



Redescription of *Gastrotheca dissimilis* (Anura: Hemiphractidae) and description of a new species of *Gastrotheca* from the Cordillera Oriental, northeastern Peru

DANIEL RODRÍGUEZ¹, JUAN C. CUSI¹ & RUDOLF VON MAY²

¹ Universidad Nacional Mayor de San Marcos, Museo de Historia Natural, Av. Arenales 1256, Jesús María, Lima, Peru

² California State University Channel Islands, Biology Program, 1 University Drive, Camarillo, CA 93012, USA

Corresponding author: RUDOLF VON MAY, e-mail: rudolf.vonmay@csuci.edu

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Abstract. *Gastrotheca peruana dissimilis* VELLARD, 1957 was considered for a long time as a subspecies of *G. peruana* BOULENGER, 1900, but recent studies indicated that it should be recognized at the species level. Here, we redescribe *Gastrotheca dissimilis* and recognize it as a full species based on a recent taxonomic revision of *G. peruana* sensu lato using independent lines of evidence (phylogenetic analyses, meristic and external morphological traits). *Gastrotheca dissimilis* can be differentiated from *G. peruana* by having a tympanum separated from eye by distance larger than the tympanum diameter, dorsal skin shagreen with abundant scattered pustules and the presence of prominent longitudinal pustular ridges, and the iris (in life) reddish copper or metallic red with fine black reticulations. Furthermore, we describe a new species of *Gastrotheca* present in the humid grasslands of the Alto Mayo Protected Forest, Departamento San Martín, northeastern Peru. It differs from all other species by having the snout acutely rounded in dorsal view and truncate in profile, relative lengths of the fingers I = II < IV < III, webbing formula I2⁺–2II2⁺–3III3–3IV3–2⁺V, shagreen dorsum, and denticulate processes of the vomers in transverse row narrowly separated between the choanae.

Key words. Amphibia, marsupial frogs, new species, phylogenetic relationships, taxonomy.

Introduction

The type species of *Gastrotheca* FITZINGER, 1843 is *Hyla marsupiatata* DUMÉRILO & BIBRON, 1841 (FITZINGER 1843). GÜNTHER (1858) proposed to change the generic name to *Nototrema*, contending that FITZINGER (1843) appeared to have believed in the existence of a pouch on the belly. The name *Gastrotheca* was derived and used by old anatomists to refer to the brain-pan. GÜNTHER (1858) disagreed with FITZINGER (1843) and did not accept the name *Gastrotheca*. As a result, *Nototrema* was commonly used for marsupial frogs until MIRANDA-RIBEIRO (1920) resurrected the genus *Gastrotheca*. In the 19th century, three species of marsupial frogs were recognized in the genus *Nototrema* in the Andes of western South America: *N. bolivianum*, *N. peruanum* and *N. marsupiatum* (DUELLMAN & FRITTS 1972).

Recognition of species of marsupial frogs, genus *Gastrotheca*, in the Cordillera Occidental from northern Peru began in the 19th century. BOULENGER (1900) described the first species of marsupial frog, *Nototrema peruanum* (*Gastrotheca peruana*), based on five syntypes (BMNH 1900.6.20-46–50) collected from “Carao” (= Caraz), De-

partamento de Ancash, Peru. Later, VELLARD (1957) examined a set of specimens of *Gastrotheca peruana* and recognized three subspecies (*G. peruana peruana*, *G. peruana dissimilis* and *G. peruana junensis*), with the name *G. peruana dissimilis* referring to populations in Departamento de La Libertad. MORALES et al. (1990) catalogued the type series of *G. peruana dissimilis* and designated as lectotype the specimen with code MUSM 7740. RODRÍGUEZ et al. (2019), in a phylogenetic analysis of *G. peruana*, recognized two non-sister clades and presented indication for new candidate species. One of these clades includes a specimen collected at the type locality of *G. peruana dissimilis*. RODRÍGUEZ (2022) reviewed the taxonomic status of *G. peruana* sensu lato using morphological data, providing support to the hypothesis that *G. peruana* includes two lineages based on the mitochondrial 16S rRNA gene. Comparison of these specimens with material deposited in the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (MUSM) as well as with literature data, confirmed that *G. dissimilis* represents a lineage at the species-level. Differentiation of the species *G. dissimilis* from other closely related species is important for various reasons. For example, the supposed geographic range

of *G. dissimilis* (RODRÍGUEZ et al. 2019, RODRÍGUEZ 2022) includes regions with mineral concessions (AGUILAR et al. 2012) and given that mining activities can negatively impact amphibian populations, using up-to-date taxonomic information will allow the correct identification of the species in the field and provide valuable data for wildlife monitoring programmes near mining areas. Additionally, conservation actions for *G. dissimilis* are often dismissed because the species is not currently listed in the IUCN Red List (IUCN 2026). A redescription will further support the potential inclusion of *G. dissimilis* on the IUCN Red List, which in turn could help the government prioritize conservation efforts. In light of new information (DNA and morphometric data), and with the aim of stabilising the taxonomic identity of the lectotype, we also provide a refined diagnosis for *G. dissimilis*.

More recently, fieldwork in the Andes of northern Peru resulted in the discovery and description of four more species of *Gastrotheca*: *G. gemma* VENEGAS, GARCÍA AYACHI, ECHEVARRÍA, PALUH, CHÁVEZ-ARRIBASPLATA, MARCHELIE & CATENAZZI 2021; *G. flavodactyla* ECHEVARRÍA, PALUH, GARCÍA AYACHI, VENEGAS, CATENAZZI, PRADEL & CASTROVIEJO-FISHER, 2022; *G. trachyplevra* ECHEVARRÍA, PALUH, GARCÍA AYACHI, VENEGAS, CATENAZZI, PRADEL & CASTROVIEJO-FISHER, 2022; and *G. mittaliiti* VENEGAS, ECHEVARRÍA, GARCÍA-AYACHI, WONG, CHÁVEZ, GARCÍA-BRAVO, CATENAZZI & CASTROVIEJO-FISHER 2026. Additionally, the status of two other nominal taxa of *Gastrotheca* from northern Peru, *G. splendens* and *G. monticola*, was clarified by KÖHLER et al. (2024). In 2014, JUAN C. CUSI and colleagues conducted a herpetological survey in the Alto Mayo Protected Forest, Departamento de San Martín, and found several species of amphibians and reptiles (CUSI et al. 2015, 2017). One of these species is a *Gastrotheca* collected in a humid grassland, which exhibits morphological differences to other species in the genus.

Here, we use independent lines of evidence, including phylogenetic analyses and external morphological traits, to characterize and diagnose *G. dissimilis* and to describe a new species of *Gastrotheca*.

Materials and methods

Field expeditions in 2012 and 2014 conducted in the Departamentos La Libertad, Cajamarca, and San Martín, all located in northern Peru, resulted in the collection of eleven specimens of *Gastrotheca*. Geographical coordinates were obtained by Garmin GPS receiver using datum WGS84. We euthanized voucher specimens with 20% benzocaine gel on the skin, and after extraction of a tissue sample, fixed them in 10% formalin for 24 hours, and stored them permanently in 70% ethanol. Specimens were deposited in the herpetological collection of the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (MUSM), Lima, Peru. Sex was determined by the presence of brood pouches or by examination of gonads. Additional specimens examined are listed in Appendix I.

The morphological characters and measurements are those used by DUELLMAN & FRITTS (1972), DUELLMAN & PYLES (1980), DUELLMAN & HILLIS (1987), LEHR & CATENAZZI (2011) and DUELLMAN (2015). All measurements are in millimeters and were taken with digital calipers (Igagin) under a microscope (Nikon SMZ800) and rounded to the nearest 0.1 mm; these are: snout–vent length (SVL), tibia length (TL), 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), orbit–jaw distance (OJ), nostril–jaw distance (NJ), tympanum diameter (TD), thumb length (FFL), finger III length (TFL) and width of disc on finger III (TFD). Webbing formula was determined by the method proposed by SAVAGE & HEYER (1967), as modified by MYERS & DUELLMAN (1982), and CISNEROS-HEREDIA & MCDIARMID (2007).

To carry out a molecular phylogenetic analysis, we used DNA sequences from a fragment of the 16S rRNA mitochondrial gene (16S) of a representative set of *Gastrotheca* samples obtained from GenBank and from specimens collected during field expeditions in northern Peru as already used by RODRÍGUEZ et al. (2019). GenBank accession numbers are provided in Supplementary document S1. Our analysis included sequences from four recently described species, *G. gemma*, *G. flavodactyla*, *G. mittaliiti*, and *G. trachyplevra*, as well as several candidate species identified in recent studies (VENEGAS et al. 2021, 2026, ECHEVARRÍA et al. 2022). We also note that one specimen (CORBIDI 862) originally identified as *G. abdita* with the associated GenBank number KJ489463 represents *Gastrotheca* sp. J (VENEGAS et al. 2021, ECHEVARRÍA et al. 2022). The GenBank number MH756008 is designated for the holotype of the new species described below (originally listed as *Gastrotheca* sp. 1 in RODRÍGUEZ et al. 2019). We used Geneious Prime 2025.2.2 (<https://www.geneious.com>) to align nucleotide (consensus) sequences with the default settings in the MUSCLE algorithm (EDGAR 2004). We used IQ-TREE (TRIFINOPOULOS et al. 2016) to perform a Maximum Likelihood (ML) analysis to infer a phylogeny of the study species. The ML analysis setting included the ultrafast bootstrap method, with 10000 bootstrap alignments. *Hemiphractus proboscideus* was used to root the tree. We used the R package ‘APE’ (Paradis et al. 2004) to estimate uncorrected pairwise distances among 16S sequences, to infer the degree of genetic divergence among focal taxa.

Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The LSID (Life

Science Identifier) for this publication is: urn:lsid:zoobank.org:pub: C3F8FE7F-DD06-482D-AFAD-DD5CA12C1103. The electronic edition of this work was published in a journal with an ISSN and has been archived and is available from the following digital repositories: www.zenodo.org and www.salamandra-journal.com.

Results

Molecular phylogenetic analysis

The ML phylogenetic tree (Fig. 1, Supplementary document S2) placed the focal taxa as part of the *Gastrotheca marsupiat* species group sensu CASTROVIEJO-FISHER et al. (2015) and ECHEVARRÍA et al. (2022). This phylogeny suggests that *G. dissimilis* is an independent evolutionary lineage that is closely related to *G. peruana* and *G. aratia*, which are sister to one another. These three species belong to a clade that currently contains five other species (*G. phelloderma*, *G. pseustes*, *G. turnerorum*, *G. aguaruna*, and *G. yacuri*). Additionally, the new species described here belongs to another clade that currently contains eight other species (*G. flavodactyla*, *G. oresbios*, *G. gemma*, *G. spectabilis*, *G. trachyplevra*, *G. mitaliiti*, *G. psychrophila*, *G. stictopleura*).

Uncorrected 16S pairwise distances suggest that there is relatively low genetic divergence between *G. dissimilis* and *G. peruana* (average 2.5%), between *G. dissimilis* and *G. aratia* (average 1.5%), and between *G. peruana* and *G. aratia* (average 1.6%). A complete table of pairwise distances is provided in Supplementary document S3.

Taxonomy

In the following, we present a redescription of *Gastrotheca dissimilis* and the description of a new species of *Gastrotheca*.

Gastrotheca dissimilis

(Figs 2, 3)

Gastrotheca peruana dissimilis – VELLARD (1957:30); Syntypes: Museo Javier Prado “MJP” 245 (47 specimens) from Huamachuco a 3650 m, en las orillas del río Condebamba afluente del Marañón, Departamento La Libertad, Perú; W. WEYRAUCH collector.

Gastrotheca peruana dissimilis – MORALES et al. (1990:5); lectotype designation (NP = Batrac. 245; NN = MHNSM 7740).

Gastrotheca dissimilis – RODRÍGUEZ et al. (2019: 463).

Lectotype: MUSM 7740, male, from Huamachuco, a 3,650 m a.s.l., en las orillas del río Condebamba afluente del Marañón, Departamento La Libertad, Perú, collected by W. WEYRAUCH.

Paralectotypes: Forty-six specimens (MHNSM 7700–7739, 7741–7746), from Huamachuco a 3650 m a.s.l., en las orillas del río Condebamba afluente del Marañón. Of these,

four are sub-adult females (MHNSM 7702, MHNSM 7707, MHNSM 7738, MHNSM 7741) and the rest are juveniles; collected by W. WEYRAUCH (assigned as paralectotypes by MORALES et al. 1990).

Additional referred material: MUSM 32123, an adult female, from Distrito Huamachuco, 7°53'52.95" S, 78°7'0.80" W, 3294 m, Provincia Sánchez Carrión, Departamento de La Libertad, collected by A. TICONA on 07 march 2012; MUSM 9813, an adult male, from Distrito Huamachuco, 7°56'24.768" S, 78°02'13.612" W, 3997 m, Provincia Sánchez Carrión, Departamento La Libertad, collected by N. CISNEROS on 1 February 1970; MUSM 32773, an adult female, from Distrito Hualgayoc, 6°43'53.02" S, 78°38'23.22" W, 3867 m, Provincia Hualgayoc, Departamento Cajamarca, collected by CARLOS DIAZ on 10 April 2014; MUSM 21973, an adult female from Distrito Quiruvilca, 7°59'10.67" S, 78°16'35.72" W, 4202 m, Provincia Santiago de Chuco, Departamento La Libertad, collected by JOSÉ PÉREZ on 1 October 2002; MUSM 27307, an adult female from Distrito Sorochuco, 6°58'40.89" S, 78°18'28.24" W, 3867 m, Provincia Celendín, Departamento Cajamarca, collected by CLAUDIA TORRES on 19 March 2008; MUSM 21970, an adult male, from Distrito Quiruvilca, 7°56'34.06" S, 78°16'41.81" W, 3776 m, Provincia Santiago de Chuco, Departamento La Libertad, collected by JUANA SUAREZ on 1 February 2004; MUSM 36678, an adult male, from Distrito Hualgayoc, Provincia Hualgayoc, Departamento Cajamarca, collected by JUAN C. CUSI on 08 July 2017; MUSM 26164, an adult male, from subcuenca Unigon, 6°57'53.29" S, 78°18'43.19" W, 3668 m, Provincia Celendín, Departamento Cajamarca, collected by JUANA SUAREZ on 21 September 2006; MUSM 34753, an adult female, from quebrada Honda, 6°57'20.50" S, 78°28'57.78" W, 3950 m, Distrito Cajamarca, Provincia Cajamarca, Departamento Cajamarca, collected by FRANK HUARI on 20 May 2016.

Diagnosis: A medium-sized species of *Gastrotheca*, with adult male SVL 33.5–51.4 mm (n = 5) and adult female SVL 33.7–52.5 mm (n = 9), with (1) TL less than 52% SVL, longer than foot; FL less than 46% SVL; (2) IOD larger than EW; (3) skin on dorsum shagreen with abundant scattered pustules and the presence of prominent longitudinal pustular ridges, not co-ossified with skull, lacking transverse ridges; (4) supraciliary processes are absent; (5) heel lacking calcar or tubercle; (6) tympanum oval or round, higher than wide, tympanic annulus distinct smooth or granular; (7) fingers I and II equal in length, or finger I slightly shorter than finger II, with discs slightly wider than digits; (8) fingers unwebbed; (9) the foot is one half webbed; (10) in life, dorsum green, brown or dark brown with dark green, brown or dark brown paravertebral markings extending from the eyelids to the sacral region (usually narrowly edged with black); (11) in life, head markings consisting of a green, brown or black canthal stripe and lacking labial stripe or bars; (12) dorsolateral stripe absent; (13) in life, flanks brown with irregularly shaped dark brown blotch from posterior corner of eye across tympanum to

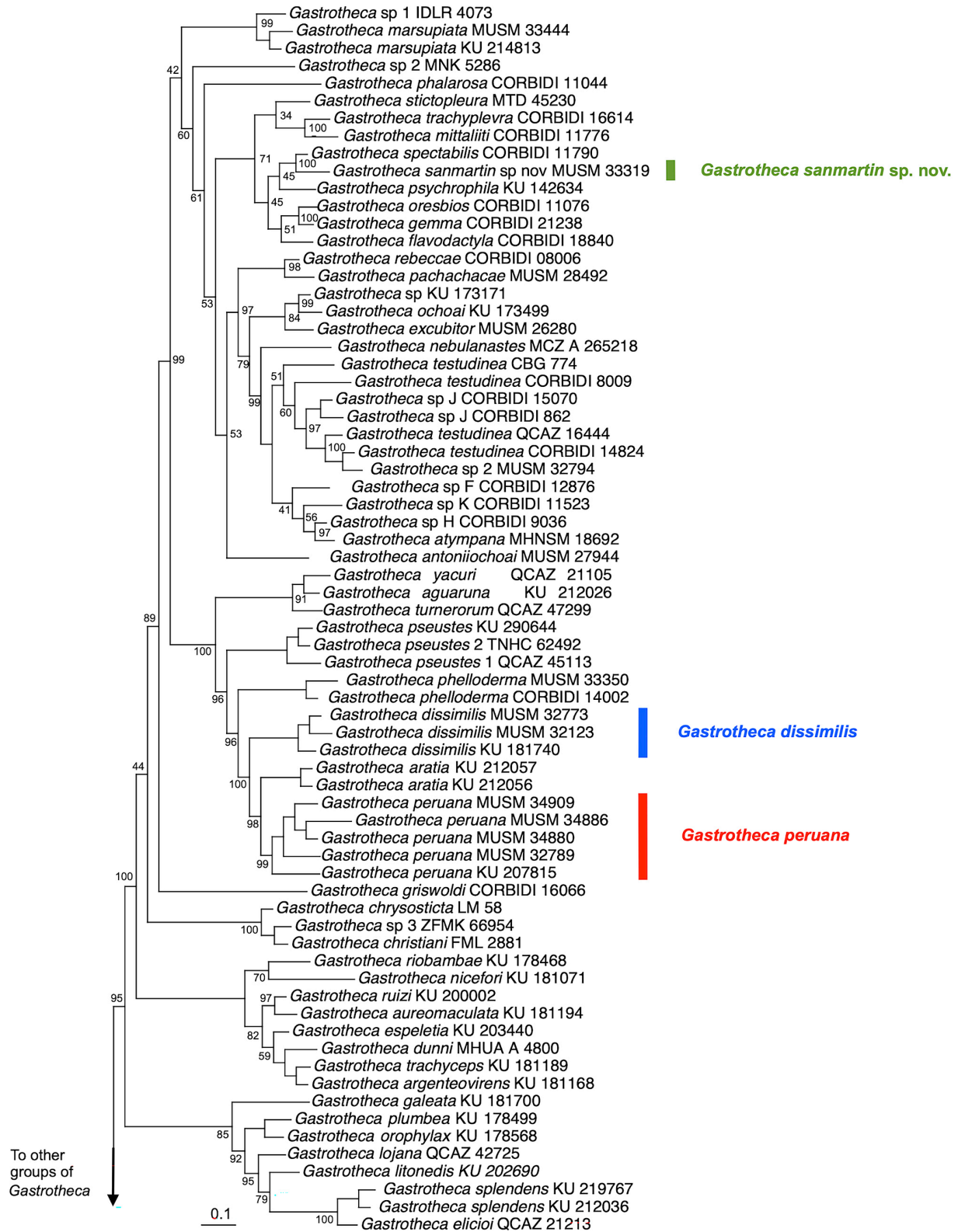


Figure 1. Maximum likelihood (ML) phylogeny of species in the *Gastrotheca marsupiata* species group, based on 524 bp of mitochondrial (16S) sequences. ML values are indicated at each node. *Gastrotheca dissimilis* and *G. peruana* are indicated with a blue and red bar, respectively, and the new species is indicated with a green bar. A complete tree including other species groups of *Gastrotheca* is provided in Supplementary document S2.

upper half of middle of flank, cloaca, anterior and posterior surfaces of thighs green, brown or dark brown lacking dark markings; (14) in life, gular region, throat, ventral surface of limbs and belly cream with or without dark spots; (15) in life, the iris is reddish copper or metallic red with fine black reticulations.

