name from the Quechua words Yacu meaning water and Quri that means gold. Ecuador's southernmost national park ranges from 2000 to 3700 meters in the Cordillera Oriental. This park of 43,090,60 hectares is unique by sheltering a series of 48 glacial lakes, and many endemic species of flora and fauna. It is a Ramsar site (The Convention on Wetlands) and part of the Podocarpus-El Cóndor Biosphere Reserve declared by UNESCO.

Comments. *Gastrotheca yacuri* belongs to the subgenus *Gastrotheca,* and is reported as Species D in Duellman (2015: Fig 12.1).

Gastrotheca litonedis Duellman & Hillis 1987

Holotype. KU 202690 (Figs. 10A, 25A), an adult female, from 10 km (by road) northeast of Girón, 2750 m (03º 07' 11.8" S, 79º 06' 28.4" W), Azuay Province, Ecuador, obtained on 7 March 1984 by William E. Duellman.

Referred specimens. (Total 28: 13 males, 15 females). Ecuador: Azuay: CJ 386−9 (females), 401−4 (females, male), 1404−8 (males), KU 335388–9 (male, female), San Fernando, Laguna de Busa, 2834 m (03° 09' 15.8" S, 79° 15' 49.03" W), collected on 9 June 2011 by Elicio E. Tapia, Sofía Carvajal-Endara and Henry Grefa; QCAZ 42734 (female), San Fernando, Laguna de Busa, 2834 m (03° 09' 15.8" S, 79° 15' 49.03" W), collected on 27 October 2007 by Sofía Carvajal-Endara, Amaranta Carvajal-Campos and Andrea Carvajal-Endara; QCAZ 42855 (female), 42857−9 (females), 42861 (female), 42866 (male), 42871 (male), San Fernando, Laguna de Busa, 2834 m (03° 09' 15.8" S, 79° 15' 49.03" W), collected on 18–20 August 2008 by Sofía Carvajal-Endara; QCAZ 49973−4 (female, male), 49976−8 (males), San Gerardo, 2854 m (03° 08' 00.17" S, 79° 11' 36.78" W), collected on 1 December 2010 by Sofía Carvajal-Endara.

Diagnosis. Included in the genus *Gastrotheca* by having a closed brood pouch on dorsum of female. A moderately large species (53.5– 62.4 mm SVL in females, n = 22; 48.9–57.4 mm SVL in males, n = 13) with tibia length 40−54% SVL, slightly longer than foot; (2) interorbital distance about 1.5 times width of upper eyelid; (3) skin on dorsum smooth, not co-ossified with skull, lacking transverse ridges; (4) supraciliary processes absent; (5) heel lacking calcar or tubercle; (6) tympanic annulus distinct, smooth; (7) Fingers I and II about equal in length, width of discs notably wider than digits; (8) fingers unwebbed; (9) webbing between external toes extending to the penultimate subarticular tubercle on Toe IV, to the distal subarticular tubercle on Toe V; (10) in life, dorsum green, brown, or tan with or without dark paravertebral marks or dark flecks; (11) head markings consisting of a pale cream labial stripe and narrow dark brown canthal stripe; (12) pale creamy white dorsolateral stripe present; (13) flanks, anterior surfaces of thighs and groin pale brown or tan slightly molted in some, posterior surfaces of thighs dark brown–gray with pale cream warts in some; (14) venter pale brownish gray; (15) brood pouch single, dorsal.

Gastrotheca litonedis most closely resembles five other species in southern Ecuador—*G. cuencana*, *G. plumbea*, *G. pseustes*, *G. turnerorum*, and *G. elicioi. Gastrotheca litonedis* differs from all of them by having a pale brownish gray venter; whereas, the venter is uniform creamy white in *G. cuencana*, cream in *G. plumbea*, cream with dark flecks or spots in *G. pseustes* and *G. elicioi*, and bronze or dark brown in *G. turnerorum*. *Gastrotheca*

litonedis, like *G. plumbea*, has smooth skin on the dorsum, whereas it is finely granular in *G. elicioi* and *G. cuencana*, weakly areolate to smooth in *G. pseustes* and areolate in *G. turnerorum*. A pale supracloacal stripe is present in *G. litonedis*, *G. pseustes*, and *G. turnerorum*, but it is absent in *G. cuencana* and *G. plumbea*. *Gastrotheca pseustes* differs further from *G. litonedis* by having a complex call structure (long and short pulsed-notes), which is simple in *G. litonedis* (only short pulsed-notes). The sister species of *G. litonedis* is the parapatric *G. cuencana*. Distinctive morphological and coloration features (compare Figs. 26–27, vs 2–4) are (character states for *G. cuencana* in parentheses): *Gastrotheca litonedis* is larger than *G. cuencana* (SVL student's t-test: t = -6.725, df = 99, $p < 0.001$), has a bluntly rounded snout in profile (rounded snout inclined anteroventrally in profile); a narrow dark brown canthal stripe is present (absent or inconspicuous), a row of barely elevated dorsolateral warts (conspicuous, elevated), green, tan or brown dorsal surfaces of fingers (fingers cream dorsally), posterior surfaces of thighs dark brown (translucent cream with pale tinge blue or green). The call of *G. litonedis* has a higher note rate, longer note duration, shorter inter-note interval, higher dominant frequency, and higher 90% bandwidth frequency compared with *G. cuencana*. Finally, these two species also differ by having a genetic distance of 1.2 % (in a DNA dataset of 438 bp, 16S gene).

Gastrotheca litonedis is syntopic with *G. lojana* and *G. pseustes* 2, from which it differs notably by the texture of skin on dorsum, ventral coloration, and call structure. The skin on the dorsum is smooth in *G. litonedis*, whereas it is finely granular in *G. lojana* and coarsely granular in *G. pseustes* 2; furthermore, both species have cream venters with dark flecks, spots, or mottling, and a complex call structure with long and short pulsed-notes (*G. lojana* call in Fig. 17H–N).

Variation. Morphometric variation of 22 females and 13 males (from Duellman 2015) is summarized in Table 3. Females are larger than males (58.0±2.4 mm; 53.8±2.8 mm). The skin on the dorsum is mostly smooth in most specimens; however, in some specimens it is weakly areolate. All adults have a moderate supratympanic fold, which usually extends from the upper part of the tympanum to a point above the insertion of the forelimb. Some individuals have several small rounded tubercles anterolateral to the tympanum. Each dentigerous vomerine process has 2–10 teeth (5.4±1.6, n = 34).

Color variation in preservative. In most specimens the dorsum is bluish gray without marks; in a few specimens faint paravertebral marks are present. The narrow canthal stripe, flanks, and posterior surfaces of thighs are dark brown. A creamy white supralabial stripe from the posterior margin of the lip to the insertion of the forelimb is prominent in all specimens. Creamy white dorsolateral, supracloacal and heel stripes are present. On the posterior part of the flanks the coloration varies from small white flecks to mottling on a dark brown ground color. The anterior surfaces of the thighs are usually gray with black flecks or spots. The ventral surfaces are uniform dull gray in most specimens; some have a pale gray venter with evenly distributed dark flecks and spots, and in CJ 1412 the venter is pale gray with black markings. Some specimens have a faint tinge of pale blue on the ventral surfaces of the shanks. Males have a cream nuptial pad on the medial surface of the thumb.

Color variation in life. (Figs. 26, 27). The dorsum varies from uniform green (QCAZ 42858), to brown (CJ 404); in some individuals dark paravertebral marks and dark brown flecks are present (QCAZ 49977). The ventral surfaces are pale gray in most specimens; some have evenly distributed dark flecks and spots, and some have a faint bluish tinge on the ventral surfaces (QCAZ 49977). A narrow dark brown canthal stripe is present; a cream supralabial stripe extends from the posterior margin of the lip to the insertion of the forelimb. The tympanum is brown, tan, or olive green. The iris is reddish bronze with dense black reticulations. The posterior surfaces of the thighs are dark brown or cream with orange flecks. A cream dorsolateral stripe is evident in most individuals. The flanks, groin, and anterior surface of the thighs usually are bronze-brown or tan with cream or dark flecks and spots. In some individuals a pink-orange tinge is present in the groin (Fig. 27). The supracloacal and heel stripes are cream or tan, and the ventral surfaces of the shanks have a faint pale blue tinge.

Tadpoles. Tadpoles belong to Type IV tadpole of Orton (1953), and the exotroph, benthic ecomorphological guild. All measurements are expressed in millimeters. The following description is based on a specimen in Stage 37 (CJ 6558), from a series of 79 tadpoles (CJ 6557) born and reared in laboratory conditions, from a mother collected when gravid in the field (CJ 6018) at Laguna de Busa, 2780 m, Azuay Province, Ecuador, by Manuel A. Morales-Mite on 06 January 2016 (Fig. 5A).

Total length 52.8; body length 19.4 (37% of total length). Body ovoid in dorsal and lateral views, slightly depressed; throat slightly concave in lateral profile, sloping from tip of snout to belly; body width at the level of spiracle 12.5, and height at same position 10.3, head width at level of eyes 10.0. Lateral line system present but

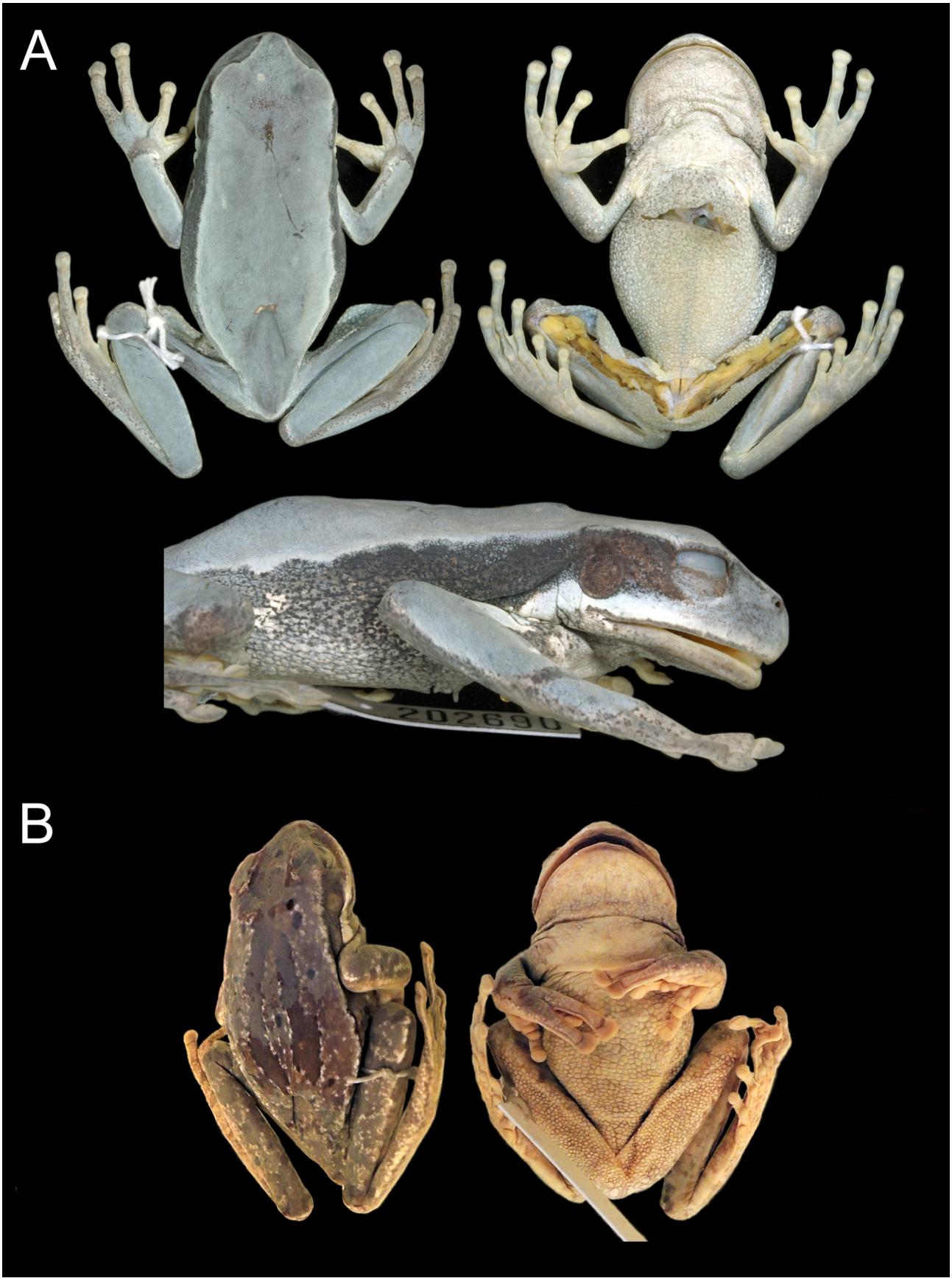

FIGURE 25. Adult female holotypes in preservative of (A) *Gastrotheca litonedis* (KU 202690, SVL = 62.4 mm), and (B) *Gastrotheca lojana* (BMNH 1947.2.31.13, SVL = 57.0 mm). Photos A by Martín R. Bustamante; B by LAC.

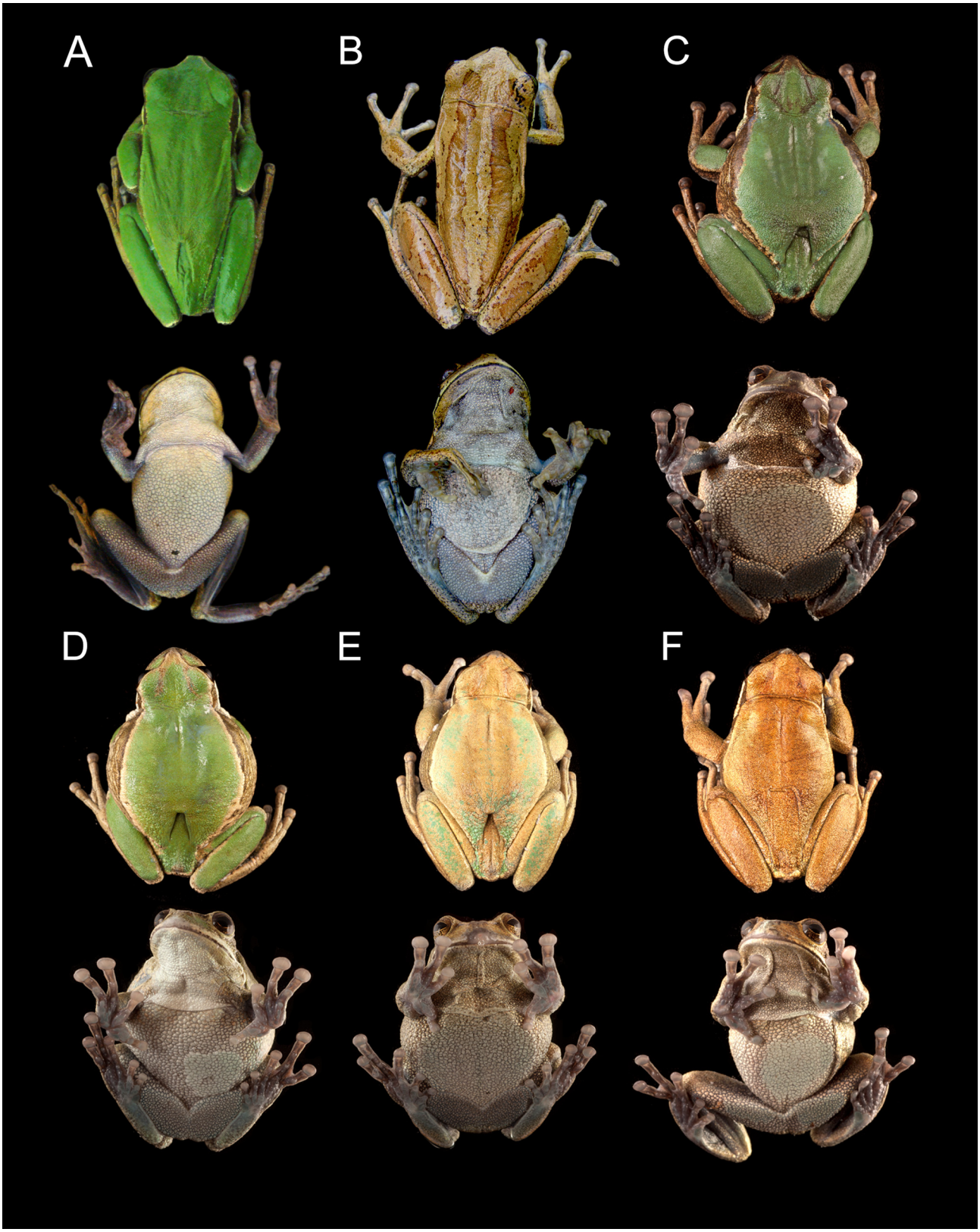

FIGURE 26. Live adults of *Gastrotheca litonedis* showing variation in dorsal and ventral color pattern: (A) QCAZ 42858, female, SVL = 56.0 mm, (B) QCAZ 49977, male, SVL = 52.4 mm, (C) CJ 401 female, SVL = not taken, (D) CJ 402, female, SVL = not taken, (E) CJ 403, female, SVL = not taken, and (F) CJ 404, male, SVL = not taken. Not to scale. Photos by LAC.

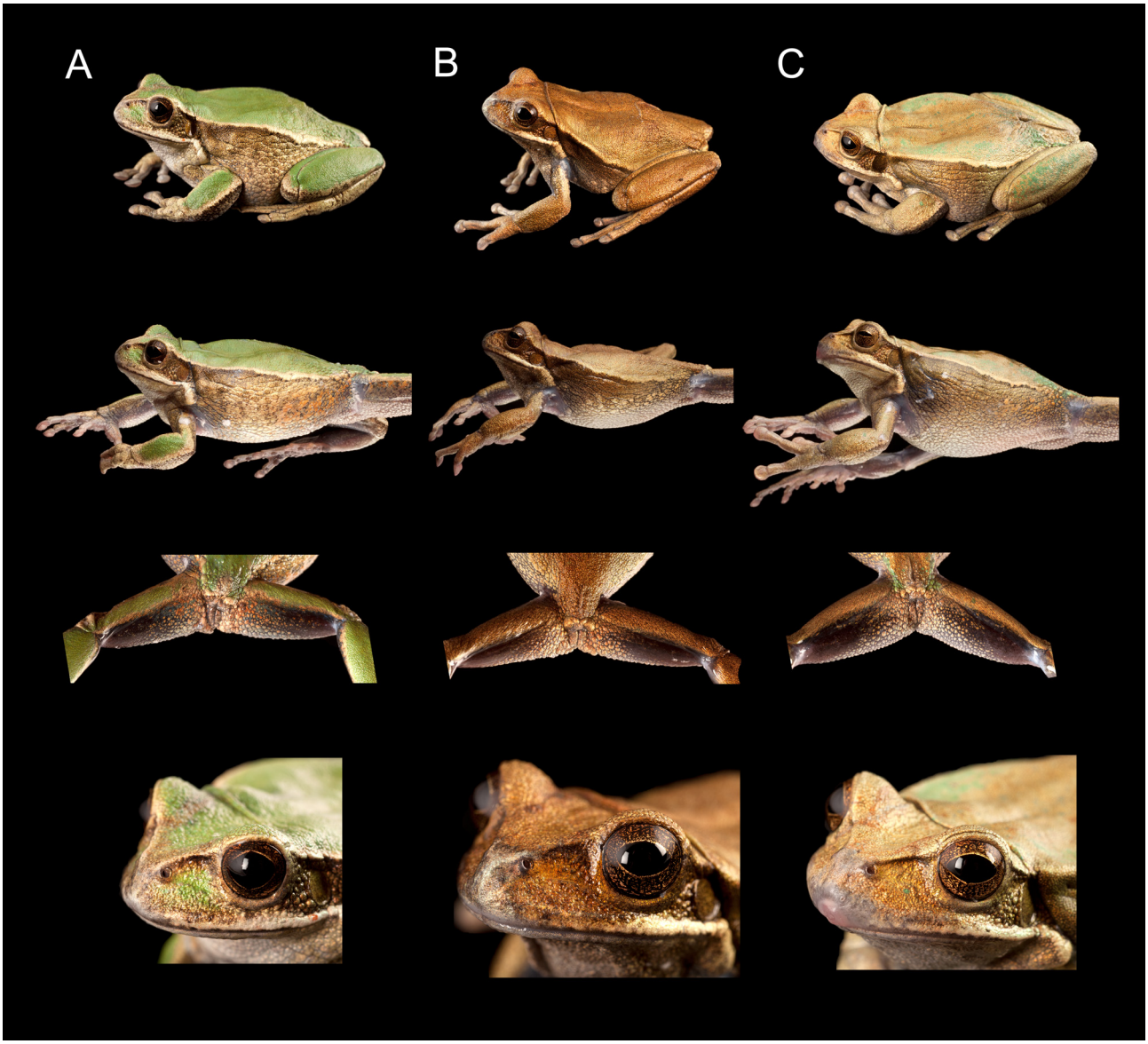

FIGURE 27. Live adults of *Gastrotheca litonedis* showing variation in lateral, groin, thighs and eye color pattern: (A) CJ 402, female, SVL = not taken, (B) CJ 404, male, SVL = not taken, and (C) CJ 403, female, SVL = not taken. Not to scale. Photos by LAC.

barely visible, supraorbital and infraorbital lines not evident at level of snout, infraorbital line present at level of the eye, touching the inferior portion of the orbit, and making contact with supraorbital line immediately behind the eye. Postorbital line represented by three stitches arranged in line and forming a 45-degree angle with the body plane. Angular line, anterior oral line and loreal lines not visible; dorsal body and middle body lines not visible. Nostril medium sized (in proportion to body length), ovoid, protruding, having a fleshy annulus, its opening directed anterolaterally. Snout–nostril distance 4.2; internarial distance 2.8. Eyes dorsally positioned; eye length 1.9, eye width 1.8; interorbital distance 5.2. Spiracle sinistral, located at midbody level, spiracular opening oriented posteriorly; distance from tip of snout to spiracular opening 12.9; end of spiracular tube rounded, attached to body wall, inner wall of spiracular tube not evident; spiracle length 2.7, spiracle transverse width 3.5. Vent tube dextral, opening oriented posteriorly, tube length 2.5, tube transverse width 2.2. Tail length 33.3; caudal musculature slender, narrowing gradually until tail terminus; caudal muscle height 4.1, width 3.6; caudal fins well developed and proportional, dorsal fin arising abruptly near tail-body junction; dorsal fin height 4.1, ventral fin height 3.7; maximum tail height 9.2; tail terminus rounded, caudal musculature not reaching fin terminus.

