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Diversity of marsupial frogs (Anura: Hemiphractidae: *Gastrotheca*) in the northern Cordillera Central, Peru, with the descriptions of two new species

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Abstract

Diversity of marsupial frogs (Anura: Hemiphractidae: *Gastrotheca*) in the northern Cordillera Central, Peru, with the descriptions of two new species. Two new species of *Gastrotheca* are represented by adult females, genomic data of these are included in a phylogenetic analysis, whereby they are placed in the northern clade of the subgenus *Gastrotheca*. One new species, *G. spectabilis,* is unique within the genus in having a color pattern consisting of white labial, rostral, and canthal stripes. The second new species, *G. oresbios,* has a dorsal color pattern of dark paravertebral markings and canthal stripe, but no pale labial stripe; thus it resembles *G. abdita,* which differs by having an inner tarsal fold, a wider interorbital distance, and smooth skin on the dorsum lacking scattered tubercles as in *G. oresbios.* Of the nine species of *Gastrotheca* in the northern Cordillera Central, only *G. spectabilis, G. ossilaginis,* and *G. oresbios* lack an inner tarsal fold. The third species is represented by two juveniles; it is briefly described but not named. Of the nine species of *Gastrotheca* known from the high elevations in the northern part of the Cordillera Central in northern Peru, only two are members of the subgenus *Duellmania* that occurs principally north of the Huancabamba Depression. Only one of the nine species of species of *Gastrotheca* in the northern part of the Cordillera Central is shared with the Cordillera Occidental in Peru, and none of the species is shared with the Ecuadorian ranges of the Andes.

Keywords: Andes, Huancabamba Depression, new species, northern Peru, subgenus *Gastrotheca,* southern Ecuador.

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Resumen

Diversidad de ranas marsupiales (Anura: Hemiphractidae: *Gastrotheca*) en el norte de la Cordillera Central de Peru, con las descripciones de dos nuevas especies. Dos especies nuevas de *Gastrotheca* se encuentran representadas por hembras adultas, datos genómicos de ambas especies en un análisis filogenético sitúan a estas en el clado norteño del subgénero *Gastrotheca*. Una de las nuevas especies, *G. spectabilis*, es la única en el género con una raya pálida labial, rostral y cantal. La segunda nueva especie, *G. oresbios*, tiene un patrón de coloración dorsal de marcas paravertebrales y raya cantal, pero no una raya labial pálida. Esta semeja a *G. abdita*, de cual se diferencia por tener pliegue tarsal interno, mayor distancia interorbital y piel lisa en el dorso, sin tubérculos dispersos, como en *G. oresbios*. De las nueve especies de *Gastrotheca* que ocurren en el norte de la Cordillera Central, solo *G. spectabilis, G. ossilaginis,* y *G. oresbios* carecen del pliegue tarsal interno. La tercera especie esta representada por dos especímenes juveniles y es brevemente descrita más no nombrada. De las nueve especies de *Gastrotheca* conocidas para las zonas altas de la porción norte de la Cordillera Central en el norte de Perú, solo dos especies son miembros del género *Duellmania,* que ocurre principalmente al norte de la Depresión de Huancabamba. Solo una, de estas nueve especies de la Cordillera Central, es compartida con la Cordillera Occidental de Perú y ninguna especie se comparte con los Andes de Ecuador.

Palabras claves: Andes, Depresión de Huancabamba, especies nuevas, norte de Peru, subgénero *Gastrotheca*, sur de Ecuador.

Resumo

Diversidade de pererecas-marsupiais (Anura: Hemiphractidae: *Gastrotheca*) no norte da Cordilheira Central, Peru, com descrições de duas novas espécies. Duas novas espécies de *Gastrotheca* são representadas por fêmeas adultas, seus dados genômicos estão incluídos em uma análise filogenética, em que são colocadas no clado do norte do subgênero. Uma nova espécie, *G. spectabilis,* é única no gênero por apresentar um padrão de coloração consistindo de faixas labial, rostral e cantal brancas. A segunda nova espécie, *G. oresbios,* possui um padrão de coloração dorsal com marcas paravertebrais e faixa cantal escuras, mas sem faixa labial clara; assim, assemelha-se a *G. abdita,* que difere pela posse de uma dobra tarsal interna, maior distância interorbital e pele lisa do dorso desprovida de tubérculos dispersos como em *G. oresbios.* Das nove espécies de *Gastrotheca* do norte da Cordilheira, apenas *G. spectabilis, G. ossilaginis* e *G. oresbios* não possuem uma dobra tarsal interna. A terceira espécie é representada por dois juvenis; essa espécie é descrita brevemente, mas não nomeada. Das nove espécies de *Gastrotheca* conhecidas de grandes altitudes da porção norte da Cordilheira Central do norte do Peru, apenas duas pertencem ao subgênero *Duellmania,* que ocorre principalmente ao norte da Depressão de Huancabamba. Apenas uma das nove espécies de *Gastrotheca* da porção norte da Cordilheira Central é compartilhada com a Cordilheira Ocidental do Peru, e nenhuma é compartilhada com as serras equatorianas dos Andes.

Palavras-chave: Andes, Depressão de Huancabamba, espécie nova, norte do Peru, subgênero *Gastrotheca,* sul do Equador.

Introduction

Frogs in the family Hemiphractidae are unique in that fertilized eggs are carried on the back of the female (*Cryptobatrachus, Hemiphractus,* and *Stefania*), in an open pouch on the back of the female (*Fritziana*), or in a closed pouch on the back of the female (*Flectonotus* and *Gastrotheca*). Molecular phylogenetic analyses place *Gastrotheca* as the most derived genus in the family (Blackburn and Duellman 2013, Castroviejo-Fisher *et al.* 2015, Duellman 2015). The greatest diversity of *Gastrotheca* is in the Andes where the elevational ranges of some species (e.g., *G. peruana* and *G. riobambae*) exceed 4000 m. Within this array of montane

frogs, some species are biphasic (aquatic larval stage) and others have direct development (no larval stage)

In their phylogenetic analysis of *Gastrotheca* Blackburn and Duellman (2013) recognized one major clade as the northern Andean clade and another as a Central Andean clade. Subsequently, Duellman (2015) defined seven subfamilies within *Gastrotheca.* The formerly recognized northern Andean clade became *Duellmania,* a subgeneric name proposed by Dubois (1987), whereas the Central Andean clade became the subgenus *Gastrotheca.* As depicted in Figure 1, the phylogenetic tree of the subgenus *Gastrotheca* contains three major clades. The northern clade contains species that have a biphasic life cycle; the group ranges from central Ecuador to northern Peru and contains the new species described herein. The Peruvian clade consists of species undergoing direct development and ranging from northern Peru to northern Bolivia. The southern clade is made up of species having both kinds of life histories; species in this clade range from central Peru to northern Argentina.