Phylogenetically, according to our results, *G. dissimilis* is most closely related to *G. aratia*, *G. peruana*, *G. phelloderma*, *G. pseustes*, *G. turnerorum*, *G. aguaruna*, and *G. yacuri*. Morphologically, *G. dissimilis* differs from these species (conditions in parentheses) by having a tibia length greater than foot length (tibia length about same length as foot in *G. aratia* and *G. aguaruna*, tibia length slightly shorter than foot in *G. phelloderma* and *G. turnerorum*, tibia length barely longer than foot length in *G. pseustes*); interorbital distance larger than the width of the upper eyelid (shorter in *G. aratia*, about equal in *G. aguaruna*); internarial area flat (slightly concave in *G. phelloderma*); diameter of eye greater than eye–nostril distance (about equal in *G. pseustes*); tympanum separated from eye by distance larger than the tympanum diameter (about equal or equal in *G. aratia*, *G. pseustes* and *G. phelloderma*, smaller in *G. peruana*, about 1.5 times in *G. aguaruna*); supratympanic fold heavy (weak in *G. aratia* and *G. phelloderma*); width of the disc on the third finger larger than half of the tympanum diameter (about equal or equal to half of the tympanum diameter in *G. aratia*, *G. phelloderma* and *G. aguaruna*, equal to tympanum diameter in *G. pseustes*); relative lengths of the fingers $I \leq II < IV < III$ ($I < II < IV < III$ in *G. aratia*, *G. turnerorum* and *G. yacuri*, $I > II < IV < III$ in *G. phelloderma* and *G. aguaruna*); supernumerary tubercles large, round (not evident in *G. aratia*, subconical in *G. phelloderma*, small, present only on proximal segments of digits in *G. aguaruna*, few, small, round only on proximal segments of fingers in *G. pseustes*); palmar tubercle bifid (absent in *G. aratia* and *G. aguaruna*); a distinct curved inner tarsal fold extending along the full length of the tarsus (fold prominent on distal half on tarsus in *G. aguaruna*, low fold on distal third of tarsus in *G. pseustes*); outer metatarsal tubercle low and round (absent in *G. aratia*, *G. phelloderma* and *G. aguaruna*, small and subconical in *G. pseustes*); inner metatarsal tubercle elliptical and visible from above (not visible from above in *G. aratia*, tubercle conical or ovoid in *G. phelloderma*, elliptical and barely visible from above in *G. aguaruna*, ovoid, flat, not visible from above in *G. pseustes*); relative lengths of the toes $I < II < III = V < IV$ ($I < II < III < IV < V$ in *G. aratia*, $I < II < V < III < IV$ in *G. phelloderma*, $I < II < III < V < IV$ in *G. aguaruna*, *G. turnerorum* and *G. yacuri*); foot one half webbed (webbing basal between toes I and II in *G. aratia* and *G. aguaruna*); webbing formula $I(1^+-2^+)-(2-2^+)II(1-2^+)-(2-3^+)III(2-2^+)-(3-3^+)IV(2-3^+)-(2-2^+)V$, ($II_2-2III_2-3IV_3-1V$ in *G. aratia*, $I_2-3II_2-3III_2-2IV_2-2V$ in *G. phelloderma*, $II_1-2III_1.5-2IV_2-1V$ in *G. aguaruna*, $II_1-2III_1-2.5IV_2-1V$ in *G. turnerorum*, $II_2-3III_2-4IV_3-2V$ in *G. yacuri*); supernumerary tubercles low, round and present on entire surface (absent in *G. aratia*, subconical more prominent along segment of toes than in between in *G. phelloderma*,

present on proximal segments of digits in *G. aguaruna* and *G. pseustes*); skin on dorsum shagreen with abundant scattered pustules and presence of prominent longitudinal pustular ridges (shagreen with scarce pustules and low or absent longitudinal pustular ridges in *G. peruana*, granular in *G. aratia*, prominent longitudinal ridges and scattered warts and pustules giving a tree bark-like appearance in *G. phelloderma*, weakly granular to smooth in *G. aguaruna*, granular in *G. pseustes*, skin weakly areolate lacking longitudinal ridges in *G. turnerorum*, weakly granular to smooth having a transverse ridge at occipital region in *G. yacuri*); skin the flanks, vocal sac, chest, and belly coarsely areolate (granular in *G. aratia*, flanks tubercular, throat and belly granular in *G. phelloderma*, flanks weakly granular to smooth, throat, belly granular in *G. aguaruna*, flanks areolate and belly granular in *G. pseustes*); absence or presence of one to three large cloacal tubercles, cloacal fold absent or present (tubercles absent in *G. aratia* and *G. aguaruna*, one to two in *G. peruana*, three in *G. phelloderma*, cloacal folds and tubercles absent in *G. pseustes*); opening of the brood pouch narrowly U-shaped (pouch opening puckered in *G. aratia* and *G. aguaruna*, pouch V-shaped in *G. phelloderma*); each dentigerous process bearing three to five teeth (six teeth in *G. aratia*, two to five teeth in *G. peruana*, four teeth in *G. phelloderma*, five teeth in *G. aguaruna*, seven teeth in *G. pseustes*); iris in life reddish copper or metallic red with fine black reticulations (silvery bronze with fine black flecks and reticulations in *G. aratia*, upper region golden with fine brown reticulations and lower region brown with fine golden spots in *G. peruana*, reddish brown with fine black reticulations and pupil with a bronze ringlet in *G. phelloderma*, dull bronze with black reticulations in *G. pseustes*, yellow-cream with brown reticulations and brown horizontal bar across the eye in *G. turnerorum*).

Description of the lectotype: Adult male (MUSM 7740); body robust; SVL 33.5 mm; vocal slits present, a median subgular vocal sac; nuptial pad on dorsal surface of thumb not recognizable; head wider than long; snout rounded in dorsal view and in lateral profile; canthus rostralis acutely rounded in cross-section; loreal region concave; lips rounded; top of head flat; interorbital distance larger than width of upper eyelid; internarial area flat; nostrils not protuberant, directed anterolaterally at the terminus of the canthus rostralis at a point above the anterior margin of the lower jaw; diameter of eye greater than its eye–nostril distance; tympanum oval, higher than wide, separated from eye by distance larger than the tympanum diameter; tympanic annulus distinct, smooth; tympanic membrane smooth; supratympanic fold heavy, extending from posterior corner of the orbit to the angle of the jaw.

Forelimb robust; ulnar tubercles absent; hand small; fingers unwebbed; fingers moderately long, bearing small round discs; width of the disc on the third finger is larger than the half of the tympanum diameter; relative lengths of fingers: $I = II < IV < III$; subarticular tubercles large and rounded, bifid; supernumerary tubercles large, round; palmar tubercle absent; prepollical tubercle elliptical.

Hind limb robust; TL 51.22% SVL; FL 45.7% SVL; calcar and tarsal tubercles absent; inner tarsal fold extends the full length of the tarsus; outer metatarsal tubercle is low and round; inner metatarsal tubercle elliptical and is visible from above; toes long; relative length of toes: $I < II < III = V < IV$; the foot is one half webbed; webbing formula $I_2-2^+II_2-3^+III_2-3^+IV_3-2^+V$; subarticular tubercles large and round; supernumerary tubercles low, round, and present on entire surface; skin on dorsum shagreen with abundant scattered pustules and the presence of prominent longitudinal pustular ridges, not co-ossified with skull, lacking transverse ridges; skin on flanks, vocal sac, chest, belly, ventral surfaces of the forearms and arms coarsely aerolate, thighs granular, tibia and tarsi smooth; cloacal tubercles and folds absent; two large tubercles ventrolateral to the cloacal opening. Dentigerous processes of vomer posteromedially inclined and narrowly separated medially between the choanae, each one bearing three teeth.

Measurements (in mm): SVL: 33.5, TL: 17.2, FL: 15.3, HL: 13.5, HW: 14.4, IOD: 4.5, EW: 2.8, IND: 2.2, ED: 3.9, EN: 3.4, OJ: 1.8, NJ: 2.8, TD: 1.8, FFL: 6.3, TFL: 11.3, TDF: 1.3.

In preservative, dorsum of the head, body, and limbs brown or gray. Dark brown markings (usually narrowly edged with black) consisting of a pair of irregulars gener-

ally interrupted paravertebral marks extending from the eyelids to the sacral region. Flanks with irregularly shaped dark grayish-brown blotch from posterior corner of eye across tympanum to upper half of middle of flank. A dark brown canthal stripe is present; upper lip stripe absent. The posterior surfaces of the thighs are brown. All ventral surfaces reddish-brown. Coloration in life unknown.