Oral disc small, ventral, located near tip of snout, not protruding laterally beyond body; transverse width 5.8. It is surrounded by a uniserial row of marginal papillae, interrupted medially on upper lip. Lower lip papillae

alternate in orientation, giving appearance of two rows; upper lip with 23 papillae on right side and 23 papillae on left side; lower lip bearing 57 marginal papillae. Upper jaw sheath medium-sized, forming a smooth arch and finely serrated, transverse width 2.9 (50% of width of oral width) and height 0.3. Lower jaw sheath V-shaped, open and finely serrated, width 2.6, and height 0.7. Labial tooth row formula 2/3(1); tooth rows lengths: A1: 4.5, A2: 4.4, P1 right row 1.65, P1 left row 2.0, P1 gap 0.2, P2: 4.1, P3: 3.95. (See also Fig. 6A of CJ 5292, Stage 35).

Color in life. Based on a specimen in Stage 34 from a series (CJ 1947) obtained from San Fernando, Laguna de Busa, Azuay Province, 2834 m, by Elicio E. Tapia, Sofía Carvajal-Endara, and Henry Grefa on 9 June 2011 (Fig. 6A). In dorsal view, body olive-gray, head and tail suffused with pink and cream. Flanks cream anteriorly to olive-gray posteriorly. In ventral view, cream anteriorly in gular region; followed posteriorly by red gills visible troughout the throat, and olive-gray guts. Caudal musculature pink proximally, gradually becoming gray posteriorly; dorsal and ventral fins translucent, with olive stippling distributed regularly along length of tail except distally, where stippling diminishes. Spiracle and oral apparatus nearly translucent. Iris gold.

Variation. Variation of 28 meristic characters of tadpoles in Stages 33–40 (CJ 5447, 5449, 5464–67, 6557, 6558) are shown in Table 8. Total length varies between 31.4 (Stage 33) and 61.9 (Stage 40) and tail length proportion varies from 58% to 69% until Stage 40. Number of marginal papillae varies among specimens and Gosner stages; variation in number of ventral papillae at lower lip is high (39–66).

We documented changes in coloration during ontogenetic development of CJ 1947 (Fig. 28A–C). At Stage 39, the dorsum and flanks are olive-gray with a diffuse pattern of gray paravertebral marks. By Stage 41, dorsum of body and limbs is green with well-defined dark green paravertebral marks; a cream dorsolateral stripe is bordered below by a fine black line; a creamy white stripe is present on face where upper lip will be formed. The flanks are greenish gray. At Stage 46, the dorsum is nearly uniform green; the paraverterbal marks are barely evident. The flanks are brown, and the iris is red. CJ 6813 is similar to the above described but has scattered cream flecks on a green dorsum.

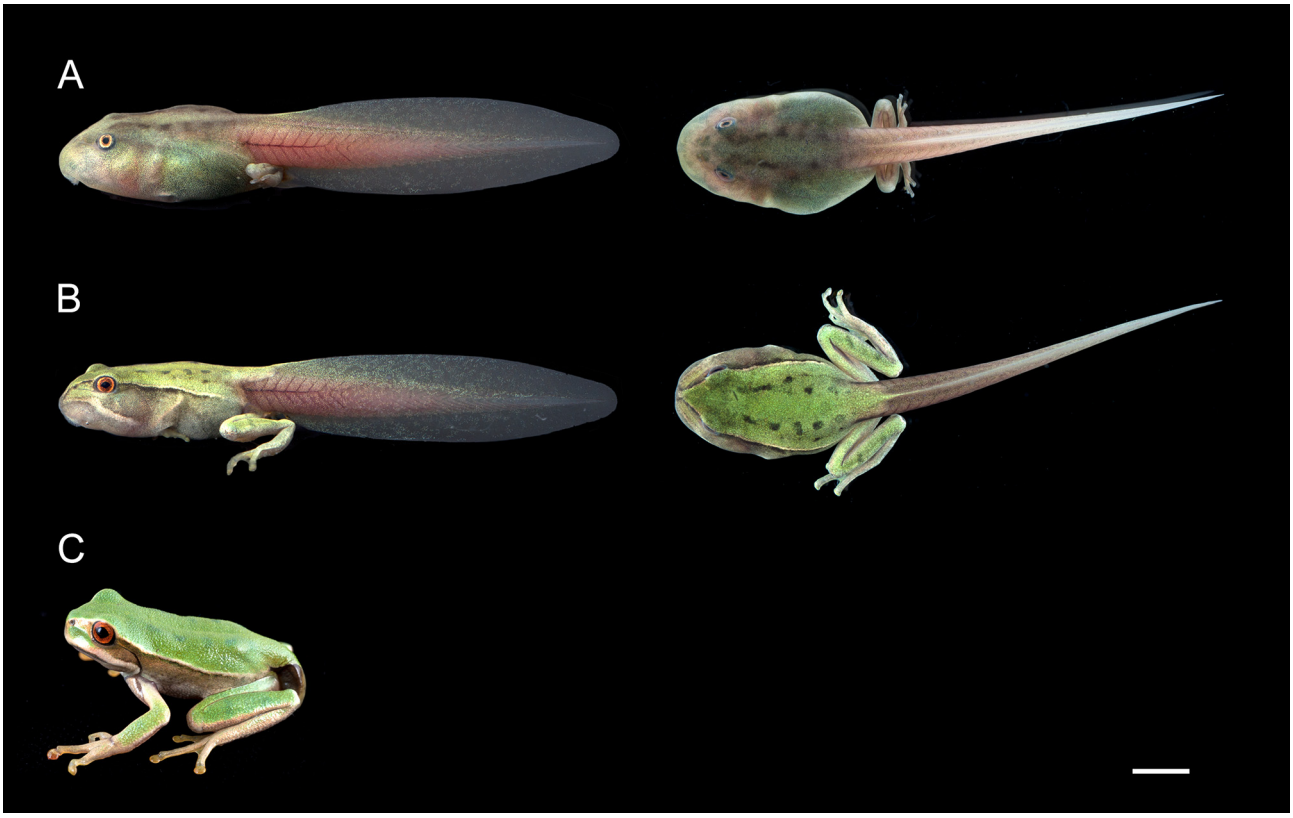

FIGURE 28. Ontogenetic changes in live *Gastrotheca litonedis* (CJ 1947) from Laguna de Busa, San Fernando, Azuay Province, Ecuador. Stages of Gosner: (A) Stage 39, (B) Stage 41, and (C) Stage 46. Scale = 5 mm. Photos by LAC.

Comparisons. Tadpoles of *Gastrotheca litonedis* may occur in sympatry with those of *G. pseustes* 2 and *G. lojana*. *Gastrotheca litonedis* differs from them by having less pigmentation on dorsum and venter (compare in Fig.

5). It further differs from *G. lojana* by having a lowest tail dorsal fin.and from *G. pseustes* by lacking a reticulated pattern on the flanks.

Vocalization. A total of nine individuals of *Gastrotheca litonedis* were recorded from two locations (6 individuals from San Gerardo and 3 from San Fernando, Laguna de Busa) in Azuay Province (Appendix III). Descriptive statistics of the acoustic variables are provided in Table 5. The advertisement call of *G. litonedis* is a simple call, composed of a series of short, single-pulsed notes, emitted at regular intervals (Fig. 8E–H). In our recordings, the calls have between 1 and 21 notes per call. The notes have a mean duration of 0.075 s (SD = 0.025) and a mean inter-note interval of 1.768 s (SD = 0.286). The mean dominant frequency of the call is 1224.0 Hz (SD = 66.415), with mean 90% bandwidth of 1114.7–1308.1 Hz. The fundamental frequency and harmonics are not clearly recognizable.

Comparisons. The advertisement call of *Gastrotheca litonedis* is similar to that of *G. cuencana*; all the other species of *Gastrotheca* species in the southern Ecuadorian Andes have complex calls. However, the call of *G. litonedis* has a higher note rate, longer note duration, shorter inter-note interval, higher dominant frequency, and higher 90% bandwidth frequency compared with *G. cuencana* (Table 5).

Distribution and ecology. *Gastrotheca litonedis* is known from three localities (ca. Girón, San Fernando (Laguna de Busa), San Gerardo) on the eastern slope of the Cordillera Occidental in Azuay Province (Fig. 9). Its elevational range is 2750–2854 m in an area of extent of occurrence of about 10.2 km^2. This nocturnal, semiarboreal species inhabits forest and disturbed areas in the Evergreen Montane Forest of Cordillera Occidental of the Andes (Ministerio de Ambiente del Ecuador 2012), where the average annual rainfall is 611–658 mm and the average annual temperature is 12.2–12.5 ºC (Fick & Hijmans 2017). Most of the specimens collected at Laguna de Busa were found among totora reeds (*Schoenoplectus californicus*) at the border of the lagoon. Males were calling from totora reeds at approximately 1–2 m above ground. Females were perched on totora reeds approximately 40 cm above ground and along small streams that were close to the lagoon. Some males also were calling from branches of shrubs around the lagoon approximately 2.5 m above ground. During the day a male and a female were basking on leaves of calla lilies (*Zantedeschia aethiopica*), which were present along irrigation ditches, bordering pastures. At this locality, *Gastrotheca litonedis* is syntopic with *G. pseustes* (*sensu lato*) and *G. lojana*; all of them have a biphasic mode of development, in which brooding females release tadpoles in ponds, where they complete their development (Figs. 10–11). In all the visits made to this locality (October 2007 and December 2007, August 2008, June 2011), gravid females were found, as well as tadpoles in small streams, temporary ponds, and at the edge of the lagoon. One of the gravid females collected on 9 June 2011 was transported to the laboratory, where it deposited 96 tadpoles. At San Gerardo, most individuals were found on the border of an irrigation ditch in a pasture. Males were calling from the grass at approximately 50 cm above ground. At this locality, *G. pseustes* (*sensu lato*) also was found. A brooding female of *G. litonedis*, showing heliophilic behavior during most of the incubation time, under captive conditions in an outdoor enclosure, is depicted in Figure 10C.

Conservation status. IUCN categorizes *Gastrotheca litonedis* as Endangered (Coloma *et al.* 2004). However, the current assessment was based on information combining the two species described in this study (*G. litonedis* and *G. cuencana*). Thus, we re-categorize this species as Critically Endangered, according with IUCN criteria and sub-criteria B1ab(i,ii,iii,iv). Currently, the known area of occurrence of *G. litonedis* is extremely small (10.2 km^2), and its area of occupancy is even smaller; although we suspect that its distribution might increase as further searches are conducted. Its populations are in heavily human populated areas. For example, the surroundings of Laguna de Busa have been deforested and modified for human activities (Fig. 11D). The lake contains two introduced, predatory fish (trout and carp) and its surroundings are greatly altered by the introduction of exotic eucalyptus and conifers. Additional threats at this site are unregulated tourisms activities.

Comments. In the original description of *Gastrotheca litonedis*, Duellman and Hillis (1987) included data on nine males and 15 females. As noted by Duellman (2015), of these specimens, only the holotype, KU 202690, is *G. litonedis*. The other specimens used by Duellman & Hillis (1987) are identified herein as *G. cuencana*. In addition, the photograph published as the holotype of *G. litonedis* by Duellman and Hillis (1987:156: Fig. 9) is not the holotype. The frog in the photograph is actually *G. lojana* (KU 148794, from 2 km SSW of Saraguro, Loja Province, Ecuador). Also, the frog QCAZ 2692 depicted in Duellman (2015: Fig. 11.12B) is *G. lojana* (not *G. litonedis*). Genetic sequences generated in this study from tissues of the holotype differ from the sequences of other specimens generated and published by Wiens *et al.* (2007) (Genbank numbers: DQ679395, DQ679355, DQ679323, DQ679287), which are more similar to sequences of *G. cuencana*.

TABLE 8. Variation of 28 meristic characters of tadpoles in Stages 33–40 of *Gastrotheca litonedis* (CJ 5447, 5449, 5464–67, 6557, 6558). Values are given in mm, mean±standard deviations (first row) and ranges (second row), number of specimens in parentheses. See Materials and methods for character abreviations.

	Stage 33 (n=2)	**Stage 34** (n=5)	**Stage 35** (n=3)	**Stage 36** (n=3)	**Stage 37** (n=2)	**Stage 38** (n=1)	**Stage 39** (n=2)	**Stage 40** (n=3)
TL		39.89±3.60	43.76±4.99	43.38±2.52				61.05±1.52
	31.40–34.35	36.07–45.37	38.70–48.68	40.74–45.75	47.55–52.77	56.58	56.80–57.55	59.30–61.95
BL		15.67±0.93	16.21±1.04	16.92±0.41				20.84±1.68
	11.41–13.14	14.63–16.78	15.47–17.40	16.48–17.30	17.08–19.52	20.78	19.90–20.32	18.99–22.28
BW		9.39±0.80	9.46±0.52	10.36±0.15				15.27±0.52
	6.87–8.01	8.44–10.32	8.97–1	10.19–10.46	11.43–12.48	11.76	13.52–13.90	14.82–15.84
BH		7.48±0.53	7.10±0.26	8.38±0.77				10.60±0.91
	6.20–6.90	6.87–8.22	6.82–7.33	7.55–9.08	8.71–10.26	9.32	10.35–10.91	9.67–11.49
HWEL		8.34±0.46	9.12±0.71	9.57±0.45				12.13±0.29
	6.40–7.22	7.59–8.80	8.37–9.78	9.06–9.88	9.96–10.23	10.72	11.31–11.38	11.86–12.44
TAL		24.22±3.05	27.55±4.24	26.46±2.75				40.21±2.98
	19.99–21.21	21.29–29.26	22.94–31.28	23.77–29.27	30.47–33.25	35.80	36.48–37.65	37.02–42.92
TLP%		60.58±2.41	62.76±3.03	60.90±2.85				65.82±3.45
	61.75–63.66	59.02–64.49	59.28–64.75	58.35–63.98	63.01–64.08	63.27	64.23–65.42	62.43–69.33
MTH		8.15±1.13	8.19±0.34	9.87±1.32				11.72±0.31
	7.49–8.14	7.18–10.04	7.97–8.59	8.96–11.39	9.57–9.61	13.07	10.26–11.28	11.54–12.08
TMW		2.51±0.37	2.76±0.31	3.11±0.21				3.92±0.24
	1.86–2.24	2.18–3.09	2.47–3.08	2.92–3.34	2.96–3.40	4.35	3.66–3.85	3.78–4.20

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TABLE 8. (Continued)

	Stage 33 (n=2)	**Stage 34** (n=5)	**Stage 35** (n=3)	**Stage 36** (n=3)	**Stage 37** (n=2)	**Stage 38** (n=1)	**Stage 39** (n=2)	**Stage 40** (n=3)
TMH		2.98±0.32	3.39±0.33	3.75±0.42				4.80±0.28
	2.63–2.92	2.57–3.43	3.04–3.68	3.26–4.00	3.77–3.91	5.05	4.15–4.45	4.48–5.00
SND		3.18±0.24	3.70±0.40	3.67±0.45				4.83±0.21
	2.10	2.90–3.50	3.30–4.10	3.20–4.10	3.29–4.20	4.10	4.30–4.80	4.60–5.00
IND		2.48±0.15	2.47±0.06	2.70±0.00				2.83±0.15
	2.20–2.40	2.30–2.70	2.40–2.50		2.00–2.53	3.00	2.70–2.90	2.70–3.00
END		1.62±0.08	1.73±0.12	1.80±0.00				2.23±0.40
	1.301.50	1.50–1.70	1.60–1.80		1.61–1.80	2.30	2.00–2.10	1.80–2.60
EL		1.46±0.17	1.63±0.06	1.83±0.06				2.33±0.12
	1.30–1.50	1.30–1.70	1.60–1.70	1.80–1.90	1.80–1.85	2.20	2.20	2.20–2.40
EW		1.38±0.15	1.53±0.06	1.83±0.06				2.40±0.10
	1.30–1.40	1.20–1.60	1.50–1.60	1.80–1.90	1.60–1.80	2.10	2.20–2.30	2.30–2.50
IOD		4.48±0.53	4.57±0.35	5.20±0.30				6.00±0.00
	3.90–4.30	3.90–5.30	4.20–4.90	4.90–5.50	4.95–5.20	5.90	5.50–5.80	
VP		54.40±7.37	59.00±6.08	56.33±4.73				55.67±3.51
	39–44	46–65	55–66	51–60	57–62	65	54–61	52–59
DP right		22.60±4.16	22.67±4.73	19.33±0.58				22.00±1.73
	14–18	16–26	19–28	19–2	19–23	19	17–19	21–24

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TABLE 8. (Continued)

	Stage 33 (n=2)	**Stage 34** (n=5)	**Stage 35** (n=3)	**Stage 36** (n=3)	**Stage 37** (n=2)	**Stage 38** (n=1)	**Stage 39** (n=2)	**Stage 40** (n=3)
MP right		5.00±3.54	4.67±2.31	3.33±3.21				5.67±0.58
		0–10	2–6	1–7	2–6	0	5–9	5–6
DP left		23.20±4.09	24.67±0.58	20±3.61				24.33±3.06
	16–17	17–28	24–25	16–23	18–23	25	21–22	21–27
MP left		4.20±2.49	4.67±3.79	2.33±0.58				7.00±1.73
		0–6	2–9	2–3	1–5	5	4–7	6–9
WOD		4.30±0.26	5.23±0.72	5.17±0.45				6.57±0.15
	3.10–3.40	4.00–4.70	4.40–5.70	4.70–5.60	5.59–5.80	6.20	6.40–6.70	6.40–6.70
WUJ		2.38±0.13	2.63±0.12	2.73±0.21				3.37±0.06
	1.70–1.80	2.30–2.60	2.50–2.70	2.50–2.90	2.90±0.00	3.40	3.20–3.30	3.30–3.40
UJP%		55.38±1.22	50.80±5.23	52.99±2.89				51.27±0.46
	52.94–54.84	54.55–57.50	47.37–56.82	5–55.77	5–51.88	54.84	49.25–5	50.75–51.56
SL		2.16±0.21	2.60±0.70	2.60±0.35				3.50±0.89
	2.50	1.90–2.40	2.10–3.40	2.40–3.00	2.30–2.70	2.90	2.80–3.50	2.50–4.20
SW		2.04±0.53	1.90±0.26	2.07±0.12				2.77±0.15
	1.80	1.70–2.70	1.60–2.10	2.00–2.20	2.40–3.50	2.70	2.50	2.60–2.90
VTL		1.96±0.17	2.40±0.62	2.57±0.70				3.50±0.10
	1.60–1.90	1.70–2.10	1.70–2.90	1.90–3.30	2.50–3.00	3.40	2.90–4.70	3.40–3.60
VTW		1.60±0.21	1.73±0.57	1.77±0.06				2.43±0.15
	1.40	1.40–1.90	1.10–2.20	1.70–1.80	1.70–2.20	2.60	2.20–2.70	2.30–2.60

Gastrotheca lojana Parker 1932

Gastrotheca marsupiata lojana Parker, 1932:25.—Holotype: BM 1947.2.31.13 (Fig. 25B) from Loja, Loja Province, Ecuador.
Gastrotheca monticola (part)—Duellman & Hillis 1987:158.
Gastrotheca (*Duellmania*) *lojana*—Dubois, 1987:33.