Recognition of species of marsupial frogs in southern Ecuador and northern Peru began slowly. Boulenger (1900) described the first species, *Gastrotheca peruana* from the northern part of the Cordillera Occidental in Peru. This was followed by the descriptions of *G. monticola* from the Huanacabamba Depression in northern Peru (Barbour and Noble 1920) and *G. lojana* from the Loja Basin in southern Ecuador. Intensive fieldwork by Duellman and his associates revealed the existence of three more species from southern Ecuador, *G. psychrophila* (Duellman 1974) and *G. litonedis* and *G. pseustes* (Duellman and Hillis 1987). *Gastrotheca galeata* (Trueb and Duellman 1978) and *G. lateonota* (Duellman and Trueb 1988) were named from the Huancabamba Depression in northern Peru and seven from northern Peru—*G. abdita* (Duellman 1987), *G. ossilaginis* and *G. phalarosa* (Duellman and Venegas 2005), *G. phelloderma* (Lehr and Catenazzi 2011), *G. dysprosita* (Duellman 2013), and *G. aguaruna* and *G. aratia*

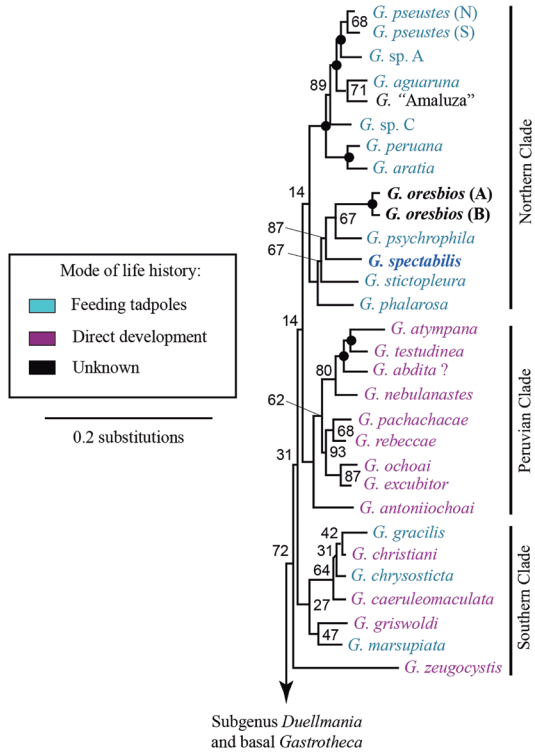

Figure 1. Maximum likelihood phylogeny of species in the subgenus *Gastrotheca,* modified from Duellman (2015). Names of species described in this paper are in bold face. See text for further explanation.

(Duellman *et al.* 2014). Most recently, Carvajal-Endara *et al.* (2017) are describing three more species from the Andes in southern Ecuador. To this conglomeration we add two more species from northern Peru. Molecular data of these three species and the two described herein were used in a previous molecular analysis (Duellman 2015).

Materials and Methods

Eleven specimens of *Gastrotheca* collected in the northern part of the Cordillera Central in Peru by PJV and studied in detail by WED form

the basis of this paper. Two new species are contained in this sample. Unfortunately one of these species is represented by only one adult female; the other is represented by an adult female, six subadults, and one juvenile. Two other juveniles probably represent another undescribed species; unfortunately tissues were not taken from these individuals.

The morphological characters and 16 measurements are those used by Duellman and Hillis (1987) and Duellman (2013, 2015) All measurements are in millimeters, and snout-vent length is abbreviated SVL. Specimens examined other than the new species are listed in Appendix I. Codes for museum collections are those listed by Sabaj Pérez (2010). The phylogenetic tree is based on the tree provided by Duellman (2015) constructed from analyses of four genes (16S, ND1, POMC, and RAG-1); see Duellman (2015) for details; Genbank accession numbers are given in Appendix II. In the tree (Figure 1), the two samples of *Gastrotheca pseustes* are labeled "N" and "S", representing northern and southern populations of that species. Of the two *G. oresbios* sp. nov., "A" is the holotype CORBIDI 11076 from Abra Barro Negro and "B" is CORBIDI 11040 from Hornillo. The associated Genbank numbers are designated *Gastrotheca* sp. E for the holotype of *G. spectabilis* sp. nov. and *Gastrotheca* sp. F for the holotype of *G. oresbios* sp. nov. (see Figure 3.1 in Duellman 2015).

In the field, elevations and geographic coordinates were obtained by Garmin® GPS using datum WGS 84.

Results

The new species are placed in the genus *Gastrotheca* because females have dorsal brood pouches. Furthermore, genomic data place them in the subgenus *Gastrotheca* (Figure 1).

***Gastrotheca oresbios* sp. nov.**
Gastrotheca sp. F, Duellman 2015, p. 282, Fig. 12.1.
(Figure 2)

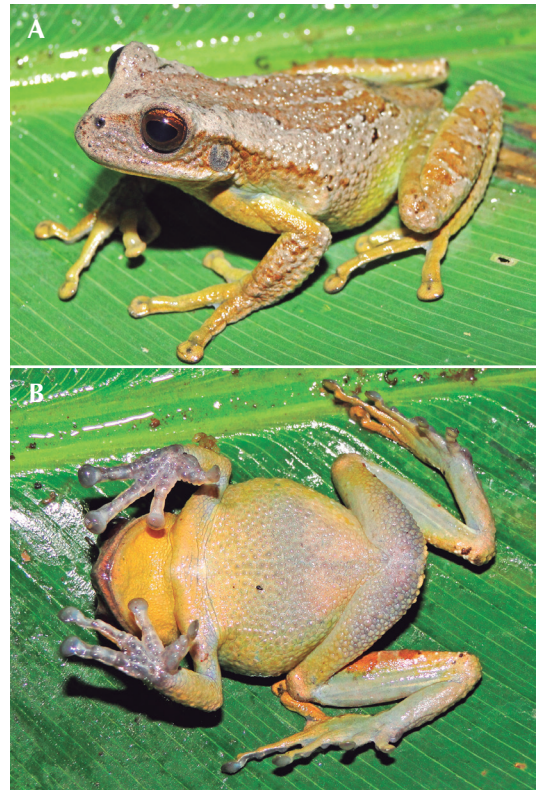

Figure 2. Holotype of *Gastrotheca oresbios,* CORBIDI 11076, female, 45.7 mm SVL. Photos by Pablo J. Venegas.