Variation: Notes on color variation in life are based on photos taken by A. TICONA from a female specimen (MUSM 32123), J. C. CUSI from male (MUSM 36678; Fig. 4) and F. HUARI from female (MUSM 34753). Dorsum green, brown or dark brown with dark green, brown or dark brown pair of irregulars generally interrupted paravertebral markings extending from the eyelids to the sacral region (usually narrowly edged with black). Head markings consisting of a green, brown or black canthal stripe, lacking labial stripe and bars. Dorsolateral stripe absent. Flanks brown with irregularly shaped dark brown blotch from posterior corner of eye across tympanum to upper half of middle of flank. Anterior and posterior surfaces of thighs lacking dark markings. All ventral surfaces creamy with or without dark spots. Iris reddish copper or metallic red with fine black reticulations. Adult males have vocal

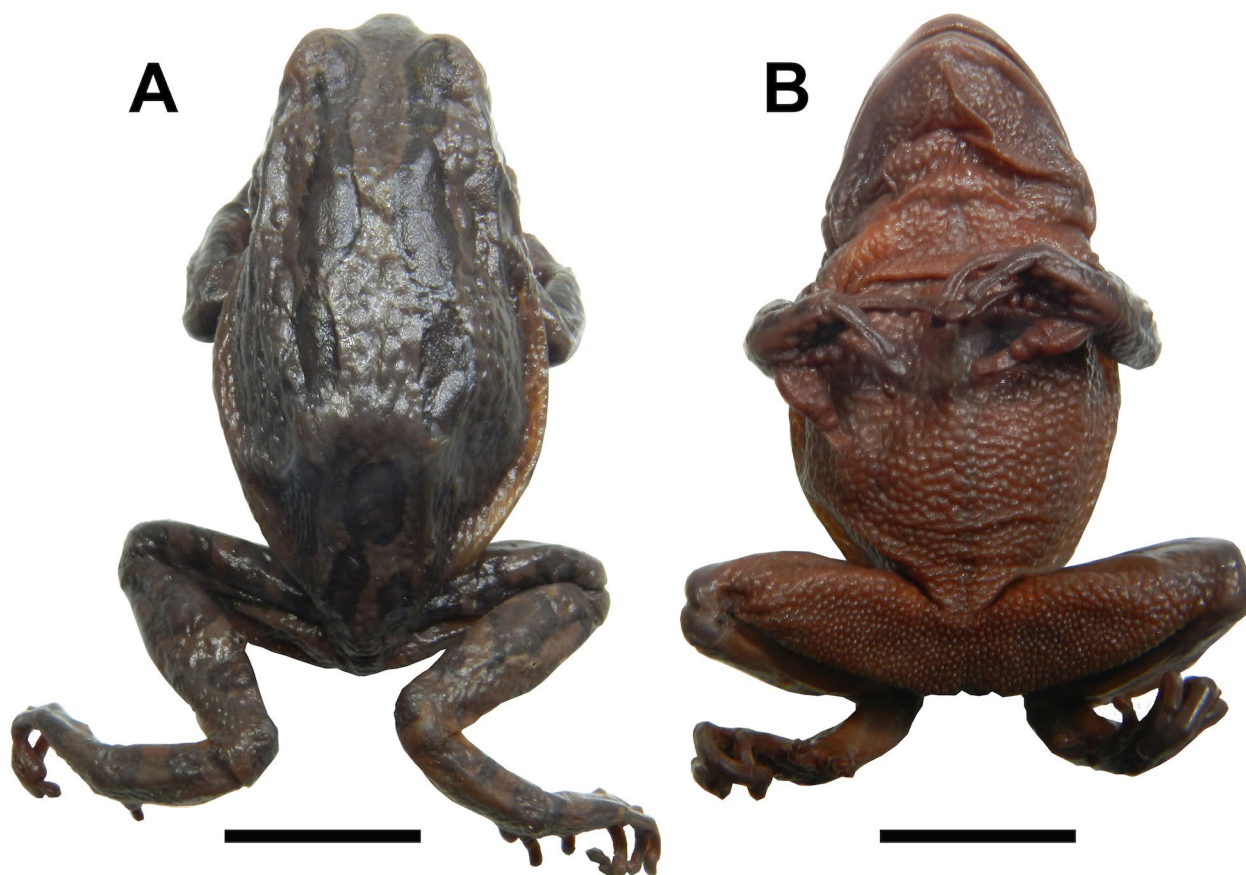


Figure 2. Preserved male lectotype of *Gastrotheca dissimilis*, MUSM 7740, 33.5 mm SVL. (A) Dorsal and (B) ventral views. Scale bars = 10 mm. Photos by D. RODRÍGUEZ.

slits, a median subgular vocal sac, and small brown nuptial excrescences on the dorsal medial surface of the thumb. For ranges and proportions of material examined (lectotype, additional material and paralectotypes) of *G. dissimilis* see Table 1.

Distribution and ecology: *Gastrotheca dissimilis* is known from several localities at elevations of 3294–4202 m a.s.l. in the northern part of the Cordillera Central in Peru (Rodríguez et al. 2019; Fig. 5).

The general landscape with records of *G. dissimilis* consists of pastures for cattle with scattered rocky outcrops, forests, puna, paramo, grasslands, containing bofedales, streams and lakes. Other sympatric anurans include *Nannophryne cophotis*, *Pristimantis cordovae*, *P. pinguis*, *P. simonsii* and *Telmatobius brevipes*. Sympatric squamates include *Petracola ventrimaculatus*, *P. waka*, *Stenocercus empetrus*, *S. melanopygus*, *S. stigmatus*, *Epictia tricolor*, *Dipsas oneilli* and *Erythrolamprus taeniurus*.

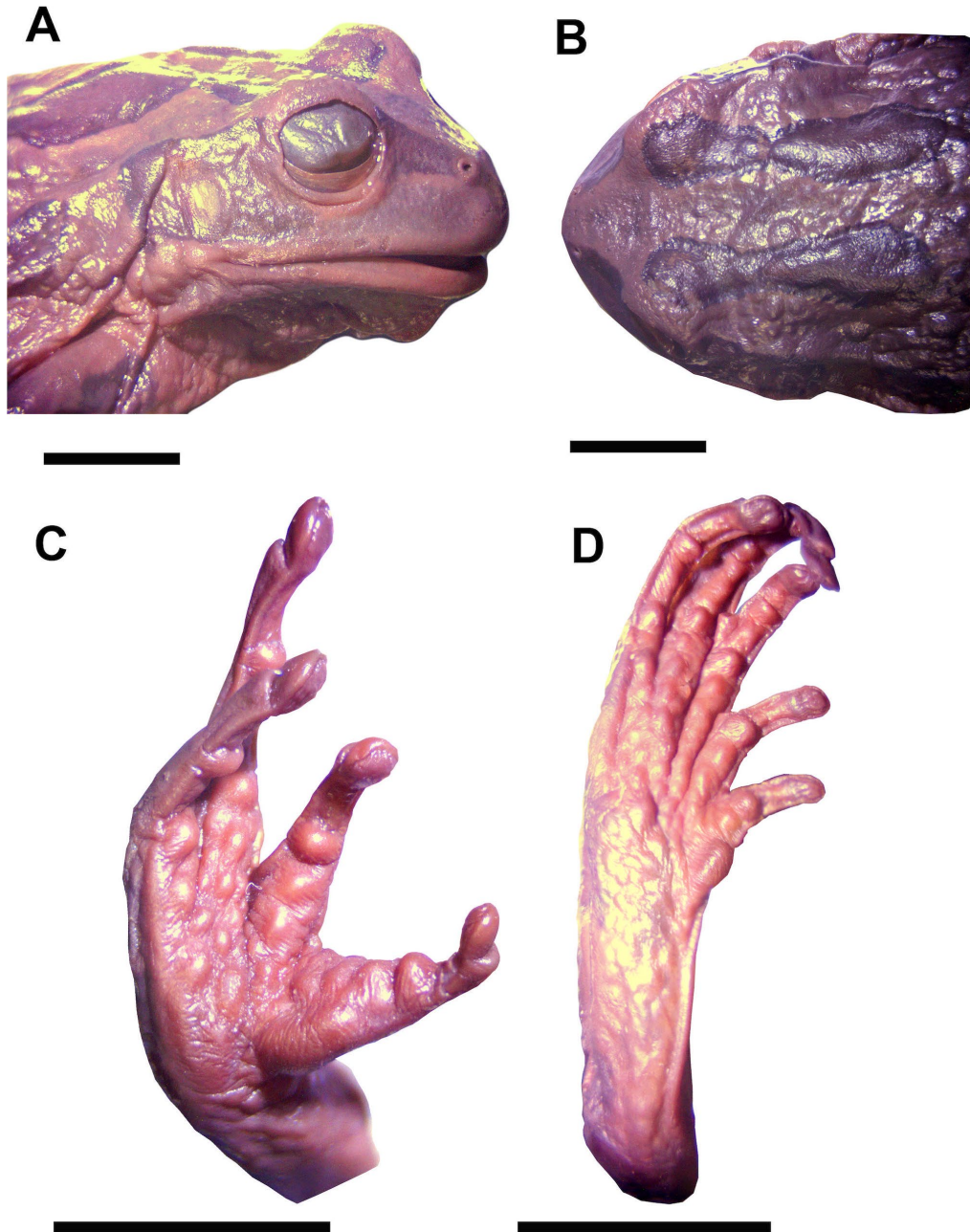


Figure 3. (A) Dorsal and (B) lateral views of the head, and views of the (C) palm and (D) sole of the preserved lectotype of *Gastrotheca dissimilis*, MUSM 7740. Scale bars = 5 mm. Photos by D. RODRÍGUEZ.