Referred specimens. Ecuador: *Azuay:* CJ 390, 401–2, from Oña, 2272 m (03° 27' 41.04" S, 79° 09' 46.47" W), on 15 June 2011 by Elicio E. Tapia, Sofía Carvajal-Endara and Henry Grefa; KU 138401–3, from Girón, 2310 m (03° 10' 00.12" S, 79° 07' 59.88" W), on 06 June 1970 by Thomas A. Fritts; QCAZ 2692, from Oña, 2272 m (03° 27' 41.04" S, 79° 09' 46.47" W), on 1 December 1999 by Luis A. Coloma and Luis E. López; QCAZ 26314–5, 26318, 26322–3, 26327–8, 26334–5, 26337–8, from Oña, 2272 m (03° 27' 40.43" S, 79° 09' 45.11" W), on 8 August 2003 by Luis A. Coloma and Ítalo G. Tapia, QCAZ 31521–3, from Oña, 2272 m (03° 27' 41.04" S, 79° 09' 46.47" W), on 27 December 2005 by Ítalo G. Tapia and Giovanni Onore; QCAZ 32212, from Oña, 2272 m (03° 27' 41.04" S, 79° 09' 46.47" W), on 2006 by Luis A. Coloma; QCAZ 32571, from Oña, 2272 m (03° 27' 40.43" S, 79° 09' 45.11" W), on 8 August 2003 by Luis A. Coloma, Erik R. Wild, Andrés Merino-Viteri, Ítalo G. Tapia and Edwin Patricio Vargas; QCAZ 42725, from San Fernando, Laguna de Busa, 2834 m (03° 09' 15.80" S, 79° 15' 49.03" W), on 22 October 2007 by Sofía Carvajal-Endara, Amaranta Carvajal-Campos, Andrea Carvajal Endara. Loja: BM 1947.2.31.6–10, BM 1947.2.31.13–18, from Loja, 2150 m (04° 00' 00" S, 79° 13' 00.12" W), on 1930–1 by Clodoveo Carrión Mora. KU 120673–4, from Loja, 2150 m (04° 00' 00" S, 79° 13' 00.12" W), on 9 June 1968 by John D, Lynch; KU 120675, from 2 km E Loja, 2100 m (03° 59' 56.4" S, 79° 13' 00.12" W), on 9 June 1968 by John D, Lynch, KU 138233, from 3 km W Loja, 2150 m (03° 58' 47.99" S, 79° 12' 54" W), on 21 June 1970 by Thomas H. Fritts; KU 138234, from 10 km W Loja, 2500 m (03° 59' 56.4" S, 70° 14' 43.08" W), on 27 June 1970 by Thomas H. Fritts; KU 138235–6, from 5 km N Loja, 2150 m (03° 52' 00.12" S, 79° 13' 00.12" W), on 28 June 1970 by Thomas H. Fritts; KU 138404–9, from Saraguro, 2412 m (03° 36' 00" S, 79° 13' 00.12" W), on 19–20 June 1970 by Thomas H. Fritts; KU 148568, from Saraguro, 2412 m (03° 36' 00" S, 79° 13' 00.12" W), on 22 May 1971 by Richard M. Montanucci; KU 178482–95, from 2 km SSW Saraguro, 2569 m (03° 38' 22.92" S, 79° 13' 59.87" W), on 5 January 1978 by John D. Lynch; KU 178496–7, from 2.1 km N Saraguro, 2575 m (03° 36' 41.76" S, 79° 13' 00.12" W), on 7 January 1978 by John D. Lynch; QCAZ 22371, from Loja Zamora Huayco, 3018 m (04° 05' 49.9806" S, 79° 10' 02.499" W), on 12 December 2002 by Diego Almeida-Reinoso; QCAZ 30788, from Saraguro, 2412 m (03° 36' 00" S, 79° 13' 00.01" W), on 20 September 1978 by MC; QCAZ 34505, from 2 km SW Saraguro, 2569 m (03° 38' 22.99" S, 79° 14' 24" W), on 5 January 1978 by John D. Lynch. *El Oro*: QCAZ 32724, from Guanazán, 2984 m (03° 27' 18.43" S, 79° 29' 23.64" W), on 3 December 2006 by Silvia Aldás Alarcón.

Diagnosis. Included in the genus *Gastrotheca* by having a closed brood pouch on dorsum of female. A moderately large species (54.1–76.1 mm SVL in females, n = 12; 40.2–61.0 mm SVL in males; n = 24) with tibia length 41−56% SVL, longer than foot; (2) interorbital distance about 1.6 times width of upper eyelid; (3) skin on dorsum finely granular, not co-ossified with skull, lacking transverse ridges; (4) supraciliary processes absent; (5) heel lacking calcar or tubercle; (6) tympanic annulus distinct, smooth; (7) Fingers I and II about equal in length, discs on fingers about twice width of digits proximal to discs; (8) fingers unwebbed; (9) webbing between external toes extending to the antepenultimate subarticular tubercle on Toe IV, to point midway between penultimate and distal subarticular tubercles on Toe V; (10) in life, dorsum green, brown, or tan with dark paravertebral marks; (11) markings on the head consisting of pale labial stripe broader at the posterior half of lip and dark interorbital bar or two blotches connected or not to paravertebral marks; (12) pale cream or white dorsolateral stripe fragmented; (13) flanks dark brown, green or tan with pale cream spots ventrally, anterior and posterior surfaces of thighs, groin, and dorsal surface of foot with contrasting pattern of heavily white mottling on a dark background, with bluish or greenish tinges; dorsal surfaces of limbs with dark brown or green bars; (14) venter creamy white with dark brown dots or marks; (15) brood pouch single, dorsal.

Gastrotheca lojana most closely resembles three other species in southern Ecuador (*G. elicioi*, *G. cuencana*, and *G. litonedis*) and one species in northern Peru (*G. monticola*). *Gastrotheca lojana* differs from *G. elicioi* in some coloration patterns (described above; also, compare in Figs. 10L, 29, 30 vs 12–14). A black canthal stripe is absent in *G. lojana*, but present in *G. elicioi*. The anterior and posterior surfaces of thighs and groin are heavily mottled in *G. lojana*, but slightly mottled in *G. elicioi*. The interorbital mark in *G. lojana* is a transverse bar that sometimes is divided into two blotches and that is usually connected with two broad paravertebral marks. In *G. elicioi* dorsal marks, when present, consist of a triangular interorbital mark, which may or may not be connected to

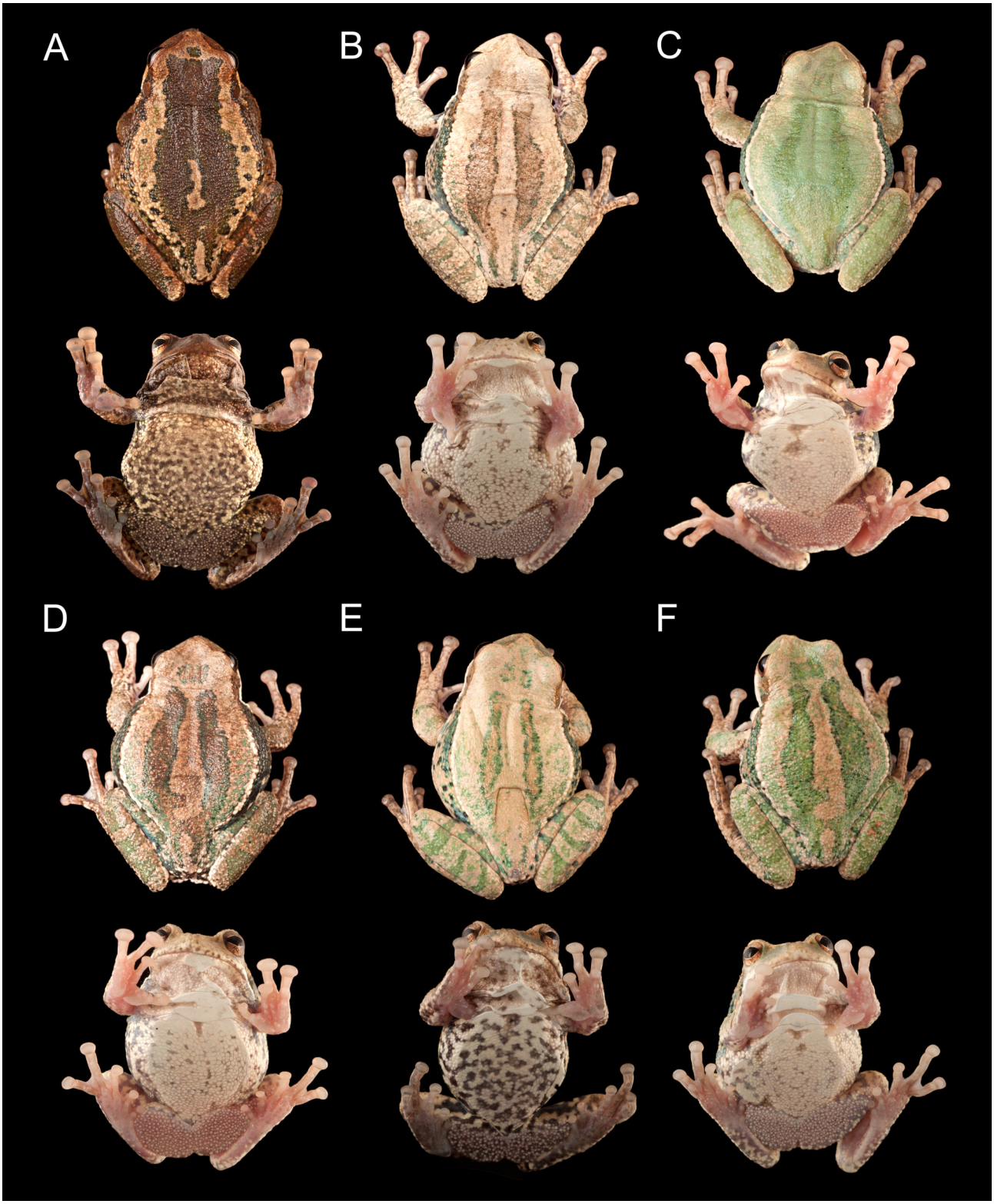

FIGURE 29. Live adults and subadults of *Gastrotheca lojana* showing variation in dorsal and ventral color pattern: (A) CJ 405, male, SVL = not taken, (B) CJ 407, female, SVL = 53.6 mm, (C) CJ 408, male, SVL = 44.9 mm, (D) CJ 409, subadult male, SVL = 45.5 mm, (E) CJ 411, female, SVL = 47.4 mm, and (F) CJ 412, male, SVL = not taken. Not to scale. Photos by LAC.

two narrow and curved paravertebral marks. *Gastrotheca lojana* has a conspicuous, elevated row of dorsolateral warts, whereas it is barely raised in *G. elicioi*. In addition, in *G. elicioi* the dark bars on limbs, when present, are shorter and less defined than in *G. lojana*. *Gastrotheca lojana* differs from its most related species, *G. cuencana* and

G. litonedis (compare Figs. 10L, 29, 30 vs 2–4, 26–27) by having: a cream venter with dark flecks or spots (uniform creamy white in *G. cuencana* and pale brownish gray in *G. litonedis*); an interorbital bar or blotches usually connected to paravertebral marks (absent in *G. cuencana* and *G. litonedis*); dorsal surfaces of limbs with dark transverse bars (irregular dark blotches in *G. cuencana* and usually unmarked in *G. litonedis*); anterior and posterior surfaces of thighs and groin heavily mottled (translucent cream without marks in *G. cuencana* and usually brown and slightly molted in some *G. litonedis*); dorsal surfaces of fingers cream or with dark brown spots (cream in *G. cuencana* and of same color of the rest of the body in *G. litonedis*); a fragmented dorsolateral stripe (continuous in *G. cuencana* and *G. litonedis*); and complex call (simple call in *G. cuencana* and *G. litonedis*). The genetic divergence between *G. lojana* and *G. litonedis* is 2.5% and between *G. lojana* and *G. cuencana* is 2.8% (in a DNA dataset of 438 bp, 16S gene). *Gastrotheca lojana* differs from *G. monticola* by having the concealed surfaces of thighs, groin and dorsal surfaces of the feet with white mottling on a dark background, whereas in *G. monticola* the axilla and groin, concealed surfaces of thighs, and dorsal surfaces of the feet are green with black spots on a green or tan background.

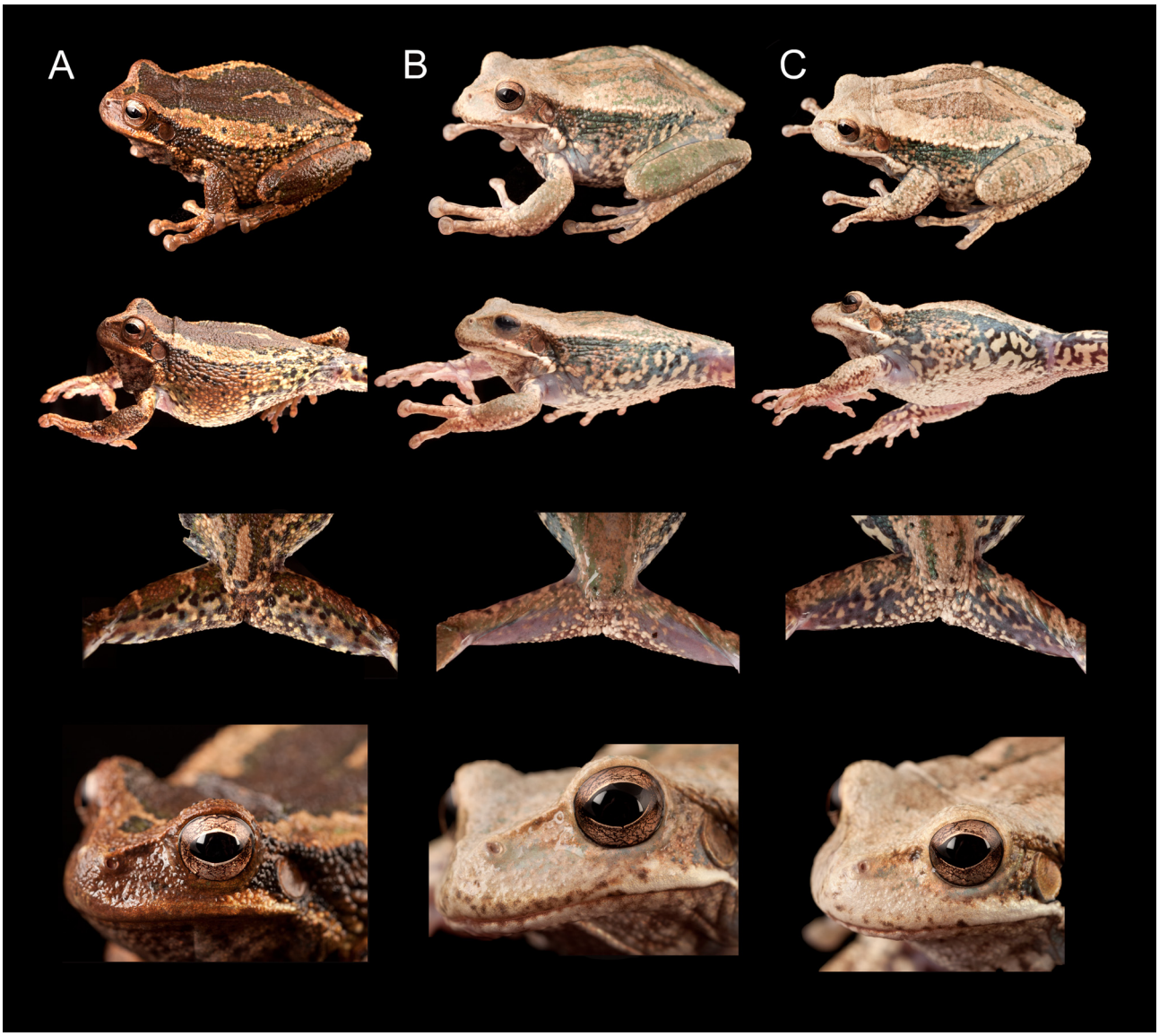

FIGURE 30. Live adults of *Gastrotheca lojana* showing variation in lateral, groin, thighs and eye color pattern: (A) CJ 405, male, SVL = not taken, (B) CJ 406, subadult female, SVL = 50.9 mm, and (C) CJ 407, male, SVL = 53.6 mm. Not to scale. Photos by LAC.

A distinctly different species, *G. pseustes*, occurs sympatrically with *G. lojana* in part of its range. *Gastrotheca lojana* differs from *G. pseustes* by having finely granular skin on the dorsum (smooth to coarsely granular in *G.*

pseustes), larger digital discs, and pale dorsolateral and supracloacal stripes. Also the call of *G. lojana* can be easily distinguished form the call of *G. pseustes* by the amplitude modulation of the longer note, shorter call duration, higher short note rate, shorter interval between notes, fewer pulses, lower pulse rate, a much lower dominant frequency, and a lower 90% bandwidth frequency.

Variation. Morphometric variation of 12 females and 24 males is summarized in Table 3. Females are larger than males (61.6±5.7 mm; 49.4±4.5 mm). All adults have a moderate supratympanic fold, which usually extends from the superior part of tympanum to point just above the insertion of forelimb. The dorsolateral row of warts can be less conspicuous in some specimens. Each vomer has four to ten teeth (5.7±1.4, n = 44).

Color variation in preservative. In most preserved specimens the dorsum is bluish gray or brown with darker interorbital, paravertebral marks and bars on the limbs. Some specimens also have dark flecks densely distributed on dorsum. All specimens lack a dark canthal stripe and have a cream white supralabial stripe, which is broader at the posterior margin of the lip and that is extended from the posterior margin of the lip to the insertion of the forelimb. Most of the specimens have a dark brown stippling on the supralabial stripe. A fragmented supracloacal and heel stripes are present; also a white mark extends laterally from the vent. The flanks are dark gray with black and white dots; the posterior part of the flanks, groin, concealed surfaces of thighs and dorsal surface of foot are heavily mottled. The venter is white and varies from having a few dark flecks to having a heavily mottled pattern.

Color variation in life. (Figs. 10L, 29, 30). In living individuals the color of the dorsum is green (CJ 408), brown (CJ 405) or tan (CJ 407) with darker interorbital and paravertebral marks. The interorbital mark is usually a bar that connects the two eyelids; however, in some individuals it is divided into two blotches (CJ 411). Paravertebral marks are broad and are usually connected with the interorbital mark (CJ 407) or, in some individuals (CJ 405), they are fused at the level of the scapular region. The venter is white in most specimens, some have dark flecks and spots evenly distributed, and others have a heavily mottled pattern. On the head there is a cream supralabial stripe, which is broader at the posterior margin of the lip and extends from the posterior margin of the lip to the insertion of the forelimb. The tympanum is brown, tan or olive green. The iris is reddish bronze with a few black reticulations. The flanks are brown, tan, or green with black and white spots. The posterior part of the flanks, groin, anterior and posterior surfaces of thighs have a heavily mottled pattern, some individuals have green or purple tinge on the groin and posterior surface of the thighs (Fig. 30). Supracloacal and heel stripes are cream or tan. The ventral surfaces of the shanks have a faint tinge of pale blue.