Holotype.—C0RBIDI 11076, an adult female, from Abra Barro Negro, 6º42'58.2" S, 77º51'53.8" W, 3290 m, Provincia Chachapoyas, Departamento Amazonas, Peru, collected by P. J. Venegas and L. Y. Echevaría on 24 May 2012.

Referred specimen.—CORBIDI 11040, a juvenile, from Quintecocha 6º51'33" S, 77º42'14.7" W, 3119 m, Provincia Marical Caceres, Departamento San Martin, Peru, collected by P. J. Venegas and L. Y. Echevaría on 19 May 2012.

Diagnosis.—Adults of this species attain a maximum snout-vent length (SVL) of 45.7 mm; tibia length less than 55% SVL, slightly longer than foot; interorbital distance about 1.5 times

width of upper eyelid; skin on the dorsum smooth with scattered tubercles, not co-ossified with skull, lacking transverse ridges. Supraciliary processes and calcars on heels absent; tympanic annulus distinct, granular. Finger I barely shorter than Finger II; discs on fingers much wider than digits proximal to discs; fingers not webbed; outer toes webbed basally. Dorsum brown with darker brown paravertebral marks; markings on head and pale dorsolateral stripe absent; flanks gray with greenish yellow-tan axillary and inguinal regions.

Gastrotheca oresbios has a nearly acuminate snout; five other species in the genus have an acute snout in dorsal view and also occur in the Andes. Of these, *G. abdita* known only from the Cordillera Colán in northern Peru differs from *G. oresbios* by having conical ulnar tubercles, an enlarged tubercle on the heel, and an inner tarsal fold on the distal two thirds of the tarsus. Furthermore, in *G. abdita* Fingers fingers I and II are equal in length, and the tympanum is vertically ovoid. The second species, the smaller *G. ochoai* (maximum SVL 30.4 mm in males, 37.5 mm in females [Duellman 2015]) is a bromeliad inhabitant in the Cordillera Oriental in southern Peru; it differs from the larger *G. oresbios* by having a vertically ovoid tympanum with a smooth annulus. *Gastrotheca pacchamama* and *G. rebeccae,* inhabitants of the Cordillera Oriental in central Peru, differ from *G. oresbios* by having a pale labial stripe and a smooth tympanic annulus. *Gastrotheca zeugocistis* also has a smooth tympanic annulus and paired brood pouches. The six remaining species in the Peruvian Andes that might be confused with *G. oresbios* have bluntly rounded snouts in dorsal view. Of these, *G. antoniiochoai* has a shagreen tan dorsum with brown and green flecks; furthermore, the interorbital distance is less than 85% of the eyelid, whereas *G. pachachacae* has a granular dorsum and tan flanks with brown spots. *Gastrotheca nebulanastes* differs from *G. oresbios* by having granular skin on the dorsum, a smooth tympanic annulus, and Finger I longer than Finger II. *Gastrotheca excubitor* and *G. griswoldi* differ from *G. oresbios* by having a smooth tympanic annulus and usually having a pale labial stripe. As the specific name implies, *G. atympana* differs from *G. oresbios* by lacking a tympanum; furthermore the snout is narrowly truncate in dorsal view and the skin on the dorsum is shagreen.

Description of holotype.—Adult female; body robust; SVL 45.7 mm; head slightly wider than long; snout acuminate in dorsal view, rounded in profile; canthus rostralis rounded in section; loreal region concave; lips rounded; top of head flat; interorbital distance 158% width of upper eyelid; internarial area flat; nostrils not protuberant, directed anterolaterally at point well posterior to anterior margin of lower jaw, below anterior terminus of canthus rostralis; diameter of eye greater than its distance from nostril; tympanum round, its diameter about two thirds that of eye, separated from the eye by distance about 5.5 times length of the tympanum; tympanic membrane smooth, annulus distinct, granular; supratympanic fold moderately heavy, tuberculate, angular in section, extending from posterior corner of orbit to point above insertion of arm, not obscuring tympanum.

Arm robust; ulnar tubercles absent; hand moderately large; fingers unwebbed; discs on fingers round, wider than digit; diameter of the disc on Finger III slightly less than length of tympanum; relative lengths of the fingers I < II < IV < III; subarticular tubercles moderately large, subconical, distal tubercle on Finger II bifid; supernumerary tubercles round, present only on proximal digits; palmar tubercle small, divided; prepollical tubercle large, ovoid, slightly elevated. Hind limbs moderately robust; tibia length 52.3% SVL; foot length 50.8% SVL; heel lacking enlarged tubercle; inner tarsal fold and outer metatarsal tubercle absent; inner metatarsal tubercle small, not elevated, ovoid, not visible from above; toes moderately long; relative lengths toes I < II < III < V < IV. Toes I–II not webbed; basal webbing between Toes III and IV and between Toes IV and V; subarticular

tubercles moderately large, subconical; supernumerary tubercles, small, subconical, present only on proximal segments of toes.

Skin on dorsum smooth with scattered small tubercles, especially numerous on supratympanic fold and on side of head posterior to eye; flanks granular anteriorly, tubercular posteriorly; skin on belly and proximal posteroventral surfaces of thighs granular; cloacal tubercles and folds absent; pair of enlarged tubercles below cloaca; opening of brood pouch U-shaped with anterior border at level of sacrum. Dentigerous processes of vomers posteromedially inclined, narrowly separated medially, between round choanae, each bearing five teeth; tongue cordiform, shallowly notched posteriorly, free behind for about one fourth of its length; nature of vocal slits unknown.