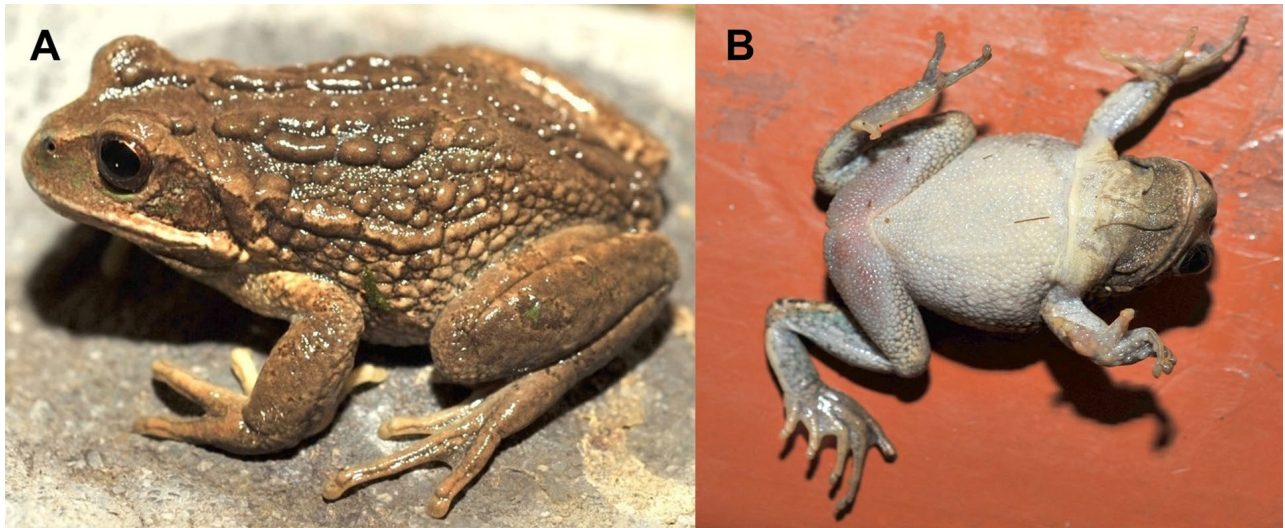


Figure 4. (A) Dorsolateral and (B) ventral views of *Gastrotheca dissimilis* (MUSM 36678) in life. Photos by J. C. Cusi.

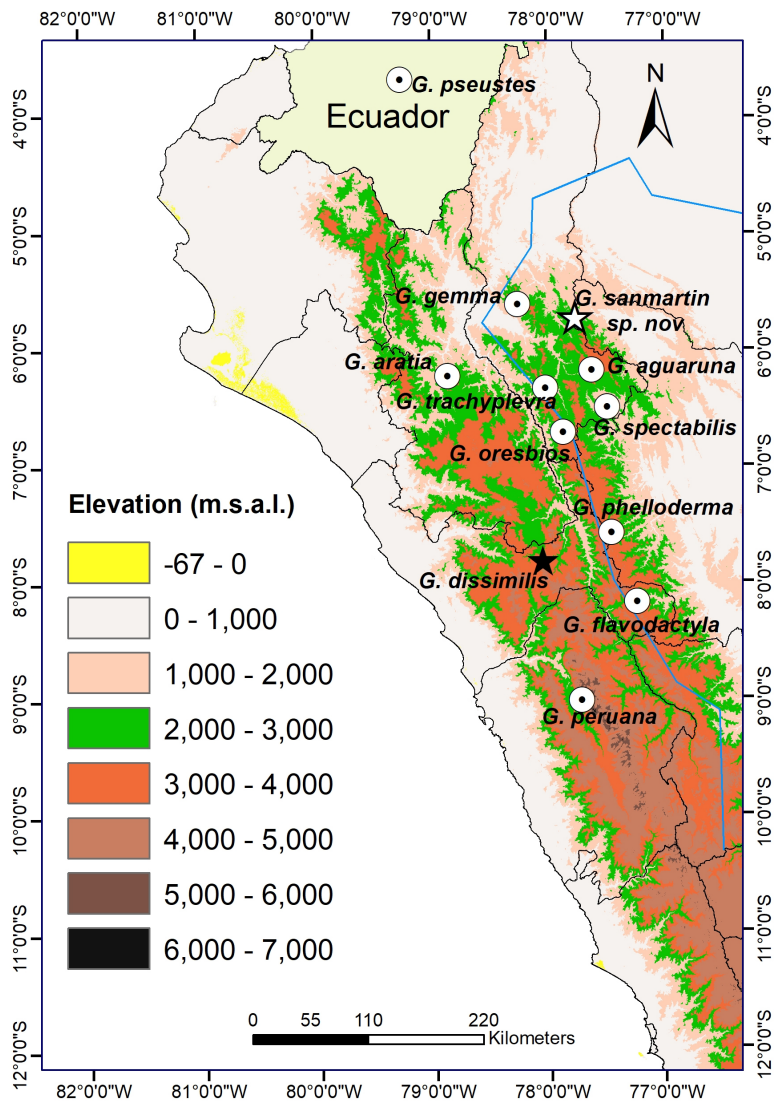


Figure 5. Map of northwestern Peru indicating the type localities of *Gastrotheca dissimilis* and *Gastrotheca sanmartin* sp. n. (black star and white star, respectively) as well as those of other selected species of *Gastrotheca*.

Table 1. Measurements (in mm) and proportions of *Gastrotheca dissimilis*. Ranges followed by means and one standard deviation in parentheses. For abbreviations used, see Material and methods.

Characters	<i>Gastrotheca dissimilis</i>	
	Females (n = 9)	Males (n = 5)
SVL	33.7–52.2 (41.8 ± 7)	33.5–50.4 (39.6 ± 8.6)
TIBL	16.4–21.9 (19.4 ± 2.1)	15.3–21.6 (18.4 ± 2.9)
FL	16.7–21.2 (18.8 ± 1.6)	13.2–21.9 (17.2 ± 4)
HL	13.5–17.4 (14.9 ± 1.4)	12.1–16.2 (13.9 ± 1.9)
HW	14.4–20.4 (16.6 ± 2.2)	13.1–19.4 (15.9 ± 3)
IOD	3.4–4.6 (4.1 ± 0.4)	3.1–5.8 (4.3 ± 1.1)
EW	2.7–4.9 (3.7 ± 0.9)	2.5–4.3 (3.3 ± 0.7)
IND	2.3–3.6 (2.8 ± 0.5)	2.2–3.2 (2.7 ± 0.5)
ED	3.8–5.0 (4.3 ± 0.4)	3.6–5.2 (4.1 ± 0.6)
EN	3.3–4.7 (3.8 ± 0.4)	2.8–3.9 (3.3 ± 0.4)
OJ	1.9–3.1 (2.4 ± 0.5)	1.6–3 (2.2 ± 0.6)
NJ	2.7–4.3 (3.4 ± 0.5)	2.6–3.4 (3 ± 0.3)
TD	1.7–2.9 (2.3 ± 0.4)	1.8–2.6 (2.1 ± 0.4)
FFL	6.0–9.3 (7.6 ± 1.2)	6.3–9.4 (7.3 ± 1.4)
TFL	11.0–16.9 (13.3 ± 2.0)	9.8–15.1 (12.2 ± 2.2)
TFD	1.3–2.0 (1.6 ± 0.2)	1.0–1.9 (1.5 ± 0.4)

***Gastrotheca sanmartin* sp. n.**

Figs 6, 7

Gastrotheca sp. 1 – RODRÍGUEZ et al. (2019: 463)

ZooBank LSID: urn:lsid:zoobank.org:act:28CF52EF-999B-4BF9-AEFB-18F3E30412B2

Holotype: MUSM 33319, an adult female, from Alto Mayo Protected Forest, 5°43'46.1" S, 77°45'25.2" W, 3245 m a.s.l., Distrito Pardo Miguel, Provincia Rioja, Departamento de San Martín, Peru, collected on 23 June 2014 by JUAN C. CUSI, ANDY BARBOZA, and RONEL ESPINAL.

Diagnosis: A medium-sized species of *Gastrotheca* with the following combination of characters: adult female SVL 48.6 mm (n = 1); (1) TL 53.9% of SVL, greater than foot length; (2) IOD slightly greater than EW; (3) skin on the dorsum shagreen, not co-ossified with skull, lacking transverse ridges; (4) supraciliary processes absent; (5) heel lacking calcar or tubercle; (6) tympanic membrane and annulus distinct, smooth; (7) fingers I and II equal in length, with discs on fingers broadly expanded; (8) finger not webbed; (9) foot one-half webbed; coloration in life unknown, (10) in preservative, dorsum of the head, body, forelimbs, shanks, feet, distal parts of digits and loreal region bluish gray; (11) pale cream labial stripe extending from a point below the orbit to the angle of the jaw; dark white canthal stripe; (12) dorsolateral stripe absent; (13) flanks gray with minute black spots; posterior surfaces of thighs brown with black brown spots and anterior surfaces cream with black brown spots; (14) gular region, throat, ventral surface of limbs and belly uniformly cream; (15) brood pouch simple, dorsal.