Tadpoles. Tadpoles belong to Type IV tadpole of Orton (1953), and the exotroph, benthic ecomorphological guild. All measurements are expressed in millimeters. The following description is based on a specimen in Stage 36, from a series (CJ 1948) obtained from a pond at Oña, 2272 m, Azuay Province, Ecuador, by Elicio E. Tapia, Sofía Carvajal-Endara, and Henry Grefa on 15 June 2011 (Fig. 5C). Total length 55.7; body length 19.8 (36% of total length). Body ovoid in dorsal and lateral views, slightly depressed; throat shape concave in lateral profile; body width at the level of spiracle 12.3, and height at same position10.2; head width at level of eyes 10.5. Lateral-line system barely visible, supraorbital and infraorbital lines both originating at tip of snout, running in parallel to the eye and making contact immediately behind the eye; angular line descending vertically from just posterior of eye to throat; anterior oral line descending vertically from level of oral disc and just anterior to level of nares to throat there it curve to parallel infraorbital line, thereby forming a continuous circuit with angular and loreal lines; dorsal body and middle body lines present.

Nostril medium sized (in proportion to body length), ovoid, protruding, with a fleshy annulus, its opening directed anterolaterally. Snout–nostril distance 2.8; internarial distance 3.2. Eye positioned and directed dorsally, not visible from below; eye length 2.1, eye width 1.9; interorbital distance 5.7. Spiracle sinistral, located ventrolaterally; spiracular opening directed posteriorly; distance from tip of snout to spiracular opening 13.7; spiracle end rounded, attached to body wall, inner wall of spiracle not evident; tube length 4.0, tube transverse width 2.9. Vent tube dextral, its opening directed posteriorly, tube length 3.7, tube transverse width 2.1. Tail length 37.0, caudal musculature slender, narrowing gradually until tail terminus; caudal muscle height 5.2, caudal muscle width 4.3; caudal fins well developed and about the same size, originating near tail-body junction; maximum height of tail 13.6; tail terminus rounded, caudal musculature not reaching fin terminus.

Oral disc small, ventral, located near tip of snout, not protruding laterally beyond body, not visible dorsally; transverse width 4.1. It is surrounded by a uniserial row of short, marginal papillae, interrupted medially on upper lip; lower lip papillae alternating in and out, giving the appearance of two series; upper lip with 21 papillae on right side and 19 papillae on left side; lower lip with 63 marginal papillae; upper jaw sheath medium-sized, forming a

finely serrated, smooth arch, height 0.4, transverse width 3.0 (48% of oral disc width); lower jaw sheath V-shaped, open and finely serrated, width 2.1, height 0.7. Labial tooth row formula 2/3(1), tooth rows lengths: A1: 4.2, A2: 4.1, P1 right row 1.9, P1 left row 1.6, P1 gap 0.3, P2: 3.2, P3: 3.5. (Fig. 6C).

Color in preservative. Dorsum dull gray, with paler (translucent) areas on the flanks and snout. Caudal muscles pale gray with small cream flecks; dorsal and ventral fins translucent with evenly distributed cream flecks, except at tip where flecks are absent. Venter translucent on throat and belly regions, guts not exposed, white pigment partially covers the belly, producing a black and white mottling; eyes lavender gray with white flecks; oral apparatus translucent.

Color in life. In dorsal and lateral views, body olive-cream; loreal and snout areas palest. Ventrally, guts not visible, belly white with gray marks; gills visible through the throat, with a reddish hue. Caudal musculature cream-gray; proximal third reddish with myomeres and medial line well defined; distal two thirds with small cream flecks; dorsal and ventral fins translucent, suffused with minute cream flecks, clustering in rounded patches near borders of fins; most dense near tail-body junction. Spiracle, oral apparatus, and legs olive-cream. Iris gold.

Variation. Variation of 28 meristic characters of tadpoles in Stages 34–41 (CJ 1948) are shown in Table 9. Total length varies between 40.9 (Stage 34) and 61.2 (Stage 41) and tail length proportion varies from 59.1 to 63.7 until stage 41; labial tooth row formula 2/3(1). Number of marginal papillae varies among specimens and Gosner stages, variation in number of ventral papillae at lower lip is moderate (60 and 69). The color of venter varies from nearly plain gray (CJ 4303) (Fig. 31) to gray flecks in a white background (CJ 1948) (Fig. 5C). Duellman (2015) described a tadpole (KU 203548) from 7.9 Km W Loja. Nonetheless, it may also belong to either *G. pseustes, G. psychrophila,* or *G. turnerorum*.

We documented changes during ontogenetic development of CJ 4303, 4304 (Figs. 31A–C, 32). At Stage 46, the dorsum is nearly uniform clear brown; the paraverterbal marks and interorbital marks are green and vary from nearly absent to well defined.

Comparisons. Tadpoles of *Gastrotheca lojana* may occur in sympatry with those of *G. elicioi*, *G. psychrophila* (tadpole unknown, see Remarks under *G. elicioi* tadpole account)*, G. pseustes* 1, and *G. turnerorum* in the Loja-Abra de Zamora region, with *G. litonedis* and *G. pseustes* 2 (tadpole not described), in the Laguna de Busa area and with at least *G. pseustes* in other localities (compare in Fig. 5). *Gastrotheca lojana* differs from *G. elicioi* by lacking a dorsal gray-pigmented fin that abruptly arises from the body, from *G. pseustes* 1 by lacking a reticulated pattern on flanks, from *G. turnerorum* by having a more pointed tail terminus and lacking bold cream marks in a dorsal line of caudal musculature, and from *G. litonedis* by having a highest tail dorsal fin.

Vocalization. Five individuals of *Gastrotheca lojana* were recorded from one location in Azuay Province (one individual from San Fernando, Laguna de Busa) and from one location in Loja Province (four individuals from Oña) (Appendix III). The advertisement call of *G. lojana* is a complex call, composed of one long pulsed note and followed (or not) by one or two short, single-pulsed notes (Fig. 17H–N). The long note had a mean duration of 0.562 s (SD = 0.125) and consisted on average of 17.59 (SD = 2.418) distinct pulses (pulse series), separated by silent intervals (amplitude modulation of 100%). The amplitude of the long note increases gradually towards the end, without falling. The short notes have a mean duration of 0.064 s (SD = 0.027) and the inter-note interval is on average of 0.356 s (SD = 0.107). The mean dominant frequency is 1118.1 Hz (SD = 126.872), with a mean 90% bandwidth of 986.1–1348.4 Hz. The fundamental frequency is not clearly recognizable; when visible, 5 to 7 harmonics are distinguishable in the short notes.

Comparisons. The advertisement call of *Gastrotheca lojana* is most similar to that of *G. testudinea,* but *G. lojana* has a shorter call duration, higher short note rate, shorter long notes, short notes duration, shorter inter-note intervals, higher pulse rate, a higher dominant frequency and a higher 90% bandwidth frequency compared with the call of *G. testudinea* (Table 5). The call of *G. lojana* can be easily distinguished form the calls of *G. yacuri* and *G. pseustes* by the amplitude modulation of the longer note, shorter call duration, higher short note rate, shorter inter-note interval, smaller number of pulses, lower pulse rate, a much lower dominant frequency, and a lower 90% bandwidth frequency. Also, *G. lojana* emits only one long note, whereas *G. yacuri* emits up to three (usually 2) long notes per call and *G. pseustes* emits a larger number of long and short notes (Table 5).

Distribution and ecology. *Gastrotheca lojana* is known in basins within Azuay, Loja, and El Oro Provinces. Its elevational range is 1682–3018 m in an area of extent of occurrence of about 1621.2 km^2.

This nocturnal, semiarboreal species inhabits mostly disturbed areas and a few forests in the Evergreen Montane Shrub in the south of the Ecuadorian Andes, the Evergreen Montane Forest of the Cordillera Occidental

of the Andes, and the Evergreen Montane Forest from the south of the Cordillera Oriental of the Andes (Ministerio de Ambiente del Ecuador 2012), where the average annual rainfall is 566–1066 mm and the average annual temperature is 12.2–18.8 ºC (Fick & Hijmans 2017). At Oña, Azuay Province, several *Gastrotheca lojana* were calling from agave leafs 50–130 cm above the ground and among grasses near the ground (LAC field notes, 8 August 2003). A male from San Fernando, Azuay Province, was calling from approximately 100 cm above the ground on a large stone. It was close to another adult and a juvenile of the same species; the stone was 7 m from a pond. Another individual was among totora reeds (*Schoenoplectus californicus*) approximately 8 cm above a small stream. A brooding female is depicted in Figure 10L. Throughout most of its distribution, *G. lojana* is syntopic with *G. pseustes*; at San Fernando, it is syntopic with *G. pseustes* and *G. litonedis*, and in the southern part of its range it is also syntopic with *G. elicioi*.

TABLE 9. Variation of 28 meristic characters of tadpoles in Stages 34–41 of *Gastrotheca lojana* (CJ 1948). Values are given in mm, number of specimens in parentheses. See Materials and methods for character abreviations.

	Stage 34 (n=1)	Stage 36 (n=2)	Stage 37 (n=2)	Stage 38 (n=2)	Stage 41 (n=1)
TL	40.88	52.12–55.68	46.75–56.46	54.12–57.01	61.23
BL	15.71	18.19–18.73	20.78–21.41	21.72–22.09	22.21
BW	9.45	11.15–12.26	11.8–14.03	12.59–14.12	12.38
BH	7.74	10.15–10.91	9.89–12.16	10.23–11.22	9
HWEL	8.64	10–10.46	10.99–12.6	12.26–13.5	11.42
TAL	25.17	33.93–36.95	25.97–35.05	32.4–34.92	39.02
TLP (%)	61.57	65.1–66.36	55.55–62.08	59.87–61.25	63.73
MTH	9.64	12.59–13.6	12.13–12.61	12.63–12.64	11.93
TMW	2.81	4.11–4.16	3.66–4.11	4.04–4.58	4.27
TMH	3.64	4.49–5.24	4.42–4.76	5.53–5.71	4.54
Dist SN	2	2.2–2.8	2.9–3.4	3.6–3.9	4
IND	2.6	3.2–3.27	2.87–3	2.87–3	3
END	1.8	2.4–2.6	2.1–2.2	2.3–2.3	2.4
EL	1.4	2.07–2.2	2–2.2	2.3–2.4	2.1
EW	1.3	1.93–2.1	1.9–2.1	2.3–2.3	2.2
IOD	4.33	5.27–5.67	5.1–5.4	5.6–5.8	6.27
VP	63	58–63	55–67	62–76	63
DP right	27	19–21	23–25	25–26	17
MP right	–	–	4	2–5	0
DP left	22	19–20	25–30	28–28	22
MP left	–	–	5	5–6	2
WOD	4.53	4.13–5.07	5–5.7	5.8–6	5.33
WUJ	2.4	2.93–3	3.07–3.2	3.47–3.5	3.93
UJP (%)	52.94	57.89–72.58	56.14–61.33	58.33–59.77	73.75
SL	1.8	3.67–4	2.47–2.6	2.13–2.33	2
SW	1.8	2.6–2.93	2.67–3.7	2.2–2.93	2.67
VTL	1.67	3.67–4.13	2.87–4.4	3.47–4.33	–
VTW	1.33	1.67–2.13	2.8–2.8	2.93–3	–

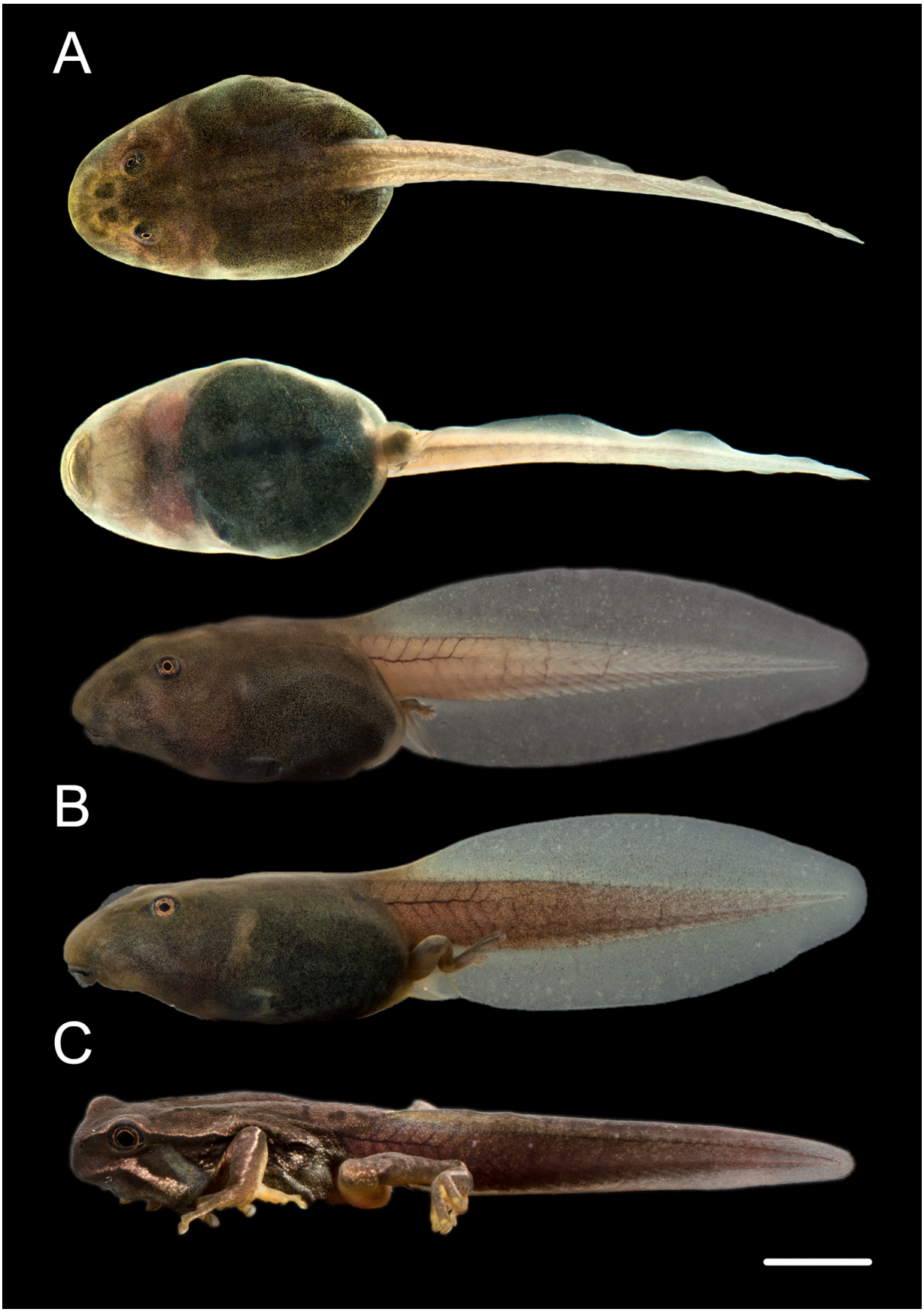

FIGURE 31. Ontogenetic changes in live *Gastrotheca lojana*. Stages of Gosner: (A) Stage 36 (CJ 4303a), (B) Stage 37 (CJ 4309), (C) Stage 43 (CJ 4303a). From Oña, Azuay Province, Ecuador. Scale = 5 mm. Photos by LAC.

FIGURE 32. Metamorph variation in live *Gastrotheca lojana* in Stage 46 of Gosner: CJ 4304, from Oña, Azuay Province, Ecuador. Photos by LAC.

Conservation status. We suggest that *Gastrotheca lojana* should be considered as Endangered according to criteria B1ab(iii,v) of the IUCN Red List. We suggest this category because its small area of occurrence (1621 km^2) is fragmented, and its habitats are in heavily human populated areas. Several search efforts (in 2010–2013, 2016, 2017) at Loja and surroundings revealed no specimens. Environs of Laguna de Busa and Oña have been deforested and modified for human activities (8D, E). The Busa lake is populated by introduced fish (trout and carp) and its surroundings by introduced eucalyptus and conifers. Additional threats at Laguna de Busa are unregulated tourism activities. None of its populations is included in the National System of Protected Areas (SNAP).

Comments. Duellman (1974) referred some specimens from 10 km W Loja, (KU 142603–8, 148549–51), Loja Province, to *Gastrotheca lojana.* These are identified here as *G. elicioi* (see below). Also we identify as *G. lojana* specimens from Girón, Azuay Province (KU 138401–138403), and Saraguro, Loja Province (KU 138404–138409) that Duellman (1974) referred to *G. monticola.* In Duellman & Hillis (1987), specimens of *G. lojana* were also included in the description of *G. monticola*. Loaiza-S (2012) provided a summary account of *G. monticola*, in which *G. lojana* was included. Duellman *et al.* (2014) and (Duellman 2015) recognized *G. lojana* as genetically distinct from *G. monticola.* Duellman (2015) provided an account of *G. lojana.* A specimen from Oña, Azuay Province (QCAZ 2692) depicted as *G. litonedis* in Duellman (2015:239, Fig. 11.12 B) belongs to *G. lojana*.

Gastrotheca pseustes Duellman & Hillis 1987

Gastrotheca pseustes was described from 7.1 km by road north of San Lucas, 2940 m (03º 41' S, 79º 15' W), Loja Province, Ecuador, in the southern Andean Cordillera. The type locality is located about midway between San Lucas and Saraguro. Current assignment of specimens to this taxon is constrained because: (1) there is a high phenotypic similarity between *G. pseustes* and *G. lateonota* from the Cordillera de Huancabamba in Peru (compare both species in Fig. 10 with Duellman 2015: Fig. 12.21); (2). There is no genetic information for topotypic *G. lateonota*, thereby precluding comparisons with specimens from southern Ecuador; (3) according to Duellman (2015), variation in morphometrics, structural characters, and coloration within *G. pseustes* presents a geographic mosaic, except for the southernmost population, Saraguro. The frogs from Saraguro are somewhat more distinctive than the others in being larger in size, and in having broader heads and some consistent characteristics of color pattern, including dark flanks with pale spots and uniformly dark posterior surfaces of the thighs; and (4) new molecular phylogeographic data (not shown) suggest that there may be at least two species in what is now recognized as *Gastrotheca pseustes*.

While awaiting ongoing analyses of molecular data and a future report with a more detailed taxonomic and phylogeographic revision of *Gastrotheca pseustes*, we provide additional data of specimens (adults, tadpoles and metamorphs) from the type locality and surrounding areas in Loja and El Oro provinces.

The recognition of *Gastrotheca lateonota* in southern Ecuador (from El Oro and Loja provinces) by Blackburn & Duellman (2013), Duellman *et al.* (2014), Yáñez-Muñoz *et al.* (2014), and Duellman (2015) was based on specimens identified as that species by Carvajal-Endara and Coloma. Subsequent examination of the specimens from Chilla, El Oro Province, reveals that they do not differ from the holotype (KU 203443, Fig. 10G) and additional specimens (Figs. 10D–F) of *G. pseustes*, from 3.7 km S Saraguro, 2800 m. Thus, we do not recognize *G. lateonota* to occur in Ecuador, and treat the specimens from Chilla as part of a series of populations we consider *G. pseustes* complex (*G. pseustes* 1, *G. pseustes* 2, Fig. 33), occurring from the Equator south to high elevations of Podocarpus National Park in southern Ecuador (see also map in Duellman 2015: Figure 12.47). Conceivably, molecular data from topotypic *G. lateonota* from 31.5 km [by road] E Canchaque, 2770 m, Cordillera de Huancabamba, Región de Piura, Peru, (Fig. 33), and additional populations from northern Peru would resolve by (1) placement of non-type populations in either *G. pseustes* or *G. lateonota*, or (2) placement of *G. lateonota* as a junior synonym of *G. pseustes*.