In preservative, dorsal surface of body and limbs dull gray with faintly darker grayish brown paravertebral marks originating on eyelids, extending posteriorly, coalescing at midlength of body, coalescing posterior to sacrum, then bifurcating and terminating at level of opening of brood pouch. Flanks pale gray above cream below; anterior and posterior surfaces of thighs and ventral surfaces of body and limbs dull cream; no transverse bars hind limbs. Markings on head consisting of dark brown canthal and postorbital regions. Axillary and inguinal regions pale greenish tan.

In life, the dorsum is tan with reddish brown middorsal mark on head and body and transverse bars on forearm, thigh, and shank (Figure 2A). Loreal region and side of head reddish brown; this color extending to point above insertion of forelimb. Anterior and posterior surfaces of thighs gray with scattered small black flecks; mid-flanks tan; groin greenish yellow. Belly and ventral surfaces of limbs pale gray; throat yellow; paracloacal tubercles yellow (Figure 2B). Iris dull bronze with fine black reticulations.

Measurements of holotype in mm are: SVL 45.7, tibia length 23.9, foot length 23.2, head length 16.1, head width 17.1, interorbital distance 7.1, internarial distance 3.3, width of eyelid 4.5, eye–nostril distance 4.1, diameter of eye 4.7, diameter of tympanum 3.5.

Variation.—The juvenile (CORBIDI 11040) has a SVL of 17.3 mm; it is the individual shown as *G. oresbios* (B) in the phylogenetic tree (Figure 1), where the holotype (CORBIDI 11076) is shown as *G. oresbios* (A). The dorsal pattern of the juvenile is identical to that of the holotype but differs by having the belly with black flecks and the ventral surface of thighs and shanks gray with black marks.

Distribution and ecology.—*Gastrotheca oresbios* is known only from two localities at elevations of 3290 m on Abra Barro Negro and at 3119 m in Quintecocha in the northern part of the Cordillera Central in northern Peru (Figure 3). *Gastrotheca dysprosita* occurs at elevations of 3370 and 3440 m on the same slope of Abra Barro Negro (Duellman, 2013) so the two species may occur sympatrically. The holotype of *G. oresbios* was found by day inside a large bromeliad fastened to a rocky outcrop. The general landscape of the type locality consists of extensive pastures for cattle with some scattered rocky outcrops, and small patches of forest from where advertisement calls of *Gastrotheca* were heard. Only *Pristimantis melanogaster* is known to be sympatric with *G. oresbios* at the type locality. At Quintecocha the juvenile (CORBIDI 11040) was perched on herbaceous vegetation by day on a trail in a patch of montane forest. Sympatric anurans in this locality were *Pristimantis corrugatus* and *Rhinella arborescandens*. *Gastrotheca ossilaginis* and *Telmatobius atahualpai* were collected at the same place in November 2003.

Etymology.—The specific name oresbios is a Greek noun meaning living on mountains.

***Gastrotheca spectabilis* sp. nov.**
Gastrotheca sp. E, Duellman 1915, p. 282, Fig. 12.1.
(Figure 4)

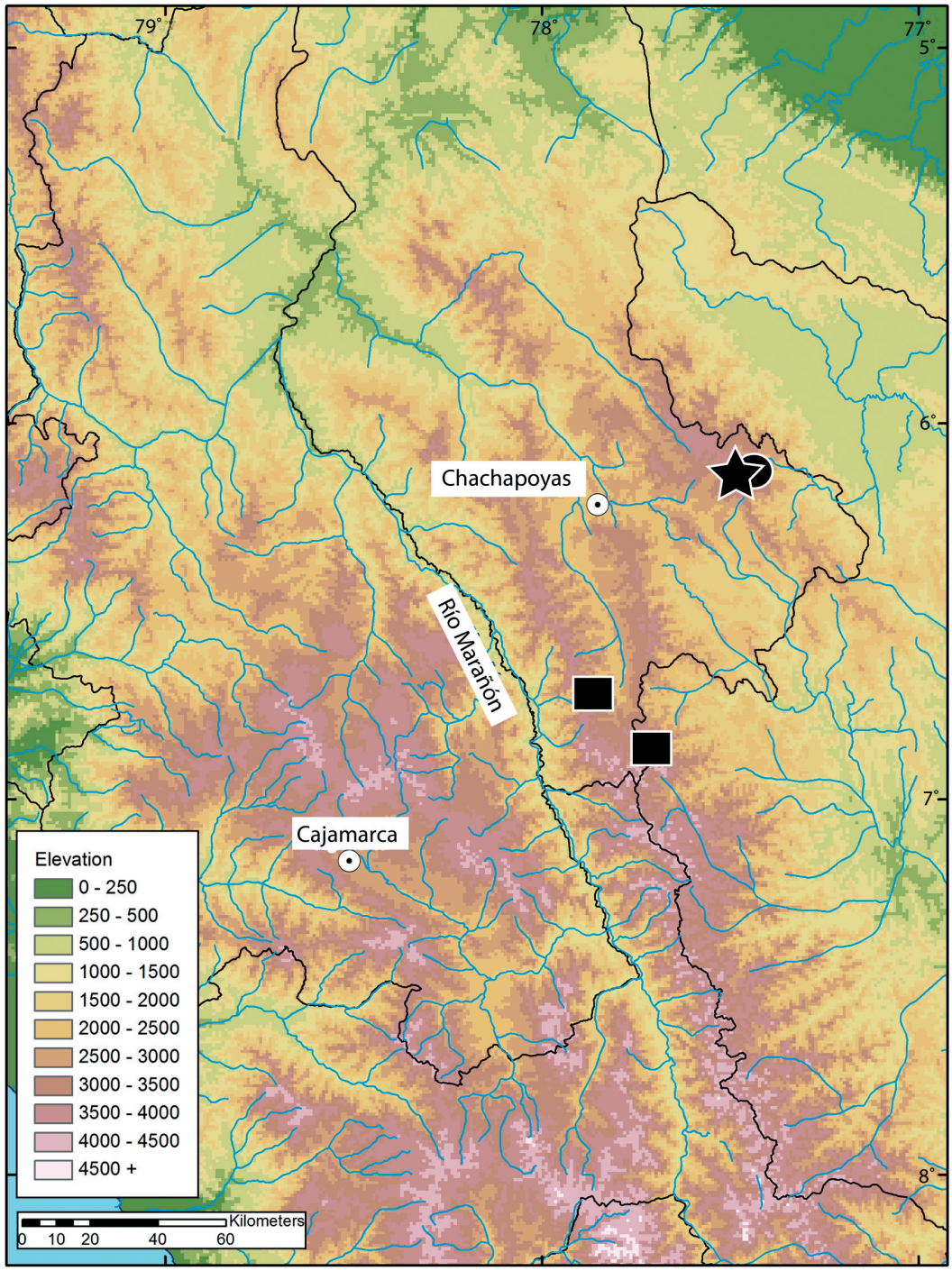

Figure 3. Northern Peru showing localities of known occurrence of three species of *Gastrotheca,* The square is *G. oresbios,* star is *G. spectabilis,* and circle is *G.* sp. D.