Phylogenetically, according to our results, *G. sanmartin* is sister to *G. spectabilis* and both species are in turn closely related to *G. flavodactyla*, *G. gemma*, *G. oresbios*, *G. psychrophila*, *G. mittaliiti*, *G. trachyplevra*, and *G. stictopleura* (Fig. 1). Morphologically, *G. sanmartin* differs from these species (conditions in parentheses) by having the snout acutely rounded in dorsal view, truncate in profile (snout acutely rounded in dorsal view with bluntly rounded in profile in *G. spectabilis*, *G. psychrophila* and *G. flavodactyla*, snout acutely rounded and inclined anteroventrally in profile in *G. trachyplevra* and *G. gemma*, snout acuminate in dorsal view, rounded in profile in *G. oresbios*; snout subacuminate in dorsal view, inclined anteroventrally in profile in *G. mittaliiti*); tibia length greater than foot length (tibia length shorter than foot in *G. spectabilis*, *G. mittaliiti*, and *G. trachyplevra*); canthus rostralis angular in cross-section (rounded in cross-section in *G. psychrophila*, *G. oresbios* and *G. gemma*, concave in *G. trachyplevra* and *G. flavodactyla*); interorbital distance greater than width of the upper eyelid (smaller than width of the upper eyelid in *G. mittaliiti* and *G. trachyplevra*); the internarial area is flat (slightly elevated in *G. spectabilis* and slightly convex in *G. trachyplevra*); eye diameter greater than eye–nostril distance (shorter in *G. spectabilis* and *G. gemma*, about equal in *G. psychrophila*); tympanum ovoid, separated from the eye by a distance larger than the tympanum diameter (round, separated by a distance equal to the tympanum diameter in *G. psychrophila*); tympanic membrane and annulus distinct, smooth (annulus distinct and granular in *G. oresbios*, annulus barely evident and wrinkled or tuberculate in *G. gemma*); width of disc on third finger longer than tympanum diameter (less than the tympanum diameter in *G. spectabilis*, *G. trachyplevra* and *G. oresbios*, equal to the tympanum diameter in *G. flavodactyla*); fingers unwebbed (the fingers II, III and IV webbed basally in *G. psychrophila*, basal webbing between fingers II and III in *G. trachyplevra*, fingers with basal webbing only between III and IV in *G. gemma*, all fingers with basal webbing in *G. flavodactyla*); relative lengths of fingers I = II < IV < III (I < II < IV < III in *G. psychrophila*, *G. oresbios*, *G. gemma* and *G. flavodactyla*, II < I < IV < III in *G. mittaliiti* and *G. trachyplevra*); subarticular tubercles large, round and non-bifid (large, subconical and with the distal tubercle on finger II bifid in *G. oresbios*, the distal tubercle on finger IV weakly bifid in some specimens of *G. psychrophila*); supernumerary tubercles few, small, round, present only on proximal segments of fingers (absent in *G. spectabilis*); palmar tubercle bifid (inconspicuous in *G. spectabilis*, trifold in *G. psychrophila*); low and curved inner tarsal fold extending along full length of the tarsus (curved inner tarsal fold on the distal two-thirds of the tarsus in *G. psychrophila*, inner tarsal fold absent in *G. oresbios*); outer metatarsal tubercle absent (small and subconical in *G. psychrophila*, present in *G. trachyplevra*); foot one half webbed (toe webbing basal in *G. trachyplevra* and *G. flavodactyla*, basal webbing between toes I and II in *G. gemma*, toes I–II lacking webbing, basal webbing between toes III to V in *G. spectabilis*); webbing formula $I_2^+ - 2II_2 - 3III_3 - 3IV_3 - 2^+V$ ($I_2 - 2II_2 - 3III_2 - 3 - 3^+IV_3 - 3^+ - 2V$ in *G. psy-*

chrophila, toes II₂ III₂⁺ and preaxial side of toe V₂⁺ in *G. trachyplevra*, toes I–II not webbed, basal webbing between toes III, IV and V in *G. oresbios*, II₁–2III₁–2½IV₂–1V in *G. gemma*, toes II₂ III₂⁺ and V₂⁺ in *G. flavodactyla*, I basal II₂⁺–3⁺III₂⁺–3½IV₄–2⁺V in *G. mittaliiti*); skin on dorsum shagreen (smooth in *G. spectabilis*, dorsal surface of the head, body and limbs smooth (29%) or areolate (71%) in *G. psychrophila*, dorsum covered with packed rounded pustules, and two prominent paravertebral longitudinal pustular ridges in *G. trachyplevra*, dorsum smooth with scattered small tubercles in *G. oresbios* and *G. flavodactyla*, dorsum uniformly granular in *G. mittaliiti*, dorsum coarsely granular in *G. gemma*); skin on flanks, belly, ventral surfaces of arms, forearms, thighs and tympanic region granular, ventral surfaces of tibia or shanks and tarsi smooth (flanks smooth with tubercles on supratympanic fold and side of head posterior to eye in *G. spectabilis*, flanks areolate, belly and proximal posteroventral surfaces of thighs granular in *G. psychrophila*, flanks covered by large ovoid pustules in *G. mittaliiti*, flanks covered by large ovoid pustules, throat and chest granular, ventral surfaces of thighs and arms granular, belly granular, ventral surface of shanks smooth, posterior surface of thighs granular in *G. trachyplevra*, flanks covered by low, round granules, throat and chest smooth, ventral surface of forelimbs smooth in *G. flavodactyla*); cloacal folds and tubercles absent (a pair tubercles is present below the cloacal opening in *G. psychrophila*, two vertical rows of enlarged brown tubercles, three on left and two on right, below the cloacal opening in *G. gemma*); pouch opening V-shaped with anterior border at level of posterior edge of sacrum (opening of brood pouch U-shaped with

border at level of sacrum in *G. spectabilis*, *G. psychrophila* and *G. oresbios*); dentigerous processes of the vomers in transverse row narrowly separated between the choanae (dentigerous processes posteromedially inclined, narrowly separated medially in *G. spectabilis*, *G. psychrophila* and *G. oresbios*, dentigerous vomerine processes narrowly separated medially in *G. trachyplevra*, *G. gemma* and *G. flavodactyla*); each process bearing five teeth (six and seven in *G. spectabilis*, from four to seven in *G. psychrophila*, four in *G. trachyplevra*, from five to six in *G. gemma*).

Description of the holotype: Adult female (MUSM 33319); body robust; SVL 48.6 mm; head wider than long; snout acutely rounded in dorsal view, truncate in profile; canthus rostralis angular in section; loreal region concave; lips rounded; top of head flat; interorbital distance width larger than upper eyelid; internarial area flat; nostrils are not protuberant, and are directed anterolaterally at the terminus of the canthus rostralis at a point formerly the anterior margin of the lower jaw; diameter of eye greater than eye-nostril distance; tympanum ovoid, its diameter half the eye diameter, separated from the eye by a distance larger than tympanum diameter; tympanic membrane and annulus distinct, smooth; supratympanic fold heavy, obscuring the upper and posterior margins of the tympanic annulus, and extends from the posterior corner of the orbit to the insertion angle of the forelimbs.

Arm moderately robust; ulnar tubercles absent; hand large; fingers unwebbed; fingers long, discs broadly expanded, elliptical, wider than digit, fingers broad lateral fringes; width of disc on third finger greater than tympan-

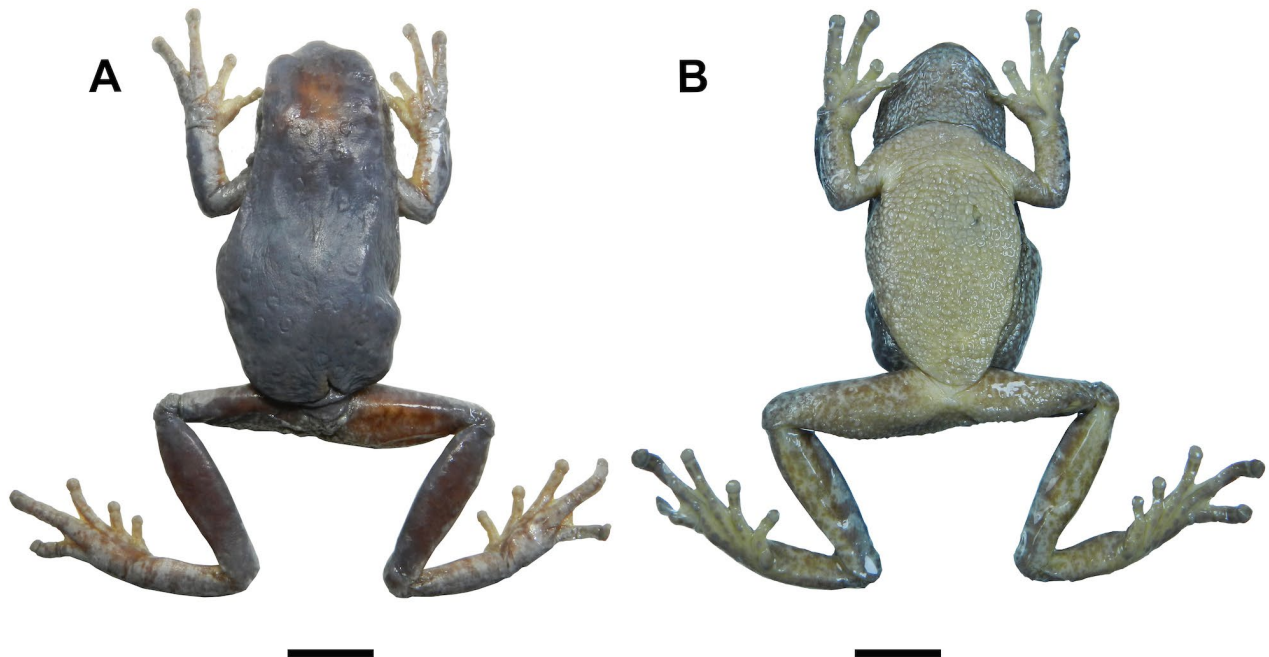


Figure 6. Preserved female holotype of *Gastrotheca sanmartin* sp. n., MUSM 33319, 48.6 mm SVL. (A) Dorsal and (B) ventral views. Scale bars = 10 mm. Photos by D. RODRÍGUEZ and J. C. CUSI.

num diameter; relative lengths of fingers I = II < IV < III; subarticular tubercles large and round; supernumerary tubercles few, small, round, present only on proximal segments of fingers; palmar tubercle bifid; prepollical tubercle elliptical. Hind limbs robust; TL 53.9% SVL; FL 51.26% SVL; calcar and tarsal tubercles absent; inner tarsal fold low, extending along the full length of the tarsus; outer metatarsal tubercle absent; inner metatarsal tubercle elliptical, visible in ventral view; toes moderately long; relative lengths toes I < II < III < V < IV. Foot one half webbed; webbing formula $I_2^+ - 2II_2^- - 3III_3 - 3IV_3 - 2^+V$; subarticular tubercles large and round; supernumerary tubercles, low, round, present

only on proximal segments of toes. Skin on dorsum shagreened; flanks, belly, ventral surfaces of the forelimbs, thighs and the tympanic region granular; skin on tibia and tarsi smooth; cloacal folds and tubercles absent; opening of the brood pouch V-shaped with anterior border at level of posterior edge of sacrum. Dentigerous processes of vomers in transverse row narrowly separated medially between the choanae, each process bearing five teeth.