Castroviejo-Fisher *et al.* (2015) included in a phylogenetic analysis a specimen UINHM 94580 from San Rafael, Azuay, Ecuador under the name *Gastrotheca riobambae*, a species that does not occur in southern Ecuador. Their analysis places it in the *G. pseustes* complex. We also found a locality named San Rafael in Azuay Province, which is located between Cuenca and Cumbe, in Parroquia Tarqui at about 2700 m asl (not in the lowlands as was stated by Castroviejo-Fisher *et al.,* 2015). This locality is well within the altitudinal and latitudinal range of *G. pseustes* 2.

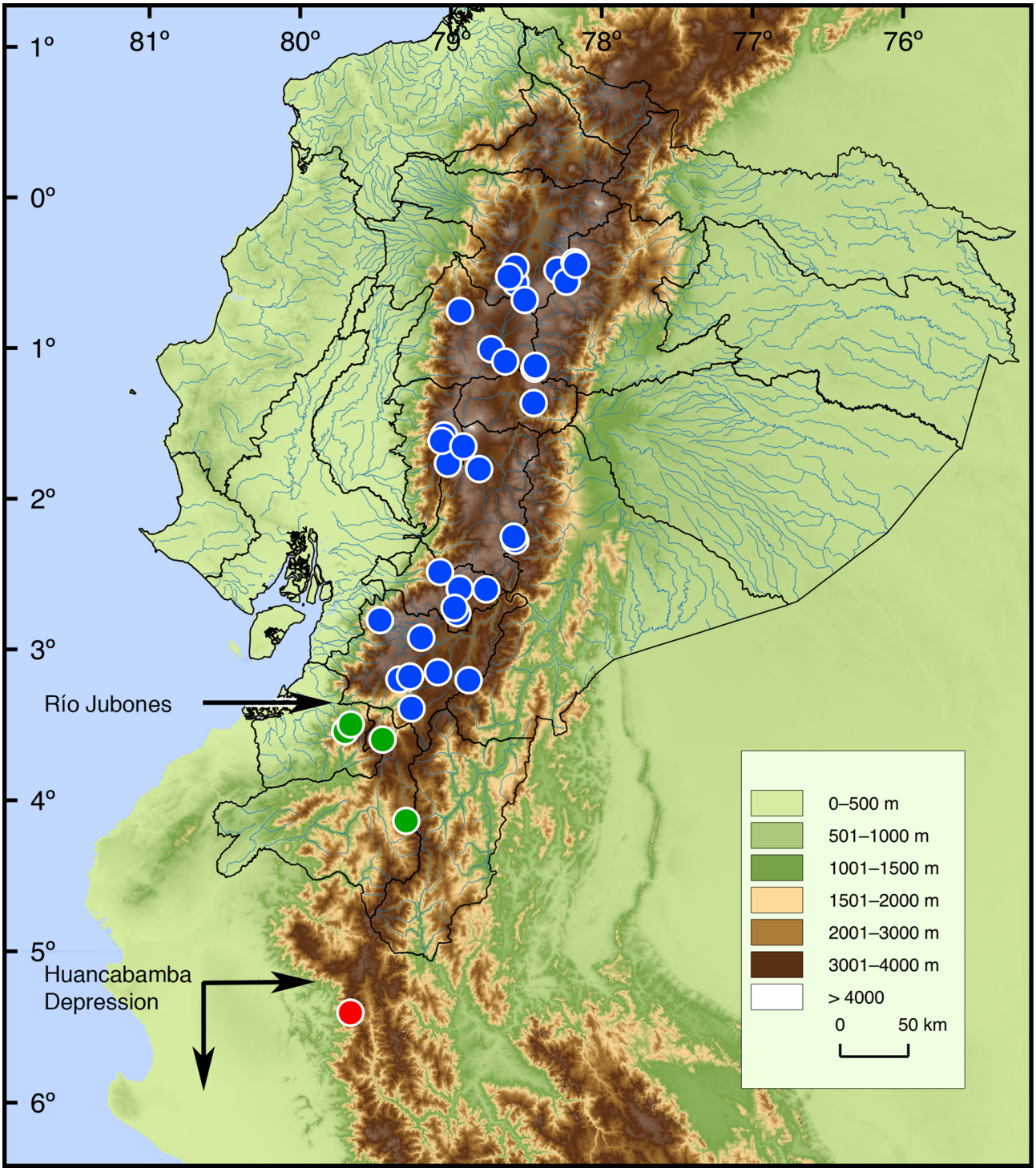

FIGURE 33. Localities of known occurrence of *Gastrotheca lateonota* (red), *G. pseustes* 1 (green), and *G. pseustes* 2 (blue). See Appendix II for detailed locality data. Some nearby localities are represented by a single symbol.

Herein, we provide meristic data from specimens of *Gastrotheca pseustes* 1 and 2 (Table 3), images depicting intrapopulation color pattern variation of metamorphs (Fig. 34), of adults of *G. pseustes* 1 from the type locality (Fig. 10G) and from Chillacocha (Figs. 10D–F). Data for additional specimens of *G. pseustes* 1 are: QCAZ 45121, 45124–5, adult males, and QCAZ 45123 adult female from Chillacocha, ~8 km SW Chilla, El Oro Province (03° 30' 39.1" S, 79° 36' 52.92" W; 3163 m) collected on 18 August 2009. The frogs were on leaves of *Gunnera* sp. (Gunneraceae) near a small stream and adjoining marshland about 10 x 5 m. The water temperature was 9.6° C. Two individuals—CJ 201 adult female and KU 335386 adult male—are from Chillacocha, ~8 km SW Chilla, El

Oro Province (03° 30' 15.37" S, 79° 37' 01.7" W; 3250 m) collected on 10 June 2011. They were in amplexus on a leaf of *Gunnera* sp. (Gunneraceae) approximately 90 cm above the ground and a small stream. Tadpoles were collected from a puddle next to the road in the vicinity of Chilla, El Oro Province (03° 27' 29.41" S, 79° 34' 52.07" W; 2452 m) on 11 June 2011; one of these was raised to be an adult male (CJ 399). Tadpoles were collected from a puddle next to the road at Manu, Loja Province (03° 33' 17.03" S, 79° 22' 6.02" W; 2876 m) on 11 June 2011; one of these was raised to be an adult female (CJ 400). Tadpoles were collected from the entrance of Parque Nacional Podocarpus, Loja Province (04° 05' 25.51" S, 79° 12' 09.97" W; 2456 m) on 14 June 2011; one of these was raised to be an adult female (KU 335387).

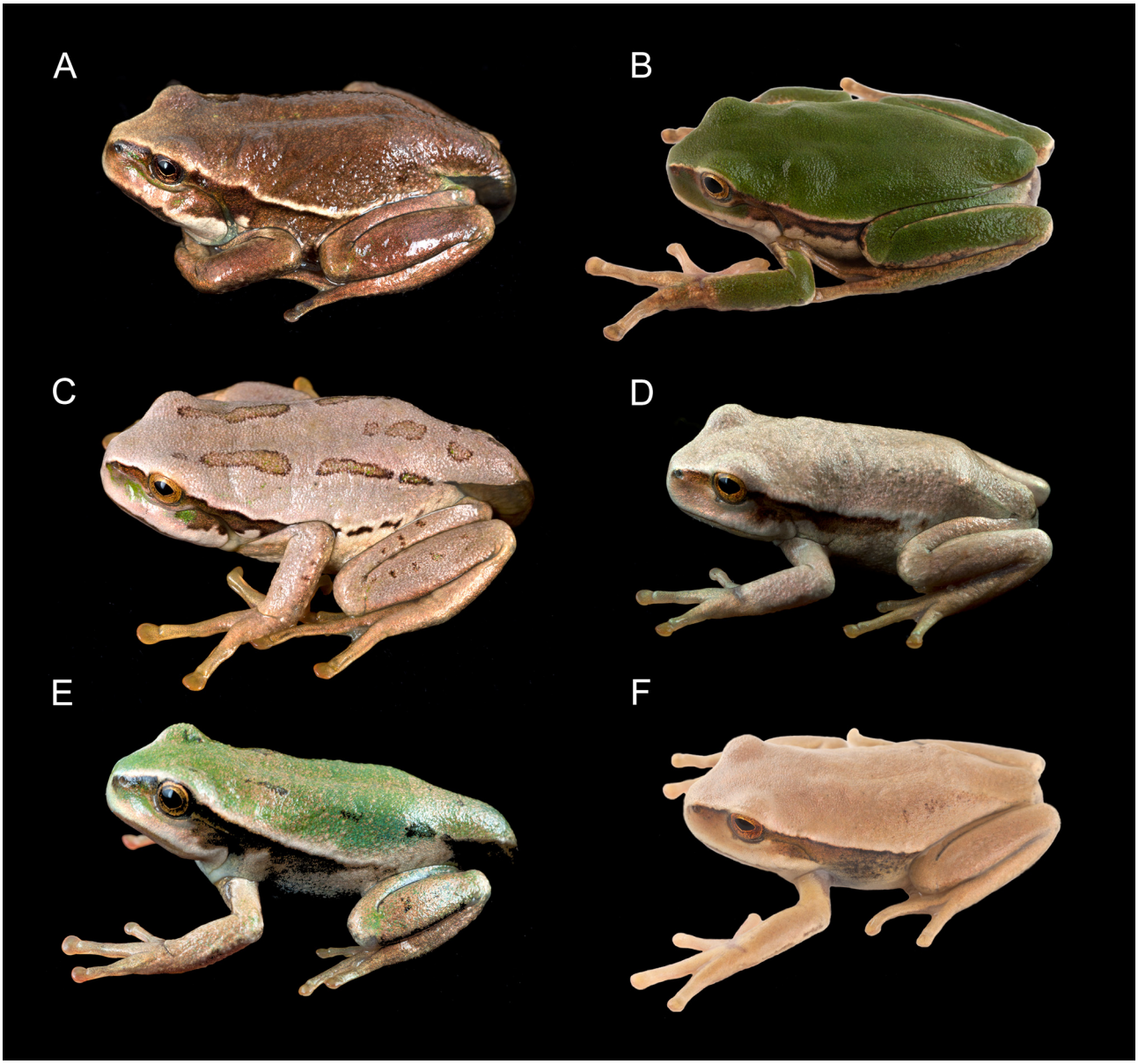

FIGURE 34. Metamorph (Stage 46 of Gosner) variation in live *Gastrotheca pseustes* 1 from Chillacocha, El Oro Province, Ecuador: (A) CJ 1954, (B) QCAZ 45126, (C) CJ 1955, (D) CJ 1953, (E) CJ 1956, and (E) from Chilla–Saraguro (CJ 1956). Not to scale. Photos by LAC.

Tadpoles. Tadpoles belong to Type IV tadpole of Orton (1953), and the exotroph, benthic ecomorphological guild. All measurements are expressed in millimeters. The following description is based on a specimen in Stage 36, from a series (CJ 1949) obtained from a pond at Chillacocha, 8 km SW Chilla, 3250 m, El Oro Province, Ecuador, by Elicio E. Tapia, Sofía Carvajal-Endara, and Henry Grefa on 10 June 2011 (Fig. 5E). Total length 58.2; body length 22.7 (39% of total length). Body ovoid in dorsal and lateral views, slightly depressed; throat concave in lateral profile, sloping from anterior margin of snout to belly; body width at level of spiracle 15.3, and height at

same position 12.9; head width at level of eyes 11.7. Lateral-line system present but barely visible, supraorbital and infraorbital lines both originating at tip of snout, running parallel to the eye and making contact immediately behind the eye; angular line descending vertically from just posterior of eye to throat; it dorsally contacts with post infraorbital line; post-supraocular present in form of a few stitches, anterior oral line descending vertically from oral disc level and behind nares level to throat, making a curve that parallels infraorbital line, forming a circuit continuous with angular and loreal lines; ventral line surrounds dorsally the spiracle; dorsal body and middle body lines not visible. Nostril medium sized (in proportion to body length), ovoid, protruding, with a fleshy annulus, its opening directed anterolaterally. Snout–nostril distance 3.9; internarial distance 3.6. Eye positioned and directed dorsolaterally, eye length 2.9, eye width 2.3; interorbital distance 7.1. Spiracle sinistral, located at midbody, spiracular opening oriented posteriorly; distance from tip of snout to spiracular opening 15.6; end of spiracle rounded, attached to body wall, inner wall of spiracle not evident; tube length 2.7, tube transverse width 3.0. Vent tube dextral, opening directed posteriorly, tube length 2.9, tube transverse width 2.8. Tail length 35.0, caudal musculature robust, narrowing gradually until tail terminus; caudal muscle height 4.5, caudal muscle width 4.3; caudal fins well developed and proportional, dorsal fin originating near tail-body junction, forming low hump; dorsal fin height 4.2, ventral fin height 3.8; maximum height of tail 12.3; tail terminus rounded, caudal musculature not reaching fin terminus.

Oral disc small, ventral, anteriorly reaching level of tip of snout, not protruding laterally beyond body, not visible dorsally; transverse width 5.9, surrounded by an uniserial row of small, marginal papillae, interrupted medially in upper lip; lower lip papillae alternating in orientation in and out, giving appearance of two rows; upper lip with 17 papillae on right side and 16 papillae on left side; lower lip with 52 marginal papillae; upper jaw sheath medium-sized, forming a finely serrated, smooth arch, with lateral processes, height 0.56, transverse width 3.7 (63% of oral disc width); lower jaw sheath V-shaped, finely serrated, width 2.9, height 0.68. Labial tooth row formula 2/3(1), tooth rows lengths: A1: 4.2, A2: 4.5, P1 right row 1.9, P1 left row 2.0, P1 gap 0.3, P2: 4.1, P3: 3.7. (Fig. 6F).

Color in preservative. Dorsum gray with darker gray areas on flanks, above eye and on throat; margin of snout paler than adjacent areas. Caudal musculature and fins with a profusion of medium-sized dots that are most dense on upper part of the musculature; fins otherwise translucent. Venter cream, speckled with white, guts not exposed; eyes lavender gray with irregular white markings, oral apparatus translucent.

Color in life. In dorsal view, body tan with black flecks. Flanks reticulated with black and tan; areas around the eyes and snout paler tan. Venter cream with black markings; throat translucent with small cream flecks; reddish gills evident. Caudal muscles reddish-pink, more evident on proximal half; myomeres barely visible; caudal muscles and fins having medium-sized cream dots, most dense on upper side of caudal muscles and near tail-body junction, forming a nearly conitnuous stripe along dorsolateral caudal musculature; otherwise caudal fins translucent. Legs cream with black markings on toes. Oral apparatus pale cream. Iris copper-yellow, with black reticulations.

TABLE 10. Variation of 26 meristic characters of tadpoles in Stages 36–42 of *Gastrotheca pseustes* (CJ 1949). Values are given in mm, mean±standard deviations (first row) and ranges (second row), number of specimens in parentheses. See Materials and methods for character abreviations.

	Stage 36 (n=1)	Stage 40 (n=1)	Stage 41 (n=2)	Stage 42 (n=3)
TL	58.23	55.02	57.6–58.66	54.61±3.1
				51.24–57.34
BL	23.19	19.13	19–19.33	16.65±1.23
				15.35–17.82
BW	15.27	11.6	11.51–11.81	9.44±1.18
				8.09–10.31
BH	12.9	9.58	8.67–8.93	8.86±1
				8.23–10.01

.....*continued on the next page*

TABLE 10. (Continued)

	Stage 36 (n=1)	Stage 40 (n=1)	Stage 41 (n=2)	Stage 42 (n=3)
HWEL	11.66	9.7	10.18–10.63	10.32±0.85
				9.33–10.82
TAL	35.04	35.89	38.6–39.33	37.96±1.87
				35.89–39.52
TLP (%)	60.18	65.23	67.01–67.05	69.52±0.57
				68.92–70.04
MTH	12.32	10.47	12.12–12.13	11.08±0.64
				10.51–11.78
TMW	4.3	4.14	4.22–4.68	4.6±0.12
				4.49–4.73
TMH	4.5	4.29	4.91–5.18	5.55±0.54
				4.95–5.99
SND	3.9	1.9	1.6–1.9	1.3±0.52
				1–1.9
IND	3.6	1.73	2–2.2	2.09±0.08
				2–2.13
END	2.9	2.07	2.13–2.4	2.2±0.07
				2.13–2.27
EL	2.3	1.67	1.67–2.1	2.01±0.22
				1.87–2.27
EW	2.2	1.53	1.73–1.9	1.77±0.12
				1.67–1.9
IOD	7.1	6.2	6.3–6.8	6.47±0.31
				6.2–6.8
VP	52	50	50–54	43±2.65
				40–45
DP right	17	22	20–20	18.67±3.21
				15–21
DP left	16	23	20–21	17.67±0.58
				17–18
WOD	5.87	4.8	5–5.1	4.9±0.1
				4.8–5
WUJ	3.67	2.7	3.7	–
UJP (%)	62.5	56.25	74	–
SL	2.73	3.4	2.3–2.7	–
SW	3	1.7	1.6–1.7	–
VTL	2.93	3	3	–

Variation. Variation of 28 meristic characters of tadpoles in Stages 36–42 (CJ 1949) are shown in Table 10. Total length varies between 55.0 (Stage 40) and 58.2 (Stage 36) and tail length proportion varies from 60% to 70% until Stage 42. Number of marginal papillae varies among specimens and Gosner stages; number of lower lip papillae is high (43–52).

We documented changes in coloration during ontogenetic development of one, mostly pale brown individual (CJ 1953) (Figs. 5E, 35). At Stage 41, the dorsum and flanks are yellowish-brown with a poorly defined pattern of brown-gray, elongated paravertebral marks and few blotches on dorsum of hind limbs. A diffuse brown-gray stripe borders the canthal and dorsolateral body, and is bordered above by a creamy-brown stripe. The iris has a reddish-gold suffusion. By Stage 45, markings on the dorsum and flanks are better defined with brown markings darkest peripherally; scattered green ill-defined flecks are present on dorsum of head, limbs, and canthus rostralis; tip of fingers are yellowish-cream. At Stage 46, paravertebral green-brown markings on dorsum of body and green flecks on limbs are contrasting to surrounding light brown areas; flanks have a dark brown stripe. Color variation in 6 metamorphs (CJ 1949, 1953–56, QCAZ 45126) in Stage 46 is depicted in Figure 34. They vary from dark brown to green with either well-defined paravertebral marks to a uniformly colored dorsum.

FIGURE 35. Ontogenetic changes in live *Gastrotheca pseustes* 1 (CJ 1953) from Chillacocha, El Oro Province, Ecuador. Stages of Gosner: (A) Stage 41, (B) Stage 45, and (C) Stage 46. Scale = 5 mm. Photos by LAC.

Comparisons. Tadpoles of *Gastrotheca pseustes sensu stricto* (in Loja and El Oro provinces) occur in sympatry with those of *G. elicioi in* the Saraguro region and with *G. elicioi*, *G. lojana*, *G. psychrophila*, and *G. turnerorum* in the Loja-Abra de Zamora region. *Gastrotheca pseustes* differs from *G. elicioi* by lacking a dorsal gray-pigmented fin that abruptly arises from the body; from *G. lojana* by having a reticulated pattern on flanks, and from *G. turnerorum* by having a less rounded tail terminus (compare in Fig. 5). For *G. psychrophila*, see remarks under *G. elicioi* tadpole account.

Vocalization. Four individuals of *Gastrotheca pseustes* were recorded from three locations in Loja Province (2 individuals from Bosque Washapamba, one from Vía Urdaneta-Tutupali, and 1 from Cerro de Arcos; see Appendix

III). Because of the taxonomic problems related to the *G. pseustes* complex we decided to use for the present analysis only the recordings obtained from populations situated nearby the type locality, south of the Jubones-Girón river valley in Loja Province (e.g. *G. pseustes* 1). Descriptive statistics of the acoustic variables are provided in Table 5. The advertisement call of *G. pseustes* is a complex call, composed of one to five long pulsed notes and followed (or not) by one to six short, single-pulsed notes (Fig. 23H–N). The long note had a mean duration of 0.878 s (SD = 0.188) and consisted on average of 32.72 (SD = 6.867) distinct pulses, partly fused, without silent intervals (amplitude modulation close but less than 100%). The amplitude of the long note increases gradually towards the end of the note after which it decreases a little by the end. The short notes had a mean duration of 0.080 s (SD = 0.046) and the inter-note interval is on average of 0.795 s (SD = 0.502). The mean dominant frequency of the call is 1359.0 Hz (SD = 37.981), with a mean 90% bandwidth of 1043.2–1483.4 Hz. The fundamental frequency is usually recognizable; when visible, 6 to 7 harmonics are distinguishable.