Holotype.—CORBIDI 11790. Brooding female, from Hornillo, 6°30'05" S, 77°29'04.9" W, 3308 m, Distrito de Vista Alegre, Provincia Rodríguez de Mendoza, Departamento de Amazonas, Peru, obtained by P. J. Venegas and V. Durán on 31 August 2012.

Paratypes.—CORBIDI 11644, 11753, 11780–81, and KU 342532, all subadults collected with the holotype.

Diagnosis.—No other Andean species of *Gastrotheca* has a color pattern like that of *G. spectabilis*; the tan dorsum with irregular brown spots and middorsal mark and a dark brown venter with cream granules are unique within the genus. Three other species of *Gastrotheca* are known from the vicinity of the type locality of *G. spectabilis.* Of these, *G. phelloderma* differs from *G. spectabilis* by having pustular ridges on the dorsum, an interorbital distance equal to the width of the upper eyelid, and an inner tarsal fold extending the entire length of the tarsus, as opposed to smooth skin on the dorsum, an interorbital distance twice the width of the upper eyelid, and no inner tarsal fold in *G. spectabilis.* The smaller *G. oresbios* differs from *G. spectabilis* by having a granular tympanic annulus and by lacking the pale stripes on the head, and *G. aguaruna* differs by having a green dorsum and flanks, an inner tarsal fold on the distal half of the tarsus, and in interorbital distance about equal to the width of the upper eyelid. Of the other species of *Gastrotheca* in the Andes in northern Peru, *G. galeata* and *G. ossilaginis* differ from *G. spectabilis* by having the skin on the head co-ossified with the underlying dermal elements of the skull; furthermore, in *G. galeata* the head is casqued with flared maxillaries and premaxillaries, and an elevated transverse occipital ridge, and *G. ossilaginis* differs further by being green and lacking pale stripes on the head. In contrast to *G. spectabilis,* five other species (*G. abdita, aratia, lateonota, monticola,* and *peruana*) in northern Peru have distinct inner tarsal folds; in these species the dorsum is tan or green with darker paravertebral marks. The only remaining species of *Gastrotheca* in the northern Cordillera Central, *G. phalarosa,* differs from *G. spectabilis* by having a black venter with white spots, pustular skin on the dorsum, and an interorbital distance about equal to the width of the upper eyelid.

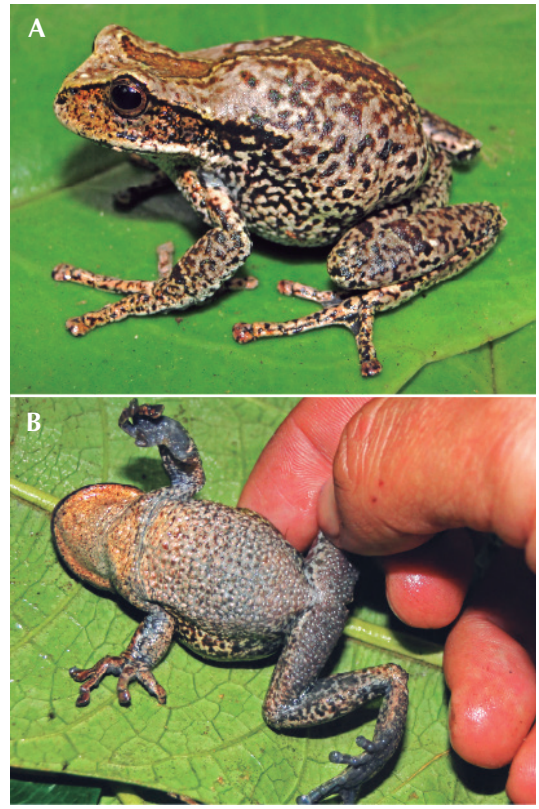

Figure 4. Holotype of *Gastrotheca spectabilis,* CORBIDI 11790, female, 47.2 mm SVL. Photos by Pablo J. Venegas.

Description of holotype.—Adult female; body robust; SVL 47.2 mm; head slightly wider than long; snout acutely rounded in dorsal view, bluntly rounded in profile; canthus rostralis angular in section; loreal region barely concave; lips rounded; top of head flat; interorbital distance 196% width of upper eyelid; internarial

area slightly elevated; nostrils not protuberant, directed laterally at point slightly posterior to anterior margin of lower jaw, below anterior terminus of canthus rostralis; diameter of eye about equal to its distance from nostril; tympanum round, its diameter about half that of eye, separated from the eye by distance twice length of the tympanum; tympanic membrane and annulus distinct, smooth; supratympanic fold moderately heavy, tuberculate, angular in section, extending from posterior corner of orbit to point above insertion of arm, not obscuring tympanum.

Arm robust; ulnar tubercles absent; hand moderately large; fingers unwebbed; discs on fingers round, only slightly wider than digit; diameter of the disc on third finger less than length of tympanum; relative lengths of the fingers I = II < IV < III; subarticular tubercles moderate in size, rounded, none bifid; supernumerary tubercles absent; palmar tubercle inconspicuous; prepollical tubercle ovoid, elevated. Hind limbs moderately robust; tibia length 48.5% SVL; foot length 50.8% SVL; heel lacking enlarged tubercle; inner tarsal fold and outer metatarsal tubercle absent; inner metatarsal tubercle elevated, ovoid, visible from above; toes moderately long; relative lengths of toes I < II < III < V < IV. Toes I–II lacking webbing; basal webbing exists between Toes III and IV and between Toes IV and V; subarticular tubercles small, subconical; supernumerary tubercles, small, rounded, present only on proximal segments of toes.