Measurements (in mm): SVL: 48.6, TL: 26.2, FL: 24.9, HL: 15.9, HW: 17.0, IOD: 4.5, EW: 4.1, IND: 3.5, ED: 4.7, EN: 4.5, OJ: 2.8, NJ: 4.1, TD: 2.4, FFL: 10.2, TFL: 16.4, TDF: 2.6.

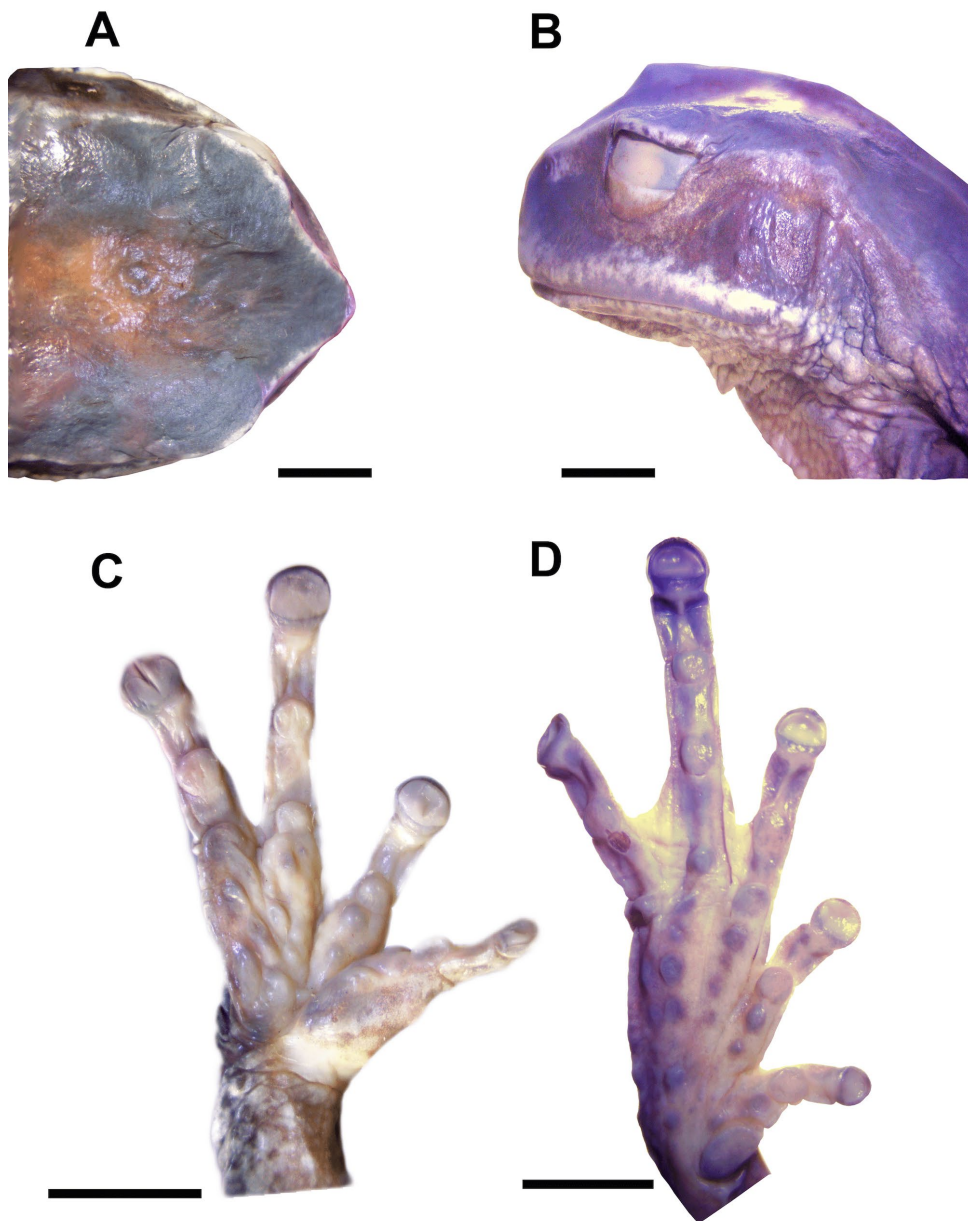


Figure 7. (A) Dorsal and (B) lateral views of the head, and views of the (C) palm and (D) sole of the preserved holotype of *Gastrotheca sanmartin* sp. n., MUSM 33319. Scale bars = 5 mm. Photos by D. RODRÍGUEZ and J. C. CUSI.

In preservative, dorsum of the head, body, forelimbs, shanks, feet, distal parts of digits and loreal region bluish gray; dorsolateral stripe absent; pale cream labial stripe extending from a point below the orbit to the angle of the jaw; dark white canthal stripe; flanks gray with minute black spots; posterior surfaces of thighs brown with black brown spots and anterior surfaces cream with black brown spots; gular region, throat, ventral surface of limbs and belly uniformly cream; cloacal region cream with black brown spots; the outer toes are bluish gray, the inner toes creamy white. Coloration in life unknown.

Distribution and ecology: *Gastrotheca sanmartin* inhabits a humid grassland and is known only from its type locality (Fig. 4) in the mountain ridge called Abra Patricia, within the Alto Mayo Protected Forest, located in the northern part of the Cordillera Oriental in Peru. The single known specimen, a gravid female with developed embryos in dorsal pouch (direct development), was caught at 00:00 hours on 23 June 2014 on top of a bush at 1.5 m above the ground. At the type locality, *G. sanmartin* occurs sympatrically with an undescribed species of *Lynchius*.

Etymology: The specific name *sanmartin* is a noun in apposition and used in reference to the type locality in San Martín department, a region that harbors a great diversity of amphibians and reptiles, especially in zone poorly explored as Alto Mayo Protected Forest.

Discussion

In this study, we used different lines of evidence and followed an integrative taxonomic approach (PADIAL et al. 2010) to solve an old taxonomic problem and to describe a new species of *Gastrotheca*. Our phylogenetic analysis suggests that *G. dissimilis* is a distinct evolutionary lineage that is closely related to, but morphologically distinct from *G. peruana* and *G. aratia*, which are sister to one another. This finding concurs with recent phylogenies of *Gastrotheca* (RODRÍGUEZ et al. 2019, VENEGAS et al. 2021, ECHEVARRÍA et al. 2022). Additionally, our results suggest that *G. sanmartin* is sister to *G. spectabilis* and both species are closely related to four other species distributed on the Cordillera Oriental (*G. flavodactyla*, *G. oresbios*, *G. gemma*, *G. trachyplevra*). All these species, including *G. spectabilis*, were described within the last ten years (2016–2025).

The general pattern of genetic divergence among taxa distributed in montane areas separated by arid river valleys agrees with previous research on vertebrates in northern Peru, which showed that population divergence and species formation may occur on both sides of a biogeographic barrier (e.g., WEIR 2009, DUELLMAN & TRUEB 2015). The distribution of divergent lineages of *Gastrotheca* on cordilleras east and west of the Río Marañón (Cordillera Occidental and Cordillera Oriental) as well as along a north-to-south axis on each cordillera supports this pattern. However, despite notable morphological differences, the relatively low

16S genetic distances among some of these lineages (Supplementary document S3) suggest relatively recent species formation. Our analysis showed that there is relatively low genetic divergence between *G. dissimilis* and *G. peruana* (average 2.5%), between *G. dissimilis* and *G. aratia* (average 1.5%), and between *G. peruana* and *G. aratia* (average 1.6%). These genetic distance values are within a 'gray' area of overlap between interspecific and intraspecific distributions of pairwise distances observed in other frog taxa.

The use of uncorrected pairwise genetic distances (UPD) is a tool for identifying potentially different species of amphibians. Although a 3% distance threshold in the 16S rRNA gene has been proposed as an indicator of distinct lineages (FOUQUET et al. 2007), various studies in South America have demonstrated that different amphibian lineages occur near or below this 3% threshold. For instance, in the *Engystomops petersi* complex (Leptodactylidae), populations with low genetic distances (2–3%) exhibit distinct advertisement calls, demonstrating reproductive isolation (FUNK et al. 2012). Similarly, within the genus *Eupsophus* (Alsodidae), lineages with genetic distances of 1–2% have remained independent based on morphology, allopatry, and karyotype (CORREA et al. 2017). In the genus *Pristimantis* (Strabomantidae), due to their rapid radiation across the Andes, authors validate lineages with UPD below 3% (1.3–2.5%) through integrative taxonomy, where fast Andean speciation generates acoustic and morphological differences (PÁEZ & RON 2019). This is consistent with ROJAS et al. (2018) who employed an integrative taxonomic approach (morphological and geographical) to validate candidate lineages with UPD < 3% as cryptic species within the genus *Amazophrynella*, revealing an underestimated diversity in the Amazon. Furthermore, PEREYRA et al. (2021) concludes that the 3% genetic distance threshold (UPD) in the 16S gene is arbitrary and insufficient for species delimitation in *Rhinella*, as lineages with lower divergence can constitute independent evolutionary units. Their research emphasizes that recent diversification with low UPD (near 1%) and total evidence (morphology, osteology) are more reliable for species identification, revealing a historical underestimation of South American diversity. And the study of AMÉZQUITA et al. (2024) used an integrative approach to validate new species of the genus *Phyllobates* with low genetic divergence (below 3% UPD), while presenting differences in coloration, morphology, and toxicity levels.