Comparisons: The advertisement call of *Gastrotheca pseustes* is most similar to that of *G. yacuri,* but *G. pseustes* has a much longer call duration, longer long notes duration, longer inter-note interval a lower dominant frequency and a lower 90% bandwidth frequency compared with the call of *G. yacuri* (Table 5). Also, *G. pseustes* usually emits 4–6 short notes compared with the only two short notes that *G. yacuri* emits. The call of *G. pseustes* can be easily distinguished from that of *G. lojana* and *G. testudinea* by the amplitude modulation of the longer note, much longer call duration, lower short note rate, longer long notes duration, longer inter-note interval, larger number of pulses, higher pulse rate, a higher dominant frequency, and higher 90% bandwidth frequency. Also, *G. pseustes* emits a larger number of long and short notes compared with *G. lojana* and *G. testudinea* (Table 5).

Morphometric variation among *Gastrotheca* species

We found significant differences in morphometric characteristic among closely related species of *Gastrotheca* from the southern Ecuadorian Andes. Fourteen morphological measurements of 167 adult specimens are summarized in Table 3. From the first PCA performed including five species of the subgenus *Duellmania* (*G. cuencana*, *G. elicioi*, *G. litonedis*, *G. lojana*, and *G. monticola*), we retained four principal components (PC) with eigen values > 1.0, which explained 60.1 % of the total variation (Table 11). The variables with highest loadings for PC 1 were interorbital distance and tibia length; for PC 2 were thumb length and foot length; for PC 3 were eye diameter and eyelid width; for PC 4 was disc width. Biplots of the three main PCs (Fig. 36A) show that specimens of *G. cuencana* tend to have smaller interorbital distance and tibia length, as well as a larger thumb and foot length than *G. litonedis* and *G. lojana*. In turn, specimens of *G. litonedis* tend to have smaller interorbital distance and tibia length, as well as a larger thumb and foot length than *G. lojana*. Specimens of *G. elicioi* and *G. monticola* showed a greater overlap in the morphospace with other species. However, they differ between each other in that specimens of *G. elicioi* tend to have larger eye diameter and eyelid width than *G. monticola*. Multivariate analysis of variance (MANOVA) performed with the PC scores revealed that there are morphometric differences among these species (Pillai's Trace: $F = 12.21$, $df = 16\ (644)$, $p < 0.01$), and the analyses of multiple comparisons of means among species (Tukey tests) showed that the morphometric differences between all pair of species from the group were significant except between *G. monticola* and *G. lojana*. Along the PC 1, PC 2, and PC 4, we found significant differences between *G. cuencana* and three species: *G. litonedis*, *G. lojana*, and *G. monticola* (p-values after adjustment for the multiple comparisons, p adj. << 0.01) Along PC 2 and PC 3, we found significant differences between *G. litonedis* and two species: *G. lojana* (p adj. << 0.01) and *G. monticola* (p adj. = 0.02, p adj. < 0.01). In addition, we found significant differences between *G. elicioi* and two species: *G. litonedis* and *G. lojana* (p adj. << 0.01) along the PC 1, and between *G. elicioi* and *G. monticola* (p adj. < 0.01) along PC 3.

From the second PCA performed with species of the subgenus *Gastrotheca*, including *G. turnerorum*, *G. yacuri*, *G. pseustes* 1 (populations from Loja and El Oro provinces), and *G. pseustes* 2 (northern populations, see Appendix I) we retained five principal components with eigen values > 1.0, which explained 60.5% of the total variation (Table 11). The variable with highest loadings for PC 1 was foot length; for PC 2 was tympanum diameter; for PC 3 was disc width; for PC 4 was eye diameter; and for PC 5 was thumb length. Biplots of the three main PCs (Fig. 36B) showed that species of this group overlap greatly in morphospace. However, specimens of *G. turnerorum* tend to have larger disc width than *G. pseustes* 1, *G. pseustes* 2, and *G. yacuri*. The MANOVA performed with the PC scores revealed that there are significant morphometric differences among these species

TABLE 11. Principal components loadings, eigenvalues, and percentage of explained variance from two Principal component analyses (PCA) based on 14 morphometric variables and applied two species groups. Group 1 included adult specimens of *Gastrotheca cuencana, G. elicioi, G. litonedis, G. lojana,* and *G. monticola* (n = 166) and Group 2 included adult specimens of *Gastrotheca pseustes* 1, *G. pseustes* 2, *G. turnerorum,* and *G. yacuri* (n = 130). Abbreviations are: snout–vent length (SVL), tibia length (TIBL), foot length (FL), head length (HL), head width (HW), interorbital distance (IOD), eyelid width (EW), internarial distance (IND), eye diameter (ED), eye–nostril distance (EN), tympanum diameter (TD), thumb length (FFL), Finger III length (TFL) and Finger III disc width (TFD).

	PCA Group 1				**PCA Group 2**				
Variables	PC 1	PC 2	PC 3	PC 4	PC 1	PC 2	PC 3	PC 4	PC5
SVL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
TIBL	0.80	-0.19	-0.28	-0.22	0.61	-0.35	-0.28	0.24	-0.28
FL	0.42	0.67	0.07	-0.09	0.74	-0.33	-0.21	0.22	-0.08
HL	0.68	0.14	-0.17	0.39	0.68	0.26	0.09	-0.12	-0.24
HW	0.69	0.09	-0.26	0.10	0.67	0.40	0.13	0.07	-0.09
FFL	0.25	0.72	0.08	0.09	0.48	-0.06	-0.16	0.15	0.68
TFL	0.52	0.58	-0.01	-0.17	0.63	-0.49	0.10	-0.01	0.31
IOD	0.82	-0.33	-0.10	-0.15	0.33	0.30	-0.55	-0.16	0.06
IND	0.29	-0.05	-0.36	0.43	0.47	0.39	0.14	-0.31	-0.07
EN	0.78	-0.38	-0.12	-0.19	0.45	0.09	0.12	-0.55	-0.19
ED	0.23	-0.14	0.67	-0.08	0.14	0.10	0.52	0.60	-0.31
TD	0.60	-0.26	0.32	0.36	-0.10	0.66	-0.34	0.14	0.14
EW	0.42	-0.04	0.66	0.37	0.19	0.53	0.37	0.31	0.34
TFD	0.45	0.02	0.27	-0.56	0.11	-0.20	0.65	-0.33	0.25
Eigenvalue	4.21	1.72	1.39	1.09	3.08	1.72	1.46	1.16	1.05
Variance explained (%)	30.10	12.32	9.94	7.76	21.97	12.29	10.45	8.28	7.48
Variance cumulative (%)	30.10	42.42	52.36	60.12	21.97	34.26	44.70	52.98	60.47

(Pillai's Trace: F = 12.32, df = 10(244), p < 0.001), and the analyses of multiple comparisons of means among species (Tukey tests) showed there are significant differences between *G. turnerorum* and *G. pseustes* 1 along PC 3 (p adj. < 0.01). Also, we found significant differences between, *G. turnerorum* and *G. pseustes* 2 along PC 3 (p < 0.01) and PC 4 (p = 0.03), and significant differences between *G. pseustes* 1 and *G. pseustes* 2 along PC 2 and PC 4 (p adj. << 0.01).

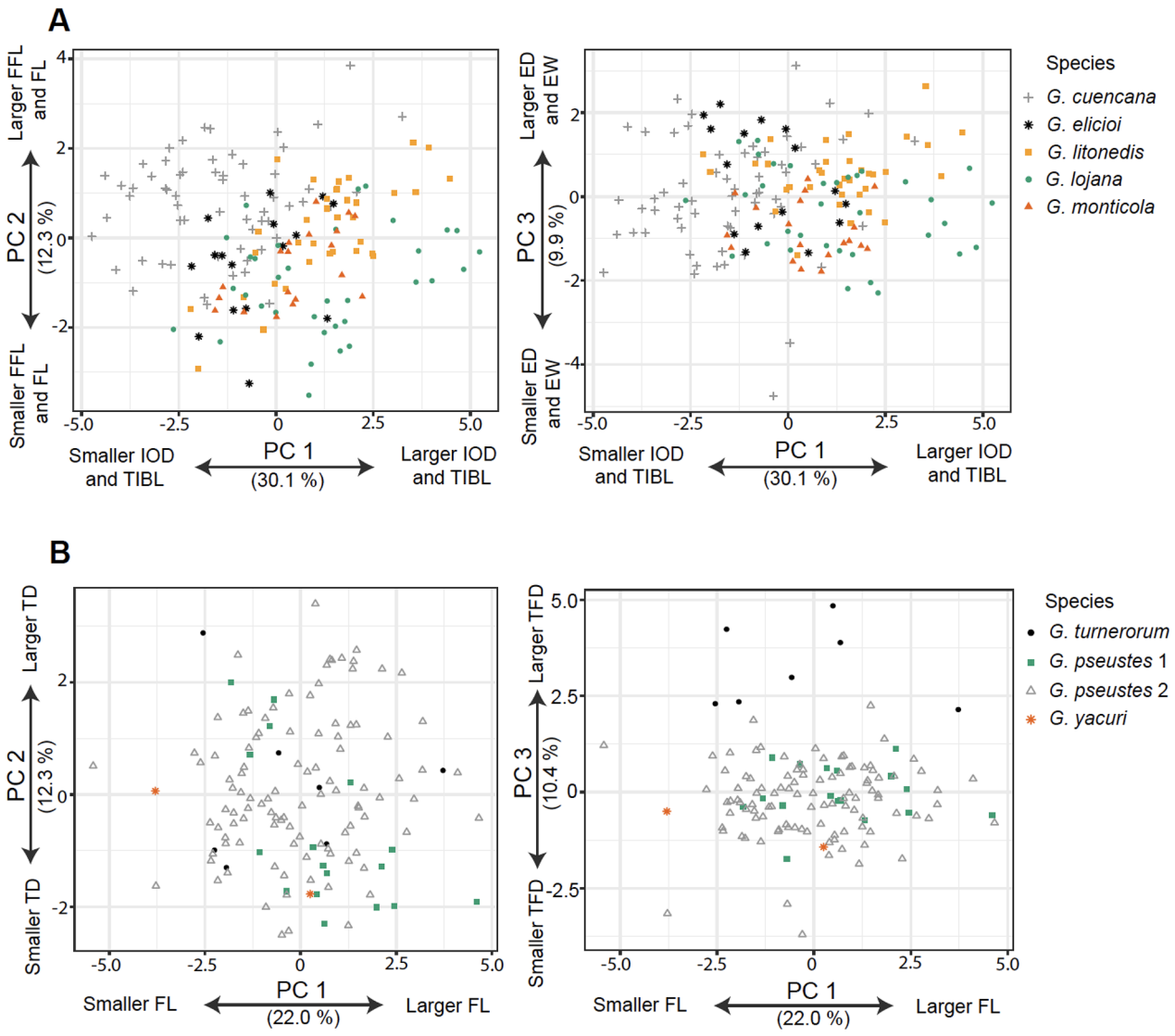

FIGURE 36. (A) Principal components analysis (PCA) based on 14 morphometric variables. (A) Biplots of the three main principal components (PC 1, PC 2, PC 3) from the PCA performed with the species group 1, including adult specimens of *Gastrotheca cuencana*, *G. elicioi*, *G. litonedis*, *G. lojana*, and *G. monticola* (n = 166). (B) Biplots of the three main principal components (PC 1, PC 2, PC 3) from the PCA performed with the species group 2 including adult specimens *G. pseustes, G. turnerorum,* and *G. yacuri* (n = 130). Percent values indicate the proportion of variation explained. Variable abbreviations are: tibia length (TIBL), foot length (FL), interorbital distance (IOD), eyelid width (EW), tympanum diameter (TD), thumb length (FFL), Finger III length (TFL), and Finger III disc width (TFD).

Vocalization of *Gastrotheca testudinea*

Six individuals were recorded from one location (5 individuals from Zuñag) in Morona Santiago Province and one individual in the Centro Jambatu (Appendix III). Descriptive statistics of the acoustic variables are provided in Table 5. The advertisement call of *G. testudinea* is a complex call, composed of one long pulsed note and followed

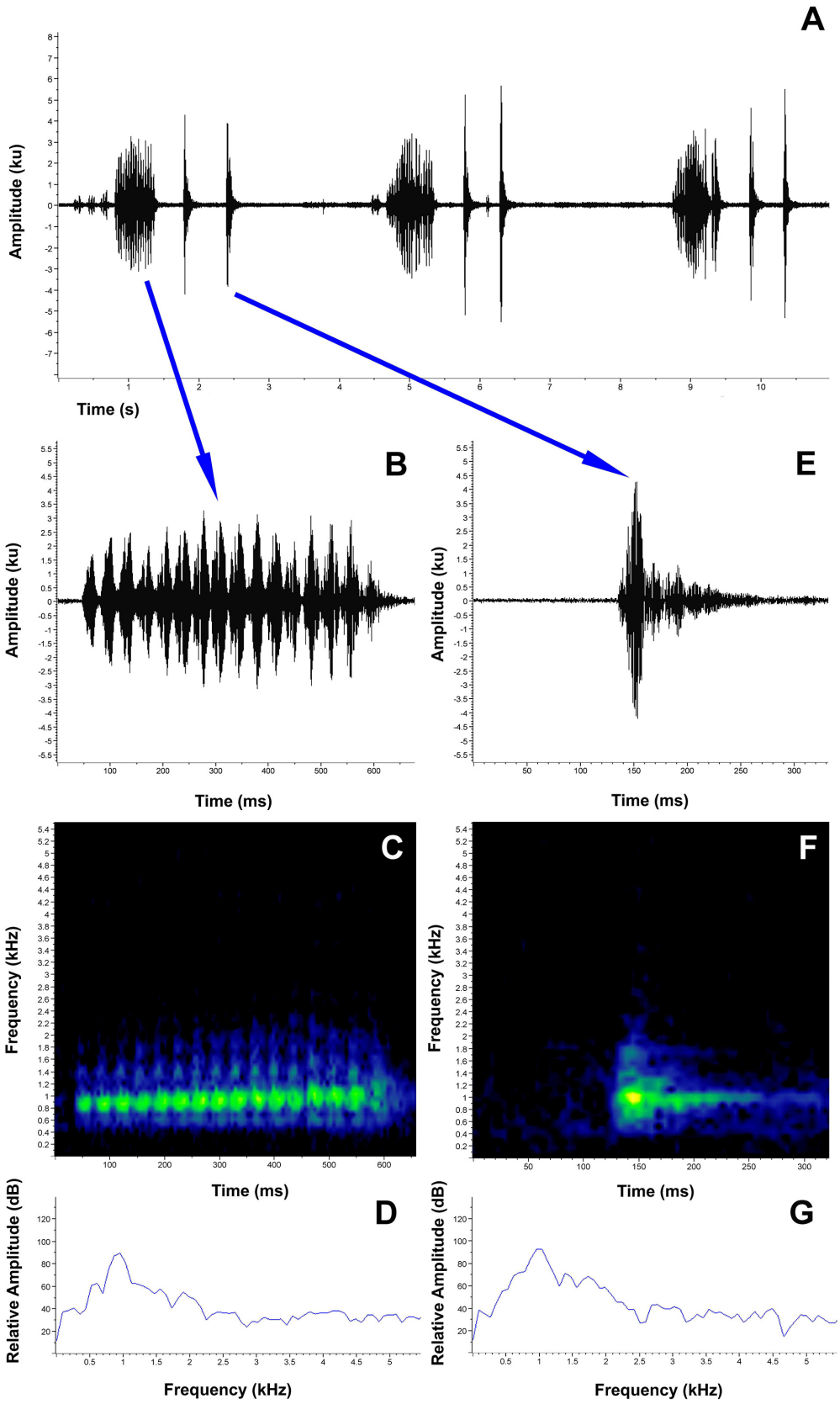

FIGURE 37. Advertisement call of *Gastrotheca testudinea*: (A) oscillogram of three consecutive calls, each of them composed of one long note and two short notes, (B) oscillogram of a single long note, (C) spectrogram of a single long note, (D) power spectrum of a single long note, (E) oscillogram of a single short note, (F) spectrogram of a single short note, (G) power spectrum of a single short note. All spectrograms at Hanning window function, 512 bands resolution. See text for details.

(or not) by one to three short, single-pulsed notes (Fig. 37A–G). The long note had a mean duration of 0.746 s (SD = 0.154) and consisted on average of 18.88 (SD = 2.870) distinct pulses (pulse series), separated by silent intervals (amplitude modulation of 100%). The amplitude of the long note increases gradually towards the end of the note after which it decreases a little by the end. The short notes have a mean duration of 0.080 s (SD = 0.040) and the inter-note interval is on average of 0.452 s (SD = 0.069). The mean dominant frequency of the call is 1069.1 Hz (SD = 86.448), with a mean 90% bandwidth frequency of 800.5.1–1205.9 Hz, having the lowest values recorded between the analyzed species. The fundamental frequency and harmonics are not clearly recognizable.

Comparisons. The advertisement call of *Gastrotheca testudinea* is most similar to that of *G. lojana*, but *G. testudinea* has a longer call duration, lower short note rate, longer long notes and short notes duration, longer inter-note intervals, lower pulse rate, a lower dominant frequency, and lower 90% bandwidth frequency compared with the call of *G. lojana* (Table 5). The call of *G. testudinea* can be easily distinguished from that of *G. yacuri* and *G. pseustes* by the amplitude modulation of the longer note, shorter call duration, smaller number of pulses, lower pulse rate, a much lower dominant and a lower 90% bandwidth frequency. Also, *G. yacuri* emits up to three (usually 2) long notes per call, and *G. pseustes* emits a larger number of long and short notes compared with the only one long note emitted by *G. testudinea* (Table 5).

Discussion

Diversity. The discovery and descritption of amphibian diversity is a major priority of the Amphibian Conservation Action Plan (Gascon *et al.* 2007). Accordingly, there have been some regional taxonomic efforts (e.g., in Ecuador). For example, from January 2005 to 5 November 2018, the known species of amphibians occurring in Ecuador increased by 121 especies (including *Gastrotheca* described here), from 471 to 591 (Centro Jambatu 2018). Thus, in Ecuador, about nine species are added per year, and these numbers have more than doubled the rate of descriptions before 2005. This increase is correlated with the increase of taxonomists in South America (Costello *et al.* 2013). Coloma *et al.* (2007) estimated that 20% of the amphibian diversity is still undescribed (the total number possibly 677–728 species); thus, at the current rate of descriptions, it will take another 10–15 years to have a complete inventory for the country. Marsupial frogs (*Gastrotheca*) are no exceptions to taxonomic efforts needed (Wheeler *et al.* 2012), although important steps in solving taxonomic problems and describing new taxa have been done in recent years (e.g., Duellman *et al.* 2011a, Blackburn & Duellman 2013, Duellman 2013, Duellman *et al.* 2014). Herein we have pointed to cases that need urgent resolution such as the *G. pseustes* complex from Ecuador and northern Peru, and the pending exploration and discovery of marsupial frogs in the complex topography of the Peruvian Andes, where four undescribed species are known from small samples.

Conservation. Many (34 species out of 74; 46%) species of *Gastrotheca* are threatened and for 23 (31%) of species the available data are deficient to evaluate their conservation status (IUCN 2018, and species included in this publication). Most monophasic species have not been seen since the late 1980s, whereas the highland biphasic species have survived the catastrophic events that led to the disappearance of many other sympatric anurans. Five of the species of *Gastrotheca* treated herein are threatened by extinction, *Gastrotheca yacuri* requires additional surveys, and *G. pseustes* is not evaluated. Although there have been no studies on their population dynamics, other lines of evidence such as a reduction of the area of occupation point to their crises. All biphasic *Gastrotheca* species included in this study tolerate some degree of habitat modification; most of them have been observed in pasture lands where lentic water is available for tadpoles. However, their habitats are in heavily human-populated areas, where the synergistic effects of agriculture, mining, cattle raising, fires, introduced species, pesticide use, road construction, and urban development are increasing, and reduction of the area of occupation suggest population size may be decreasing. The distribution of most of these species is indeed narrow and fragmented (as reported here for at least *G. cuencana*, G. *elicioi,* and *G. lojana*); thus it is a cause of concern as geographically restricted species are often at risk of extinction because of demographic stochasticity. Important threats in their areas of occurrence are extreme climatic abnormalities and pathogens, key factors implicated in abrupt anuran declines and extinctions in the southern highlands of Ecuador (Merino-Viteri *et al.* 2005; Pounds *et al.* 2006; Pounds & Coloma 2008; Coloma *et al.* 2007, 2010). It is noticeably that the chytrid fungus, *Batrachochytrium dendrobatidis,* which has been worldwide implicated in anuran declines (Lips *et al.* 2008), has been present in most species of *Gastrotheca* since, at least, 1974 (when no sudden declines were noticed) (Manzano Pasquel 2014), and is present contemporaneously in most Andean frogs (Guayasamin *et al.* 2014; Manzano Pasquel 2014, Tapia *et al.* 2017).