Skin on dorsum and flanks smooth with minute tubercles on supratympanic fold and on side of head posterior to eye; skin on belly and proximal posteroventral surfaces of thighs granular; cloacal tubercles and folds absent; opening of brood pouch U-shaped with anterior border at level of sacrum. Dentigerous processes of vomers posteromedially inclined, narrowly separated medially, between round choanae, bearing six and seven teeth; tongue cordiform, shallowly notched posteriorly, free behind for about one fourth of its length; nature of vocal slits unknown.

In preservative, dorsum dull grayish brown with brown middorsal mark narrowly outlined with black; middorsal mark originating on eyelids, extending posteriorly, bifurcating at midlength of body, coalescing posterior to sacrum, terminating at opening of brood pouch. Many irregularly shaped, dark brown spots lateral to midorsal mark; flanks pale gray with many irregularly shaped black spots; narrow dark brown transverse bars on hind limbs—four on thigh, three on shanks, two on foot; those on thighs extending onto posterior surfaces; ventral surfaces of body and limbs dull gray. Markings on head consisting of distinct grayish white labial stripe continuous with narrow rostral stripe bifurcating into narrow canthal stripe extending onto edge of eyelid; loreal region and side of head posterior to eye dark brown.

In life, dorsum of head and body tan (Figure 4A). The broad middorsal mark on the body is reddish brown; it is narrowly outlined with black, which in turn is bordered by creamy tan. Lateral to the middorsal mark are irregular dark brown spots; on the dull cream flanks these spots become smaller and black. The dorsal surfaces of the limbs are dull brown with darker brown irregular spots and on the hind limbs one transverse bar on the thigh and another on the shank. The posterior surfaces of the thighs are dark brown with cream granules. The loreal and tympanic regions on the head are reddish brown with small black flecks. The diffuse labial stripe and narrow rostral and canthal stripes are dull cream. The throat is dull grayish brown; the belly and distal ventral surfaces of the thighs are dark brown with cream granules, whereas the proximal surfaces of the thighs are gray (Figure 4B). The iris is brown with orange flecks.

Measurements of holotype (in mm) are: SVL 47.2, tibia length 22.9, foot length 24.0, head length 16.2, head width 17.7, interorbital distance 8.0, internarial distance 3.9, width of eyelid 4.1, eye–nostril distance 5.6, diameter of eye 5.4, diameter of tympanum 3.0.

Variation.—The five subadult paratypes have SVLs of 22.3–34.2 ($\bar{x}$ = 28.9) mm. They are like the holotype in structural features and coloration.

Distribution and ecology.—*Gastrotheca spectabilis* is known only from type locality at an elevation of 3308 m in northern Departamento de Amazonas, Peru (Figure 3). The holotype was collected at night walking on moss near the edge of a patch of montane forest on a slope covered by páramo. The subadult paratypes were collected by day inside bromeliads 2–4 m above the ground in the same patch of montane forest. No other anurans were found in the same patch of forest; however, several individuals of *Pristimantis* sp., *G. aguaruna,* and *G. phalarosa* were collected at the surrounding páramo.

Etymology.—The specific name *spectabilis* is a Latin adjective meaning showy. The name refers to the unusual dorsal color pattern.

Unnamed Species *Gastrotheca* species D. (Figure 5)

This species is represented by two small juveniles, CORBIDI 11664–65, having SVLs of 15.5 and 16.8 mm, respectively. Both were collected in Quebrada Salas, 2575 m, Distrito Vista Alegre, Provincia Rodríguez de Mendosa, Departamento Amazonas, Peru (Figure 3). Both specimens were collected by night (21:00 h) on leaves 1.5 m above the ground near a trail in primary montane forest. Sympatric anurans were *Hypodactylus* sp., *Pristimantis corrugatus, P. schultei,* and *P.* sp. Advertisement calls of *Gastrotheca* were heard from the canopy of forest at the same place.

The skin on the dorsum is smooth with a few minute tubercles. The dorsum is pale brown with slightly darker markings consisting of an interorbital bar connected to paravertebral marks that extend to the sacrum and transverse bars on the thigh and two on the shank (Figure 5A). The belly is dark grayish brown. The distinguishing color markings are a black inguinal region with large cream spots and dull red anterior and ventral surfaces of the thigh and shank (Figure 5B). The iris is dull bronze with fine black reticulations.

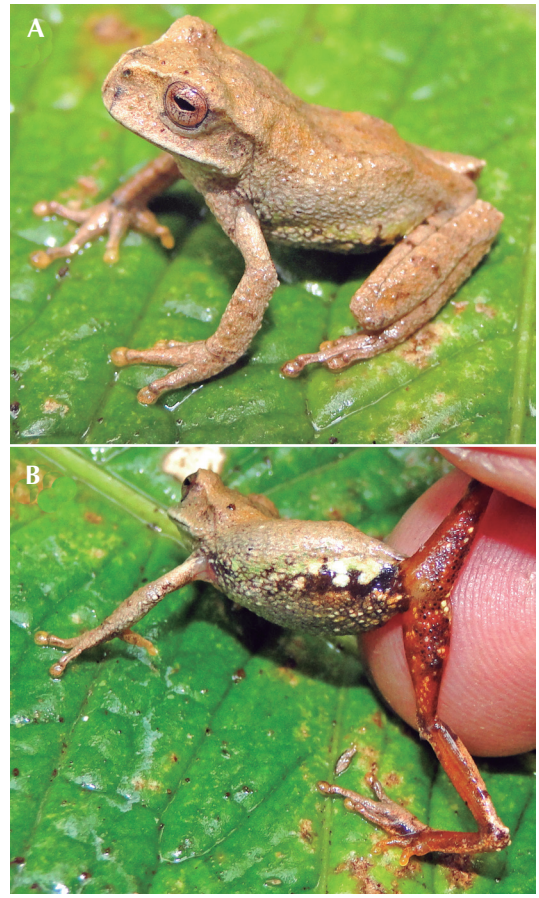

Figure 5. Juvenile of *Gastrotheca* species D, CORBIDI 11655, 16.8 mm SVL. Photos by Pablo J. Venegas.