Data from other taxa show a similar trend. For example, some sibling species of Madagascan frogs in the genus *Mantella* (Mantellidae) exhibit uncorrected pairwise distances around 1–3% (VENCES et al. 2005) whereas several species of South American frogs (e.g., Hylineae) exhibit interspecific pairwise distance values below 3% (FOUQUET et al. 2007). However, FOUQUET et al. (2007) indicated that there is a risk in using a lower threshold value (e.g., 1–2%), because one may incorrectly identify conspecific lineages as candidate species. While the 16S pairwise distances between *G. aratia* and both *G. dissimilis* and *G. peruana* fall within this lower value, the morphological differences among species would support their recognition as separate species.

Gastrotheca sanmartin exhibits greater 16S pairwise distances with respect to closely related species: pairwise distance values of 2.2% to *G. spectabilis*, 5.7% to *G. flavodactyla*, 5.9% to *G. oresbios*, 5.6% to *G. gemma*, 6.3% to *G. trachyplevra*, 5.9% to *G. psychrophyla*, 6.1% to *G. stictopleura*, and 7.7% to *G. mittaliiti* (Supplementary document S3). Although the genetic distance between *G. sanmartin* and *G. spectabilis* is below the 3% threshold, several morphological differences support the recognition of *G. sanmartin* as a separate species (tibia length greater than foot in *G. sanmartin* vs. tibia length shorter than foot in *G. spectabilis*, *G. mittaliiti*, and *G. trachyplevra*; eye diameter greater than eye–nostril distance in *G. sanmartin* vs. eye diameter shorter than eye–nostril distance in *G. spectabilis* and *G. gemma*). We consider these morphological traits useful for species delimitation in *Gastrotheca*.

The embryo recovered from the pouch of the holotype provides evidence for *G. sanmartin* having direct development (i.e., no larval stage). Two other species in the north-eastern part of Cordillera Oriental of the Peruvian Andes, *G. gemma* and *G. trachyplevra*, exhibit a similar reproductive mode (i.e., produce eggs that undergo direct development and hatch as froglets) and occur at high elevations (> 3000 m a.s.l.).

There is considerable variation in the currently known elevational distribution of species of *Gastrotheca* in northwestern Peru (Figure 8). Several species are known from a single locality only (*G. sanmartin*; *G. trachyplevra* occurs at 3434 m a.s.l.; *G. spectabilis* occurs at 3308 m a.s.l.), or have a narrow known elevational ranges (*G. gemma*, 3130–3180 m a.s.l.; *G. flavodactyla*, 3298–3336 m a.s.l.; *G. phelloderma*, 3380–3470 m a.s.l.) (LEHR & CATENAZZI 2011, VENEGAS et al. 2021, ECHEVARRÍA et al. 2022). In contrast, other species have greater elevational distributions: *G. dissimilis* (3294–4202 m a.s.l.); *G. peruana* (3726–4388 m a.s.l.); *G. pseustes* (2200–4080 m a.s.l.) (DUELLMAN 2015); *G. aratia* (2560–2875 m a.s.l.) (DUELLMAN et al. 2014), and *G. aguaruna* (2360–3308 m a.s.l.) (DUELLMAN et al. 2014). Additionally, several species pairs occur at non-overlapping elevations (*G. peruana* and *G. aratia*, *G. stictopleura* and *G. trachyplevra*, *G. spectabilis* and *G. sanmartin*; Fig. 8).

The recent discovery of many new species in the Tropical Andes Hotspot highlights the conservation value of this region (YOUNG et al. 2015). In Peru, the Critical Ecosystem Partnership Fund (CEPF) proposed as a priority north-eastern Peru as a biological corridor, that includes Abra Pardo de Miguel as a key biodiversity area (KBA). However, this corridor is threatened by roads, dam projects, ag-

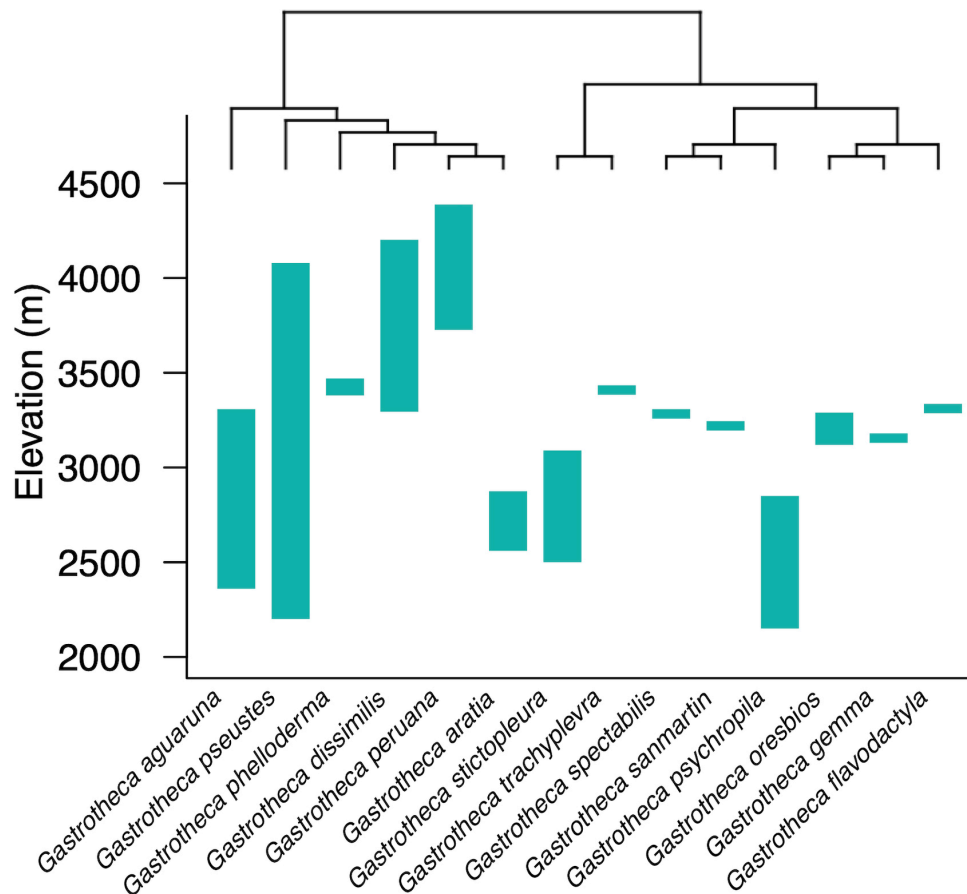


Figure 8. Diagram showing the known elevational distribution of *Gastrotheca* species in northwestern Peru (green bars). The simplified phylogeny (top) depicts the relationship among the focal species and their closest relatives.

riculture and land trafficking. Alto Mayo Protected Forest, located in Pardo de Miguel district, is an important natural area for local communities because it protects the headwaters of streams and provides research opportunities and attractive spots for tourism. The discovery of a new species of marsupial frog in this corridor highlights the importance of this area between the Cordillera Central and Oriental in northern Peru, which likely harbors additional species yet to be discovered.

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Appendix I

Comparative material examined

Gastrotheca peruana – Peru: Ancash: Huaylas, Caraz, 9°1'24.35" S, 77°42'55.54" W, 3726 m, MUSM 36589 (topotype).

Gastrotheca aratia – Peru: Cajamarca, Cutervo, 8 km (by road) NW of Cutervo, 6°14'00" S, 78°51'24" W, 2560 m, KU 212067 (holotype).

Gastrotheca phelloderma – Peru: San Martín, Mariscal Cáceres, Huicungo, Parque Nacional del Río Abiseo at Pampa del Cuy, 7°34.8' S, 77°27.0' W, 3400 m, MUSM 27739 (holotype).

Gastrotheca aguaruna – Peru: Amazonas, Chachapoyas, Molinapampa, 6°10'50" S, 77°37'01" W, 2400 m, KU 212022 (holotype).

Gastrotheca pseustes – Ecuador: Loja, 7.1 km by road north of San Lucas, 03°41' S, 79°15' W, 2940 m, KU 203443 (holotype).

Gastrotheca spectabilis – Peru: Amazonas, Rodríguez de Mendoza, Vista Alegre, 6°30'05" S, 77°29'04.9" W, 2940 m, CORBIDI 11790 (holotype).

Gastrotheca psychrophila – Ecuador: Loja, between Loja and Zamora, 13–14 km E by road of Loja, 2850 m, KU 120760 (holotype).

Gastrotheca trachyplevra – Peru: Amazonas, Luya, Colcamar, 6.335803° S, 78.0132069° W, 3434 m, CORBIDI 16614 (holotype).

Gastrotheca oresbios – Peru: Amazonas, Chachapoyas, Abra Barro Negro, 6°24'58.2" S, 77°51'53.8" W, 3290 m, CORBIDI 11076 (holotype).

Gastrotheca gemma – Peru: Amazonas, Utcubamba, Cajaruro, 5°36'58.7" S, 78°14'58.8" W, 3180 m, CORBIDI 18839 (holotype).

Gastrotheca flavodactyla – Peru: Amazonas, Rodríguez de Mendoza, Vista Alegre, 8.175510° S, 77.231355° W, 3298 m, CORBIDI 18840 (holotype).

Supplementary data

The following data are available online:

Supplementary document S1. GenBank accession number for 16S sequences used in this study.

Supplementary document S2. Maximum likelihood (ML) phylogeny of *Gastrotheca*, based on 524-bp of mitochondrial (16S) sequences.

Supplementary document S3. 16S pairwise distances.