Regarding conservation of the biphasic marsupial species treated herein, it is increasingly obvious that despite their ability to adapt to modified environments—even in neighborhood of cities where some standing water is available (e.g., irrigation ditches, water reservoirs)—they are threatened because of the synergistic and additive effects of many threats (Wake 2012) acting on fragmented populations and small ranges of distribution (10–1600 km^2). Moreover, some species occur in relatively large cities (e.g., Cuenca, Loja) where the availability of lentic water is not granted. Within green areas of the cities, their *in situ* conservation could be greatly enhanced by regulations to preserve and built water bodies of almost any size surrounded by natural vegetation, especially including plants such as bromeliads, *Agave* spp., *Schoenoplectus* sp. (totora). These policies should be accompanied of educational campaigns to change peoples´perception about frogs, and to encourage conservation as a moral duty. Failure to find species such as *G. psychrophila* is intriguing. It was originally collected in 1968–71, but several subsequent searching efforts at the type locality have been unsuccesful. Thus, integrated species conservation plans (Gascon *et al.* 2007), including conservation *in situ* and *ex situ*, are urgently needed, as well as studies of population dynamics for all species of biphasic *Gastrotheca* treated herein, as insistently claimed for amphibians (see Zippel & Mendelson III 2008, Bishop *et al.* 2012, Stuart 2012, Byers *et al.* 2013).

Phylogeny and speciation. The phylogenetic relationships estimated here are mostly congruent with previous phylogenetic hypotheses for the group (Wiens *et al.* 2007, Blackburn & Duellman 2013, Duellman *et al.* 2014, Duellman 2015, Castroviejo-Fisher *et al.* 2015). Nonetheless, there are some differences. One of them is the placement of *Gastrotheca galeata*. According to Blackburn & Duellman (2013), and Duellman (2015), *G. galeata* is sister species to all species in the Andean clades, subgenera *Duellmania* and *Gastrotheca*. In contrast, Castroviejo-Fisher *et al.* (2015) and our analyses (Fig. 1) place *G. galeata* within the subgenus *Duellmania* as sister taxa of a clade that includes 7 species from the Andes of southern Ecuador and northern Peru. Castroviejo-Fisher *et al.* (2015) hypothesis differs from that of Duellman (2015) and our hypothesis in the placement of *G. plumbea, G. orophylax, G. nicefori* and *G. griswoldi.* These topology differences may lead to distinct interpretations of character evolution. For example, the evolution of direct development in *G. orophylax* and *G. plumbea* was represented as potentially convergent with that ocurring in *G. galeata* by Castroviejo-Fisher *et al.* (2015: Fig. 2); however, according to our hypothesis it is due to common ancestry. Further analyses are needed to resolve these important discrepancies.

Lynch & Duellman (1997) highlighted the potential importance of geographic barriers as promoters of diversification in Andean anurans, but only few studies include explicit phylogenies and discuss the impact of geographic barriers (see Graham et al. 2004, Kieswetter & Schneider 2013, Hutter *et al.* 2013, Guayasamin *et al.* 2010, 2015). The inferred phylogeny presented in this work contains numerous well-supported clades and an intensive taxon sampling of *Gastrotheca* (Fig. 1). This allows us to discuss the evolutionarly scenarios that likely have been involved in shaping the diversity of the genus. The main pattern is that most sister species in *Gastrotheca* are allopatric because of Andean orogenesis. For example, *G. plumbea* and *G. orophylax* both inhabit cloud forest and subpáramo at similar elevations, but on opposite sides of the Andes; *G. plumbea* is found on the Pacific slope of the Andes, whereas *G. orophylax* is found on the Amazonian slope. Thus, the uplift of the Andes is likely the barrier that produced speciation between these species.

In other sister species, transverse Andean river valleys seem to play an important role in diversification processes (Graves 1988) by promoting conditions that act as dispersal barriers. A putative species pair (of the *Gastrotheca pseustes* complex) that fits this scenario is *G. pseustes* 1 + *G. pseustes* 2, with the Jubones-Girón river valley acting as a dispersal barrier (Fig. 34). Similarly, the Huancabamba depression is the most likely barrier between *G. monticola* and *G. elicioi*.

Differentiation between the sister and allopatric species *Gastrotheca litonedis* and *G. cuencana* is difficult to explain given the absence of an evident geographic barrier between them. Interestingly, a similar pattern of discordance between morphological and genetic data (clear morphological differenciation and low genetic distances) is found in other amphibian taxa in the same general area in Cañar-Azuay provinces (e.g., *Atelopus bomolochos*, *A. exiguus*, *A. nanay*, and *A. onorei*). The scenarios that could explain these patterns of speciation were discussed by Guayasamin *et al.* (2010).

Tadpoles. The importance of tadpole features in anuran systematics is increasingly recognized (Haas 2003); thus tadpole features are being used in recent taxonomic reviews of several anuran taxa, including glassfrogs (Terán-Valdez *et al.* 2009), dendrobatids (Páez-Vacas *et al.* 2010), and treefrogs (Coloma *et al.* 2012; Lynch & Suárez Mayorga 2011). Within biphasic *Gastrotheca*, tadpole features generally have received little attention,

either to distinguish among species or in a phylogenetic context. According to Duellman and Hillis (1987) only minor, inconsistent differences were encountered among tadpoles of species of Ecuadorian *Gastrotheca*. Their failure to find discrete consistent differences is explained by the unresolved species limits (e.g., unsolved differentiation between *G. monticola* and *G. lojana*, the occurrence of cryptic species such as *G. elicioi*, *G. cuencana* and *G. turnerorum*), and the probability of erroneous assigments of sympatric tadpoles. Tadpoles living in the same ponds have been collected for *G. pseustes* 2 and *G. litonedis* at Laguna de Busa. Sympatry of adults of especies of *Gastrotheca* varies from two to five species. In Laguna de Busa (Azuay province) three species (*Gastrotheca litonedis*, *G. lojana*, and *G. pseustes* 2) occur in the same habitats, whereas in a region such as the Loja-Abra de Zamora five species of *Gastrotheca* with aquatic tadpoles (two *Duellmania* and three *Gastrotheca*: *G. elicioi*, *G. lojana*, *G. pseustes*, *G. psychrophila*, and *G. turnerorum*) have been recorded. Thus, if the allocation of tadoples to a particular species relied on the collection of tadpoles and adults at the same site, errors in the identification of tadpoles probably occurred. For example, the species assignment among tadpoles of *Gastrotheca lojana* and *G. psychrophila* that were recently described by Duellman (2015) is not unequivocal, as specifically commented in the tadpole section of this paper. Erroneous or doubful assigments might have occurred as well among 15 additional species (out of 26 with an exothropic tadpole) of *Gastrotheca* for which descriptions have been published. Our descriptions of tadpoles of the species of *Gastrotheca* from southern Ecuador reveal useful diagnostic characters that can be used for identification and incorporated in future species descriptions and phylogenetic analyses. For example, consistent differences among species are observed in tail shape, coloration, density of chromatophores, and patterns on the dorsum, venter, tail, and iris. Nonetheless, caution should be taken when identifying tadpoles until more knowledge of intra and interpopulation variation of tadpoles are acquired. Additionally, metamorph color and variation shows remarkable polymorphisms and differences among species. It is noticeable, for example, that metamorphs of *G. psesutes* are extremely polymorphic, whereas *G. turnerorum* metamorphs are only green or brown. The selective mechanisms maintaining these patterns need to be investigated and marsupial frogs are a rich source of color phenotypes.

Vocalizations. The advertisement call features have proved to be a reliable taxonomic tool in anuran systematics (De la Riva 1995; Sinsch & Schneider 1996; Wells 2007) and the application of comparative bioacoustical analyses has resulted in the identification and description of many morphologically cryptic anuran species (Glaw & Köhler 1998; Wells 2007; Vences & Köhler 2008). Advertisement calls were successfully used for species delimitation purposes in several *Gastrotheca* species (Sinsch & Juraske 2006a; Sinsch & Juraske 2006b), providing a useful tool for species identification in the case of morphologically similar species like the ones herein studied.

We included in our advertisement call analysis the calls of seven of the nine currently known *Gastrotheca* species from the Andes of Southern Ecuador (the call of *G. psychrophila* is unknown and we were not able to secure good quality calls of *G. turnerorum*), along with the call of the only monophasic species from the region, *G. testudinea*. Our analysis revealed clear differences amongst taxa with two species having simple calls and five complex ones (or composed of different types of notes). In the majority of the cases the calls are so characteristic and different that an acoustic identification of the species is possible in the field. The only problematic calls are those of the allopatric species *G. litonedis* and *G. cuencana*, which have a similar simple advertisement call. However, we identified significant differences in the measured acoustic parameters, especially for the note rate, note duration, inter-note interval, the dominant frequency, and 90% bandwidth frequency. In general, in the call of *G. cuencana* the notes tend to be shorter and are emitted less frequently.

Besides the significant importance of call descriptions in the integrative taxonomy of hemiphractid frogs, the correct knowledge and identification of advertisement calls of the species of marsupial frogs from this region also can have a very important and practical role in the conservation efforts of these endangered animals. The marsupial frogs are usually somewhat difficult to encounter (especially in the dense vegetation of the subpáramo forests), but very easy to hear as the advertisement call is characteristic and sufficiently loud to be detected from long distances. Additionally, the identification based on only morphological features of the marsupial frogs from Andes in southern Ecuador can be sometimes quite difficult (especially in the field) and so the calls can be very helpful in the correct identification of the species. We think that identifying these species by their advertisement calls can become a very useful tool for the monitoring of the populations of *Gastrotheca*, thereby aiding in the gathering of vital distributional information needed in any conservation actions.

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APPENDIX I. Specimens measured and their associated locality data.

Gastrotheca cuencana

ECUADOR: *Azuay:* CJ 1390–7 from Cuenca, 2579 m; KU 120676, 120705, 120709–10, 120713 120718–9, 120721 from Cuenca, 2600 m; KU 129779– 82, 129795 from Río Matadero, 12 km E Cuenca; KU 138616, 138620–1 from 4 km E Cuenca 2540 m; KU 141572 from 2.1 km S Cutchil, 2720 m; QCAZ 1239 from Sigsig, 2480 m; QCAZ 26309, 26353–4, 26357–64 from Cumbe, 2740 m; QCAZ 31477, 31509, 31511 from Sigsig, 2424 m; QCAZ 34131, 42720–1 from Cuenca, 2579 m; QCAZ 37375–6, 37379–81, 37386, from unknown locality; QCAZ 38232 from Carmen del Guzho, 2666 m; QCAZ 39384–5 from Tarqui, Patapamba, 2600 m; QCAZ 47106 from Tarqui, 2741 m. *Cañar:* KU 141571, 141573, 142620–4, 147113 from Biblián, 2620 m; QCAZ 42826, 42835, 42841 from Papaloma de la Nube, 3011 m.

Gastrotheca elicioi

ECUADOR: *Loja:* CJ 1398–402 from Parque Nacional Podocarpus entrance, 2456 m; KU 142603, 142608, 148549–50 from 5.5 km W Loja, 2330 m; KU 202688 from 5.2 km W Loja, 2310 m; KU 217511–2 from 6.8 km E Loja ca. Loja-Zamora borderline; CJ 4313 from Loja-Abra de Zamora; QCAZ 22370, 46319–20 from Zamora Huayco, Loja, 3018 m; CJ 4310, 4312 from Puntzará Grande, Loja, 2311 m.

Gastrotheca lateonota

PERU: *Piura:* KU 181730 from El Tambo, 31.5 km E Canchaque, Cordillera de Huancabamba, 2770 m.

Gastrotheca litonedis

ECUADOR: *Azuay*: CJ 386−9, 401−4, 1383−4, 1404−18 from San Fernando, Laguna de Busa, 2834 m; KU 202690 from 10 km (by road) northeast of Girón, 2750 m; QCAZ 42734, 42855, 42857−9, 42861, 42866, 42871, CJ 6813 from San Fernando,

Laguna de Busa, 2834 m; QCAZ 49973−4, 49976−8 from San Gerardo, 2854 m; CJ 5458–9 from Hacienda El Cristal, San Gerardo, 2800 m.

Gastrotheca lojana
ECUADOR: *Azuay*: CJ 390, 406–10 from Oña, 2272 m; CJ 4303–04 from Oña, 2407 m; CJ 4309 from El Tablón; KU 138401–2 from Girón, 2310 m; QCAZ 2692, 26314–5, 26318, 26322–3, 26327–8, 26334–5, 26337–8, 31521–3, 32212, 32571, 32724 from Oña, 2272 m; CJ 405, 411–2, QCAZ 42725 from San Fernando, Laguna de Busa, 2834 m. *Loja*: KU 138408, 148568, QCAZ 30788 from Saraguro, 2412 m; KU 178482, 178486–9, KU 178491 from 2 km SSW Saraguro, 2569 m; KU 178496–7 from 2.1 km N Saraguro, 2575 m; QCAZ 22371 from Loja Zamora Huayco, 3018 m; QCAZ 34505 from 2 km SW Saraguro, 2569 m.

Gastrotheca monticola
PERU: *Amazonas*: KU 181742–5, 181749–56, 181758–9, 181761–66 from Pomacochas (Florida), 2180 m.

Gastrotheca pseustes 1
ECUADOR: *El Oro*: CJ 201, 1949, 1953–5, KU 335386, QCAZ 45121, 45123–6 from Chillacocha, 8 km SW Chilla; CJ 1956 from Manu, on road Chilla-Saraguro, 2876 m. *Loja:* CJ 1403 from Parque Nacional Podocarpus entrance, 2456 m; CJ 6006 from El Salado de Jimbura.

Gastrotheca pseustes 2
ECUADOR: *Azuay*: CJ 396, QCAZ 42724, 42727–30, 42732, 42862–4 from San Fernando, Laguna de Busa, 2834 m; CJ 4320 from near Nabón, on road Cuenca-Oña; QCAZ 49979–82, 37842 from San Felipe de Molleturo, 3400 m; QCAZ 24508 from between El Ideal-Sigsig, 2911 m. *Bolívar*: QCAZ 14262 from 8 km N Guaranda; QCAZ 42873, 42876, 42878–80, 42882–3, 42885–7 from Guanujo, 2909 m. *Cañar*: QCAZ 240–4 from Ingapirca, 3148 m; QCAZ 26308 from Cashapamba, 3082 m; QCAZ 27575–6, 32668 from Reserva Mazar, Campamento La Libertad, 2895 m; QCAZ 34667, 34672, 34674, 34686 from Biblián, Hacienda Papaloma, 2748 m; QCAZ 42827, 42837–40, 42845, 42851 from Papaloma de la Nube, 3011 m. *Chimborazo*: QCAZ 749, 751 from Río Tililag, 67 Km E Guaranda, 3780 m; QCAZ 40580 from Lagunas de Atillo, 3434 m; QCAZ 42889, 42892, 42896, 42906–8 from Laguna de Colta, 3322 m. *Cotopaxi*: QCAZ 13930 from between Pujilí-Paguaje, 2950 m; QCAZ 24437 from Río Zumbahua, 3543 m; QCAZ 29245, 29662, 42742, 42750, 42753–5, 42778, 42823 from Sigchos, 3010 m; QCAZ 42719, 42738 from Parque Nacional Cotopaxi, Laguna de Limpiopungo, 3850 m; *Napo:* QCAZ 14279 from Parque Nacional Llanganates, 3800 m; QCAZ 17846, 17847–8, 42790–4, 42796, 42798–801, 42805, 42807–10, 42812 from Papallacta, 3150 m; QCAZ 17951 from NW Papallacta, 3360 m; QCAZ 34634–5 from Parque Nacional Llanganates, 3800 m. *Pichincha*: QCAZ 2364 from Quito, QCAZ 14247, 14254, 14270–1 from Páramo del Antisana, Laguna Muertepungo 4080 m; QCAZ 14319, 34573, 34577–8, 34580, 34911, 34914 from Machachi, 2915 m; QCAZ 34528 from Tambillo, Barrio El Rosario, 2768 m; QCAZ 34644 from Aloag, 2870 m. *Tungurahua*: QCAZ 22635 from between Baños-El Triunfo, 2486 m; QCAZ 23008 from Parque Nacional Llanganates, Poaló, 3400 m.

Gastrotheca turnerorum
ECUADOR: *Loja:* CJ 392–5, 1386, KU 335390 from Laguna Negra de Jimbura, Parque Nacional Yacuri, 3406 m; *Zamora Chinchipe:* MUTPL 221 from Reserva Tapichalaca, 3073 m.

Gastrotheca yacuri
ECUADOR: *Loja:* CJ 7822 from El Salado de Jimbura, at about 2.5 km (by road) west from the entrance in the Parque Nacional Yacuri, 2914 m; QCAZ 21105 from El Salado de Jimbura, 2712 m.

APPENDIX II. Localities used in this study to describe the distribution of *Gastrotheca*.