Discussion

The South American tectonic plate separated from Africa in the Early to Middle Cretaceous and arced northwestward to encounter the Nazca Plate, the subduction of which was largely responsible for the orogenic events resulting in

the rise of the Andes. There is a major structural deflection of the Andes in what is now southern Ecuador and northern Peru; this is the Huancabamba Deflection, physiographically referred to as the Huancabamba Depression. Significant differences exist in the origins of the Andes north of the depression and those to the south of the depression (Gregory-Wodzicki 2000). As summarized by Duellman (1999), the Huancabamba Depression is a complex system of relatively low mountain ranges separated by low basins. In the depression the major cordilleras of the Ecuadorian Andes and the Peruvian Andes terminate or are fragmented into isolated ranges usually no more than 3500 m high and separated by valleys mostly between 1000 and 2000 m above sea level. The Cordillera Colán is one of those isolated highlands with crests above 3500 m. Within the depression, the valleys mostly are covered with dry scrub forest consisting mainly of legumes and cacti. Dramatically different vegetation is found on windward and leeward slopes of north–south mountain ranges, such as the Cordillera de Huancabamba. On the leeward slopes of this range, scrub forest extends nearly to 3000 m. On the windward slopes scrub forest extends to about 1700 m, above which humid mountain forest prevails to about 3000 m; above this elevation there is elfin forest with dwarfed trees, a great amount of moss, and many terrestrial and arboreal bromeliads (Duellman and Wild 1993). Elevations above 3000 m in the northern Cordillera Central are characterized by regions of grassland (puna); the puna dominated by bunch grass (*Stipa*) with small bushes (principally *Baccharis*) and terrestrial bromeliads and with deep mosses in some places.

Frogs of the genus *Gastrotheca* in the high Andes (mostly above 2500 m) make up the subgenera *Duellmania* (14 species) and *Gastrotheca* (36 species including two unnamed ones). The distributions of these 50 species range from northern Colombia to northwestern Argentina. The enigmatic *Gastrotheca galeata* in the Huancabamba Depression was placed in its own subgenus, *Edaphotheca,* by Duellman (2015). No species of high-Andean *Gastrotheca* cross the Huancabamba Depression. Two other species, *G. testudinea* and *G. weinlandii,* occur at elevations mostly below 2500 m in the cloud forests on the eastern slopes of the Cordillera Oriental in Ecuador and the Cordillera Central in Peru. The new species from southern Ecuador and northern Peru necessitate a revision of the patterns of distribution of *Gastrotheca* provided by Duellman and Venegas (2005).

We now recognize eight species of *Gastrotheca* in southern Ecuador; of these, five occur in the southern Cordillera Oriental; of the 14 species recorded from northern Peru, nine occur in the northern Cordillera Central (Table 1). Among the Ecuadorian species, *G. pseustes* and *G.* sp. C inhabit páramo; the former descends into subparamo and montane forests. *Gastrotheca psychrophila* inhabits terrestrial bromeliads in subpáramo; the single specimen of *Gastrotheca* "Amaluza" was found in humid montane forest. The other species (*G.* sp. A, *G.* sp. B, *G. litonedis, G. lojana*) have restricted distributions in Andean shrub and montane forests; *G.* sp. A also inhabits pasturelands, and *G. lojana* frequents agaves in dry farmland (Carvajal-Endara *et al.* 2017). Of the Ecuadorian species, *G. pyschrophila, G.* sp. C, and "Amalusa" are not sympatric with any other species of the genus. However, *G. psychrophila* and "Amalusa" are known from single localities, and *G.* sp. C is known from only two localities. In contrast, the widely distributed *G. pseustes* is sympatric with *G.* sp. A and *G. lojana* throughout most of their ranges and also occurs sympatrically with *G. litonedis* and *G.* sp. B (Carval-Endara *et al.,* 2017).

Three species of *Gastrotheca* are known from the low to moderate elevations in the Huancabamba Depression, where *G. galeata* and *G. lateonota* are endemic but allopatric. The third species, *G. monticola,* also inhabits the extreme northern part of the Cordillera Occidental and the northern part of the Cordillera Central. Two species, *G. aratia* and *G. peruana* occur only in the Cordillera Occidental, and *G.*

Table 1. Distribution of *Gastrotheca* in the Andes of Southern Ecuador and Northern Peru.

Species	Elevation (m)	Distribution
	ECUADOR	
G. species A	2407–3172	Southern Cordillera Occidental and southern Cordillera Oriental
*G. "*Amaluza"	2002	Southern Cordillera Oriental
G. species B	2177–3018	Loja Basin and surrounding slopes
G. litonedis	2750–2854	Eastern slopes of southern Cordillera Occidental
G. lojana	1682–3018	Andean Basins in provincias Azuay, El Oro, and Loja
G. pseustes	2200–4080	Southern Cordillera Occidental and southern Cordillera Oriental
G. psychrophila	1750–2850	Southern Cordillera Oriental
G. species C	3205–3406	Southern Cordillera Oriental
	PERU	
G. abdita	2970–3330	Cordillera Colán
G. aguaruna	2360–3308	Northern Cordillera Central
G. aratia	2560–2875	Northern Cordillera Occidental
G. dysprosita	3320–3440	Northern Cordillera Central
G. galeata	1720–2130	Huancabamba Depression
G. lateonota	2770	Huancabamba Depression
G. monticola	2800–3480	Huancabamba Depression and northern Cordillera Occidental and northern Cordillera Central
G. oresbios	3290–3308	Northern Cordillera Central
G. ossilaginis	3000–3100	Northern Cordillera Central
G. peruana	2200–3520	Cordillera Occidental
G. phalarosa	3119–3435	Northern Cordillera Central
G. phelloderma	3308–3400	Northern Cordillera Central
G. spectabilis	3308	Northern Cordillera Central
G. species D	2575	Northern Cordillera Central

abdita is endemic to the Cordillera Cólan in the Huancabamba Depression. Eight species are endemic to elevations of 2360–3435 m in the Cordillera Central. None of the species of *Gastrotheca* in the high Andes in Ecuador and Peru cross the Huancabamba Depression, which obviously is a barrier to latitudinal dispersal in the Andes. However, one species (*G. pseustes*) of the southern subgenus *Gastrotheca* occurs in Ecuador south of the equator, and two species (*G. dysprosita* and *G. monticola*) of the northern subgenus *Duellmania* are known only from northern Peru. According to the timetree in Duellman (2015), the two subgenera split in the

mid-Miocene, a time when the Andes were lower than they are now (Gregory-Wodzicki, 2000), whereas the species in both subgenera differentiated from one another in the mid-Late Pliocene. Thus, as the cordilleras attained higher elevations in the Pliocene and Pleistocene, the ranges of proto-species of *Gastrotheca* (and other genera) became isolated and species differentiated allopatrically.