Species	Locality	Latitude	Longitude
Gastrotheca cuencana	ECUADOR: Azuay: Cuenca, 2501 m.	-2.883330	-78.983330
Gastrotheca cuencana	ECUADOR: Azuay: Río Matadero, 12 km E Cuenca, 2457 m.	-2.883330	-78.966670
Gastrotheca cuencana	ECUADOR: Cañar: Biblián, 2807 m.	-2.700000	-78.866670
Gastrotheca cuencana	ECUADOR: Azuay: 2.1 km S Cutchil, 2720 m.	-3.100000	-78.800000
Gastrotheca cuencana	ECUADOR: Azuay: 0.8 km S Cutchil, 2556 m.	-3.083330	-78.800000
Gastrotheca cuencana	ECUADOR: Azuay: 8.8 km NW Cuenca, 2803 m.	-2.866670	-79.066670
Gastrotheca cuencana	ECUADOR: Azuay: 16 km NW Cuenca, Laguna de Zurucuchu, 3172 m.	-2.840000	-79.130000
Gastrotheca cuencana	ECUADOR: Azuay: Sigsig, 2407 m.	-3.050000	-78.800000
Gastrotheca cuencana	ECUADOR: Azuay: Sigsig, 2480 m.	-3.052333	-78.802933
Gastrotheca cuencana	ECUADOR: Azuay: Cumbe, 2754 m.	-3.083420	-79.009150
Gastrotheca cuencana	ECUADOR: Azuay: Cumbe, 2740 m.	-3.098790	-79.007980
Gastrotheca cuencana	ECUADOR: Azuay: Cumbe, 2724 m.	-3.101420	-79.008700
Gastrotheca cuencana	ECUADOR: Azuay: Sigsig, 2424 m.	-3.052333	-78.802933
Gastrotheca cuencana	ECUADOR: Azuay: Sigsig, 3104 m.	-3.059432	-78.795922
Gastrotheca cuencana	ECUADOR: Azuay: Cuenca, 2579 m.	-2.899420	-79.031330
Gastrotheca cuencana	ECUADOR: Azuay: Cuenca, Carmen del Guzho, 2666 m.	-2.933333	-79.050000
Gastrotheca cuencana	ECUADOR: Azuay: Tarqui, Patapamba, 2600 m.	-3.010600	-79.031510
Gastrotheca cuencana	ECUADOR: Cañar: Papaloma de la Nube, 3011 m.	-2.672650	-78.905910
Gastrotheca cuencana	ECUADOR: Azuay: Cuenca, Challuabamaba, 2534 m.	-2.853600	-78.900073
Gastrotheca cuencana	ECUADOR: Azuay: Tarqui, 2741 m.	-3.015880	-79.044480
Gastrotheca elicioi	ECUADOR: Loja: Loja, Parque Nacional Podocarpus entrance, 2456 m.	-4.090420	-79.202770
Gastrotheca elicioi	ECUADOR: Loja: 5.5 km W Loja, 2330 m.	-4.013610	-79.230830
Gastrotheca elicioi	ECUADOR: Loja: 5.2 km W Loja, 2310 m.	-3.982980	-79.267280
Gastrotheca elicioi	ECUADOR: Loja: 6.8 km E Loja ca Loja-Zamora line, 2366 m.	-3.988610	-79.156110
Gastrotheca elicioi	ECUADOR: Loja: 10 km from Loja, 2250 m.	-3.979730	-79.180370
Gastrotheca elicioi	ECUADOR: Loja: San Cayetano, 2177 m.	-3.979050	-79.177833
Gastrotheca elicioi	ECUADOR: Loja: Zamora Huayco, 3018 m.	-4.097217	-79.167361
Gastrotheca elicioi	ECUADOR: Loja: Loja, Barrio Putzará Grande, 2311 m.	-4.043680	-79.214070
Gastrotheca elicioi	ECUADOR: Loja: Reserva privada Madrigal del Podocarpus, 2278 m.	-4.04363	-79.17313
Gastrotheca elicioi	ECUADOR: Loja: Quebrada Minas, 2078 m.	-4.00377	-79.18514
Gastrotheca elicioi	ECUADOR: Loja: Quebrada El Salado, 2077 m.	-3.96451	-79.18901
Gastrotheca elicioi	ECUADOR: Loja: PUEAR, 2176 m.	-4.03701	-79.19620
Gastrotheca elicioi	ECUADOR: Loja: Quebrada Paccha, 2046 m.	-3.94838	-79.20924
Gastrotheca elicioi	ECUADOR: Loja: Quebrada Shucos, 2026 m.	-3.93942	-79.21694

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APPENDIX 2. (Continued)

Species	Locality	Latitude	Longitude
Gastrotheca lateonota	PERU: Piura: El Tambo, 32.5 km (by road) E Cachanque, 2770 m.	-5.366667	-79.550000
Gastrotheca litonedis	ECUADOR: Azuay: San Fernando, Laguna de Busa, 2834 m.	-3.154390	-79.263620
Gastrotheca litonedis	ECUADOR: Azuay: 10 km (by the road) NE of Girón, 2854 m.	-3.083330	-79.100000
Gastrotheca litonedis	ECUADOR: Azuay: San Gerardo, 2750 m.	-3.133380	-79.193550
Gastrotheca lojana	ECUADOR: Azuay: San Fernando, Laguna de Busa, 2834 m.	-3.154390	-79.263620
Gastrotheca lojana	ECUADOR: Azuay: Girón, 2310 m.	-3.166670	-79.133330
Gastrotheca lojana	ECUADOR: Azuay: Santa Isabel, Valle de Yunguilla, Chalcápac, 1682 m.	-3.233333	-79.200000
Gastrotheca lojana	ECUADOR: Azuay: Oña, 2271m.	-3.461230	-79.162530
Gastrotheca lojana	ECUADOR: Azuay: Oña, 2272 m.	-3.461400	-79.162910
Gastrotheca lojana	ECUADOR: Azuay: Oña, 2326 m.	-3.469270	-79.162530
Gastrotheca lojana	ECUADOR: Loja: El Tablón, 2363 m.	-3.477030	-79.179700
Gastrotheca lojana	ECUADOR: Loja: 2.1 km N Saraguro, 2575 m.	-3.611670	-79.249440
Gastrotheca lojana	ECUADOR: Loja, Saraguro, 2412 m.	-3.600000	-79.216670
Gastrotheca lojana	ECUADOR: Loja: 2 km SW Saraguro, 2569 m.	-3.639720	-79.240000
Gastrotheca lojana	ECUADOR: Loja: 2 km SW Saraguro, 2560 m.	-3.620250	-79.235810
Gastrotheca lojana	ECUADOR: Loja: Loja, 2177 m.	-4.000000	-79.216670
Gastrotheca lojana	ECUADOR: Loja: 10 km W Loja, 2500 m.	-3.999170	-79.246390
Gastrotheca lojana	ECUADOR: Loja: Zamora Huayco, 3018 m.	-4.097217	-79.167361
Gastrotheca lojana	ECUADOR: Loja: Paraíso del Celén, 2680 m.	-3.579780	-79.338120
Gastrotheca lojana	ECUADOR: El Oro: Guanazán, 2984 m.	-3.455120	-79.489900
Gastrotheca pseustes 1	ECUADOR: Loja: Loja, Parque Nacional Podocarpus entrance, 2456 m.	-4.090420	-79.202770
Gastrotheca pseustes 1	ECUADOR: El Oro: Chillacocha, ~8 km SW Chilla, 3250 m.	-3.504270	-79.617140
Gastrotheca pseustes 1	ECUADOR: El Oro: ca. Chilla, 2452 m.	-3.458170	-79.581130
Gastrotheca pseustes 1	ECUADOR: Loja, Manu, 2876 m.	-3.554730	-79.368340
Gastrotheca pseustes 2	ECUADOR: Cotopaxi: Between Pujilí-Paguaje, 2950 m.	-0.951310	-78.693410
Gastrotheca pseustes 2	ECUADOR: Pichincha: Páramo del Antisana, Laguna Muertepungo, 4080 m.	-0.418834	-78.262633
Gastrotheca pseustes 2	ECUADOR: Napo: Páramo del Antisana, 4819 m.	-0.494660	-78.201660
Gastrotheca pseustes 2	ECUADOR: Bolívar: 8 km N Guaranda, 3103 m.	-1.529000	-78.996000
Gastrotheca pseustes 2	ECUADOR: Tungurahua: Parque Nacional Llanganates, 3800 m.	-1.074400	-78.403383
Gastrotheca pseustes 2	ECUADOR: Pichincha: Machachi, 2915 m.	-0.507390	-78.540270
Gastrotheca pseustes 2	ECUADOR: Bolívar: Bosque Protector Cashca Totoras, 2998 m.	-1.716667	-78.966670
Gastrotheca pseustes 2	ECUADOR: Napo: NW Papallacta, 3360 m.	-0.363930	-78.150450
Gastrotheca pseustes 2	ECUADOR: Tungurahua: Between Baños-El Triunfo, 2486 m.	-1.304000	-78.405000
Gastrotheca pseustes 2	ECUADOR: Tungurahua: Parque Nacional Llanganates, Poaló, 3400 m.	-1.074400	-78.403383

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APPENDIX 2. (Continued)

Species	Locality	Latitude	Longitude
Gastrotheca pseustes 2	ECUADOR: Cañar: Ingapirca, 3148 m.	-2.545366	-78.874391
Gastrotheca pseustes 2	ECUADOR: Cotopaxi: Río Zumbahua, 3543 m.	-1.031940	-78.598330
Gastrotheca pseustes 2	ECUADOR: Chimborazo: Laguna de Frutatian, 3730 m.	-2.220000	-78.511000
Gastrotheca pseustes 2	ECUADOR: Azuay: Between El Ideal-Sigsig, 2911 m.	-3.151100	-78.804500
Gastrotheca pseustes 2	ECUADOR: Cañar: Cashapamba, 3082 m.	-2.436530	-79.006860
Gastrotheca pseustes 2	ECUADOR: Azuay: 3 Km S La Paz, Nieves-Oña, 2985 m.	-3.344390	-79.180690
Gastrotheca pseustes 2	ECUADOR: Azuay: Cumbe, 2724 m.	-3.101420	-79.008700
Gastrotheca pseustes 2	ECUADOR: Cañar: Reserva Mazar, Campamento La Libertad, 2895 m	-2.546589	-78.698375
Gastrotheca pseustes 2	ECUADOR: Cotopaxi: Sigchos, 3010 m.	-0.700970	-78.905150
Gastrotheca pseustes 2	ECUADOR: Azuay: San Felipe de Molleturo, 3400 m	-2.762712	-79.400160
Gastrotheca pseustes 2	ECUADOR: Pichincha: Tambillo, Barrio El Rosario, 2768 m.	-0.403200	-78.540900
Gastrotheca pseustes 2	ECUADOR: Pichincha: Aloag, 2870 m.	-0.467240	-78.582190
Gastrotheca pseustes 2	ECUADOR: Cañar: Biblián, Hacienda Papaloma, 2748 m.	-2.707910	-78.887180
Gastrotheca pseustes 2	ECUADOR: Azuay: Bosque Protector Mazán, 3115 m.	-2.874840	-79.123830
Gastrotheca pseustes 2	ECUADOR: Tungurahua: Parque Nacional Llanganates, Laguna de Pisayambo, 3599 m.	-1.056970	-78.397610
Gastrotheca pseustes 2	ECUADOR: Chimborazo: Lagunas de Atillo, 3434 m.	-2.193953	-78.521600
Gastrotheca pseustes 2	ECUADOR: Cotopaxi: Parque Nacional Cotopaxi: Laguna de Limpiopungo, 3850 m.	-0.620839	-78.476246
Gastrotheca pseustes 2	ECUADOR: Napo: Papallacta, 3150 m.	-0.381020	-78.141290
Gastrotheca pseustes 2	ECUADOR: Cañar: Papaloma de la Nube, 3011 m.	-2.672650	-78.905910
Gastrotheca pseustes 2	ECUADOR: Azuay: San Fernando, 2834 m.	-3.154390	-79.263620
Gastrotheca pseustes 2	ECUADOR: Bolívar: Guanujo, 2909 m.	-1.566030	-79.011240
Gastrotheca pseustes 2	ECUADOR: Chimborazo: Laguna de Colta, 3322 m.	-1.748970	-78.758860
Gastrotheca pseustes 2	ECUADOR: Azuay: San Gerardo, 2854 m.	-3.133380	-79.193550
Gastrotheca pseustes 2	ECUADOR: Chimborazo: Río Tililag, 67 Km E Guaranda, 3780 m.	-1.600000	-78.866700
Gastrotheca psychrophila	ECUADOR: Zamora-Chinchipe: 13.5 km E Loja, 2800 m.	-3.980000	-79.070000
Gastrotheca turnerorum	ECUADOR: Loja: Laguna Negra de Jimbura, Parque Nacional Yacuri, 3406 m.	-4.712290	-79.428440
Gastrotheca turnerorum	ECUADOR: Zamora Chinchipe: Parque Nacional Podocarpus, Lagunas del Compadre, 3205 m.	-4.174790	-79.116540
Gastrotheca turnerorum	ECUADOR: Zamora Chinchipe: Reserva Tapichalaca, 3073 m.	-4.482106	-79.158267
Gastrotheca yacuri	ECUADOR: Loja: Lagunas Negras, Parque Nacional Yacuri, 3492 m.	-4.708836	-79.430447
Gastrotheca yacuri	ECUADOR: Loja: El Salado de Jimbura, 2914 m.	-4.702325	-79.450025
Gastrotheca yacuri	ECUADOR: Loja: El Salado de Jimbura, 2712 m.	-4.686956	-79.444379

APPENDIX III. Data of call recordings used in the present study (Dist = distance from the focal male; Temp = air temperature; H = air humidity).

Species	FonoZoo ID	Voucher	Locality	Coordinates	Altitude (m)	Date	Time	Dist. (m)	Temp. (°C)	H. (%)
Gastrotheca cuencana	11170	no	Ecuador: Azuay: Cuenca	2° 53' 57.9" S 79° 1' 52.8" W	2579	2011.06.08	21:00	2	16	–
Gastrotheca cuencana	11171	no	Ecuador: Cañar: Papaloma de la Nube	2° 40' 21.5" S 78° 54' 21.3" W	3011	2008.08.14	14:00	2.5	10.3	84.2
Gastrotheca cuencana	11172	no	Ecuador: Cañar: Papaloma de la Nube	2° 40' 21.5" S 78° 54' 21.3" W	3011	2008.08.14	14:30	3	10.3	84.2
Gastrotheca cuencana	11173	no	Ecuador: Azuay: Cuenca	2° 53' 57.9" S 79° 1' 52.8" W	2579	2011.06.08	22:41	2	15.4	–
Gastrotheca cuencana	11174	no	Ecuador: Azuay: Cuenca	2° 53' 57.9" S 79° 1' 52.8" W	2579	2011.06.08	23:58	3	13.8	–
Gastrotheca cuencana	11175	no	Ecuador: Azuay: Río Mazán	2° 51' 59.1" S 79° 6' 42.0" W	3000	1986.08.03	22:00	–	–	–
Gastrotheca cuencana	11176	no	Ecuador: Azuay: Río Mazán	2° 51' 59.1" S 79° 6' 42.0" W	3000	1986.08.12	–	–	–	–
Gastrotheca cuencana	11177	no	Ecuador: Azuay: Río Mazán	2° 51' 59.1" S 79° 6' 42.0" W	3000	1986.09.08	–	–	–	–
Gastrotheca elicioi	11213	CJ 4308	Ecuador: Loja: Loja, road Loja-Parque Eólico Villonaco	4° 0' 55.76" S 79° 14' 8.34" W	2327	2016.01.27	22:20	2.5	13.6	–
Gastrotheca elicioi	11214	no	Ecuador: Loja: Loja (captive recorded in Quito at 2455 m)	–	–	2014.03.20	20:00	1	13.1	–
Gastrotheca elicioi	11215	no	Ecuador: Loja: Loja (captive recorded in Quito at 2455 m)	–	–	2014.03.20	20:20	1	13.1	–
Gastrotheca elicioi	11216	no	Ecuador: Loja: Loja, Universidad de Loja, PUEAR	4° 2' 13.8" S 79° 11' 42.6" W	2224	2016.11.30	17:58	4.5	18.5	74.5
Gastrotheca elicioi	11217	no	Ecuador: Loja: Loja, Universidad de Loja, PUEAR	4° 2' 13.8" S 79° 11' 42.6" W	2299	2016.11.30	18:21	6.5	17.5	76.5
Gastrotheca elicioi	11218	no	Ecuador: Loja: Loja, Universidad de Loja, PUEAR	4° 2' 13.8" S 79° 11' 42.6" W	2453	2016.11.30	19:09	4	15	81.5
Gastrotheca elicioi	11219	no	Ecuador: Loja: Loja, Quebrada El Salado	3° 58' 0.2" S 79° 11' 22.7" W	2064	2017.12.26	21.21	4.5	16.5	82
Gastrotheca litonedis	11221	no	Ecuador: Azuay: San Gerardo	3° 8' 0.2" S 79° 11' 36.8" W	2854	2010.12.01	16:12	2.5	16.1	–
Gastrotheca litonedis	11222	no	Ecuador: Azuay: San Gerardo	3° 8' 0.2" S 79° 11' 36.8" W	2854	2010.12.01	17:20	2.5	15.1	–
Gastrotheca litonedis	11223	QCAZ 49974	Ecuador: Azuay: San Gerardo	3° 8' 0.2" S 79° 11' 36.8" W	2854	2010.12.01	20:24	2	13.4	–
Gastrotheca litonedis	11224	QCAZ 49974	Ecuador: Azuay: San Gerardo	3° 8' 0.2" S 79° 11' 36.8" W	2854	2010.12.01	20:24	2	13.4	–
Gastrotheca litonedis	11225	QCAZ 49977	Ecuador: Azuay: San Gerardo	3° 8' 0.2" S 79° 11' 36.8" W	2854	2010.12.01	21:15	2	13.4	–
Gastrotheca litonedis	11190	QCAZ 49977	Ecuador: Azuay: San Gerardo	3° 8' 0.2" S 79° 11' 36.8" W	2854	2010.12.01	22:23	2	13.1	–

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APPENDIX 3. (Continued)

Species	FonoZoo ID	Voucher	Locality	Coordinates	Altitude (m)	Date	Time	Dist. (m)	Temp. (°C)	H. (%)
Gastrotheca litonedis	11191	no	Ecuador: Azuay: San Fernando, Laguna de Busa	3° 9' 15.8" S 79° 15' 49.0" W	2834	2011.06.09	22:07	3	8.8	96
Gastrotheca litonedis	11192	CJ 1404	Ecuador: Azuay: San Fernando, Laguna de Busa	3° 9' 15.8" S 79° 15' 49.0" W	2834	2011.06.09	22:45	5	8.6	96
Gastrotheca litonedis	11193	no	Ecuador: Azuay: San Fernando, Laguna de Busa	3° 9' 15.8" S 79° 15' 49.0" W	2834	2011.06.09	23:00	2.5	8.3	98
Gastrotheca lojana	11194	QCAZ 42725	Ecuador: Azuay: San Fernando, Laguna de Busa	3° 9' 15.8" S 79° 15' 49.0" W	2834	2007.10.24	20:10	1.5	10.8	–
Gastrotheca lojana	11195	CJ 4300	Ecuador: Loja: Oña	3° 27' 46.9" S 79° 09' 15.6" W	2368	2016.01.26	19:55	2	14.6	–
Gastrotheca lojana	11196	no	Ecuador: Loja: Oña	3° 27' 46.9" S 79° 09' 15.6" W	2368	2016.01.26	21:50	–	14.6	–
Gastrotheca lojana	11197	no	Ecuador: Loja: Oña	3° 27' 46.9" S 79° 09' 15.6" W	2368	2016.01.26	21:50	–	14.6	–
Gastrotheca lojana	11198	CJ 4302	Ecuador: Loja: Oña	3° 27' 46.9" S 79° 09' 15.6" W	2368	2016.01.26	21:50	2	14.6	–
Gastrotheca pseustes	11199	no	Ecuador: Loja: Bosque Washapamba	3° 39' 36.9" S 79° 16' 14.8" W	2912	2017.07.09	20:26	4	13.8	48
Gastrotheca pseustes	11200	no	Ecuador: Loja: Bosque Washapamba	3° 39' 32.4" S 79° 16' 23.9" W	2872	2016.04.01	20:02	5	16	72.5
Gastrotheca pseustes	11201	no	Ecuador: Azuay: Vía Urdaneta - Tutupali	3° 35' 27.7" S 79° 8' 27.9" W	2963	2016.08.04	22:01	6	10	86.5
Gastrotheca pseustes	11202	no	Ecuador: Azuay: Vía Urdaneta - Tutupali	3° 35' 27.7" S 79° 8' 27.9" W	2963	2016.08.04	22:10	3	10	90
Gastrotheca pseustes	11203	no	Ecuador: Loja: Cerro de Arcos	3° 34' 3.6" S 79° 25' 59.3" W	3327	2017.07.22	20:57	3	6	93.5
Gastrotheca testudinea	11204	no	Ecuador: Morona Santiago: Zuñag	2° 11' 30.0" S 78° 21' 27.1" W	2359	2012.12.07	–	–	–	–
Gastrotheca testudinea	11205	no	Ecuador: Morona Santiago: Zuñag	2° 11' 30.0" S 78° 21' 27.1" W	2359	2012.12.07	–	–	–	–
Gastrotheca testudinea	11206	no	Ecuador: Morona Santiago: Zuñag	2° 11' 30.0" S 78° 21' 27.1" W	2359	2012.12.07	–	–	–	–
Gastrotheca testudinea	11207	no	Ecuador: Morona Santiago: Zuñag	2° 11' 30.0" S 78° 21' 27.1" W	2359	2012.12.07	–	–	–	–
Gastrotheca testudinea	11208	no	Ecuador: Morona Santiago: Zuñag	2° 11' 30.0" S 78° 21' 27.1" W	2359	2012.12.07	1:30	–	10.8	–
Gastrotheca testudinea	11209	no	Ecuador: Morona Santiago: Zuñag (captive recorded in Quito at 2455 m)	–	–	2014.03.20	20:30	–	12.6	–
Gastrotheca yacuri	11210	CJ 7822	Ecuador: Loja: El Salado	4° 42' 8.4" S 79° 27' 0.1" W	2914	2016.04.09	1:48	3	10.5	96.5
Gastrotheca yacuri	11211	no	Ecuador: Loja: El Salado	4° 42' 8.4" S 79° 27' 0.1" W	2914	2016.07.29	21:50	4	8.5	93
Gastrotheca yacuri	11212	no	Ecuador: Loja: El Salado	4° 42' 8.4" S 79° 27' 0.1" W	2914	2016.07.30	21:40	4	8.5	93