The anuran fauna is rich and diverse in the Andes of southern Ecuador and northern Peru and the intervening Huancabamba Depression. This is especially true of strabomantid (Craugastorid) frogs (Duellman and Lehr 2009, Lynch 1979). Ten species of strabomantids are known from elevations of 2400–3370 m in the northern part of the Cordillera Central (2 *Hypodactyus,* 1 *Noblella,* and 7 *Pristimantis*); nine of these are endemic to the region. Undoubtedly, the Cordillera Central in northern Peru contains many more species of anurans awaiting discovery, description, and phylogenetic placement. The high elevations of this cordillera have one of, if not, the richest anuran fauna in any high-elevation region in the Andes.

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Appendix I. *Comparative material examined.*

Gastrotheca abdita. PERU: *Amazonas:* Cordillera Colán, 2970-3330 m, E La Peca, KU 96833 (holotype), 196834–35.

Gastrotheca aguaruna. PERU: *Amazonas:* Molinapampa, 2400 m, KU 212022 (holotype). 212023–28, 212030–31.

Gastrotheca aratia. PERU: *Cajamarca:* Cutervo: KU 212060, 212062–66, 8 km NW Cutervo, KU 212067 (holotype).

Gastrotheca dysprosita. PERU: *Amazonas:* west slope Abra Barro Negro, 3440 m, KU 212078 (holotype).

Gastrotheca excubitor, PERU: *Cusco:* N slope Abra Acjanaco, 3270–3520 m, KU 139193–201.

Gastrotheca galeata. PERU: *Piura;* 15 km (by road) E Canchaque, 1740–1890 m, KU 174361–63, 181700, 219765–66.

Gastrotheca griswoldi. PERU: *Junín:* Pacha, 9.5 km NW La Oroya, KU 139140–61.

Gastrotheca lateonota. PERU: *Piura:* El Tambo, 31.5 km E Canchaque, 2180 m, KU 181730–39.

Gastrotheca litonedis. ECUADOR: *Azuay:* 10 km NE Girón, 2750 m, KU 202690; (holotype); San Fernando, Laguna de Busa, 22834 m, KU 335388–89.

Gastrotheca lojana. ECUADOR: *Azuay:* Girón, 2310 m, KU 138401–03. *Loja:* Loja, 2150 m, KU 120673–74; 5 km N Loja, 2150 m. KU 138235–36; Saraguro, 2412 m, KU 138404–09; 2 km SSW Saraguro, 2569 m, KU 178482–95.

Gastrotheca monticola. PERU: *Piura:* Huancabamba, 1960 m, KU 219771; 1.8 km N Huancabamba, 1980 m, KU 219767–68; 4 km N Huancabamba, 1900 m, KU 219769–70.

Gastrotheca nebulanastes. PERU: *Cusco:* Buenos Aires, 2280 m, KU 123208–09, 123210 (holotype), 123211–17.

Gastrotheca ochoai. PERU: *Cusco:* Chilca, 10 km N Ollantaytambo, 2760 m, KU 138628–65.

Gastrotheca ossilaginis. PERU: *San Martín:* Lago Quindecocha, 3100 M, KU 117293.

Gastrotheca pacchamama. PERU: *Ayacucho:* Abra Tapuna, 7 km N Mahuayara, 3710 m, KU 163279–99.

Gastrotheca pachachacae. PERU: *Apurimac:* Ccerabamba-Andina Chinchay cloud forest, 30050 m, MUSM 18489–92.

Gastrotheca peruana. PERU: *Cajamarca:* 8 km S Cajamarca, 3050 m, KU 212070; Cutervo, 2620 m, KU 212055–57, 212060–66.

Gastrotheca phalarosa. PERU: *San Martín:* Esperanza, 3435 m, MUSM 19462, 19487 (holotype).

Gastrotheca phelloderma. PERU: *Amazonas:* Hornillo, 3308 m, CORBIDI 11778. *San Martín:* 24 km NE Pataz, 3400 m. KU 331039–40.

Gastrotheca pseustes. ECUADOR: Saraguro, 2500 m, KU 141571, 142609–13, 148563–67.

Gastrotheca psychrophila. ECUADOR: *Loja-Zamora-Chinchipe:* 13–15 km E Loja, 2770–2850 m, KU 120760 (holotype), 120761–62, 141586, 142631–37, 148599, 164233–34.

Gastrotheca rebeccae. PERU: *Ayacucho:* Ccarpa, below Tambo on Valle de Apurimac trail, 2470 m. LU 196806–11.

Gastrotheca sp. A. ECUADOR: *Azuay:* Cuenca, 2600 m, KU 120672, 120683–84, 120709–10, 120718–19, 120721–22; Laguna de Zurucuchu, 3200 m, KU 203441.

Gastrotheca sp. B. ECUADOR: *Loja:* 5.2 km W Loja, 2310 m, KU 202688; 5.5 km W Loja, 2330 m, KU 142603–08, 148549–51.

Gastrotheca sp. D. ECUADOR: *Loja:* Laguna de Jimbura, Parque Nacional Yacuri, Amaluza, 3406 m, KU 335390.

Appendix II. *Specimens used in phylogenetic analysis with associated GenBank numbers.*

Species	Voucher Number	ND1	16s	POMC	RAG1
Gastrotheca oresbios	CORBIDI 11040	KJ489508	KJ489460	–	KJ489507
Gastrotheca oresbios	CORBIDI 11076	KJ489509	KJ489461	KJ489552	KJ489588
Gastrotheca spectabilis	CORBIDI 11790	KJ489513	KJ489464	KJ489554	KJ489592