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Two new species of marsupial frogs (Anura: Hemiphractidae) from the Central Andes of northern Peru

Lourdes Y. Echevarría[1], Daniel J. Paluh[2], Luis A. García-Ayachi[3,4], Pablo J. Venegas[3,4,5],
Alessandro Catenazzi[3,4,6], Renzo Pradel[3,4] & Santiago Castroviejo-Fisher[1,7]

[1] Laboratório de Sistemática de Vertebrados, Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS), Porto Alegre, Brazil

[2] Department of Natural History, Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA

[3] Instituto Peruano de Herpetología (IPH), Lima, Peru

[4] División de Herpetología, Centro de Ornitología y Biodiversidad (CORBIDI), Lima, Peru

[5] Rainforest Partnership, 4005 Guadalupe St., Austin, Texas 78751, USA

[6] Department of Biological Sciences, Florida International University, Miami, Florida, USA

[7] Division of Vertebrate Zoology (Herpetology), American Museum of Natural History, New York, NY 10024, USA

Corresponding author: Lourdes Y. Echevarría, e-mail: lourdese.20@gmail.com

Abstract. We describe two new species of *Gastrotheca* from the humid montane forests and grasslands of La Libertad and Amazonas departments, respectively, in the northern portion of the central Peruvian Andes. Our phylogenetic analysis recovered the new species as part of the *Gastrotheca marsupiata* species group and closely related to *G. gemma*, *G. oresbios*, *G. psychrophila*, *G. spectabilis*, *G. stictopleura*, and one undescribed species. The new species from La Libertad department can be differentiated from the aforementioned congeners by being of moderately small size (SVL = 33.3–41.9 mm, N = 3), having an acutely rounded snout in dorsal view, a rounded snout in lateral view, smooth skin on the dorsum with low granules, and smooth tympanic annulus and supratympanic fold. The new species from Amazonas department (SVL = 33.5–43.9 mm, N = 2) differs from other *Gastrotheca* species by having the dorsum covered with large and closely packed rounded pustules, two prominent paravertebral longitudinal pustular ridges, and a distinctly thick and elevated supratympanic fold extending from the top edge of the tympanum to the flank and being continuous or fused with the dorsolateral row of elongated pustules. In addition to external morphological characters, we include detailed descriptions and illustrations of the skeleton of the holotypes based on 3D models obtained from CT-scans.

Key words. Amphibia, CT-scan, *Gastrotheca*, osteology, phylogeny, taxonomy.

Introduction

Gastrotheca Fitzinger, 1843 is the most species-rich and geographically widespread genus of the family Hemiphractidae. It includes 76 species distributed from Central America and Chocó, along the Andes to northern Argentina, the Amazon Basin, the Cordillera de la Costa in Venezuela, and the Atlantic Forest in Brazil (Duellman 2015, Frost 2021). This monophyletic group is popularly known as marsupial frogs because females carry their fertilized eggs in a dorsal pouch with a posterior opening (Castroviejo-Fisher et al. 2015). This group exhibits outstanding behavioural and developmental variation, with some species having a biphasic life cycle including a free-living tadpole while others are direct developers (Duellman 2015). During development inside the pouch, the embryos ex-

change gases with the mother (del Pino et al. 1975) and the mother may transfer nutrients to the embryos (Warne & Catenazzi 2016).

Marsupial frogs are particularly diverse in the Andes, where 61 species (80% of the total diversity) are found at altitudes of up to 4660 m a.s.l. (Frost 2021, Steigerwald et al. 2021). New species of *Gastrotheca* are continued to be found in this region, with 21 Andean species having been described during the last 20 years (Frost 2021). Species of *Gastrotheca* known to occur in Peru correspond to the *G. longipes* and *G. marsupiata* species groups, and the highest diversity of marsupial frogs is currently concentrated in the northern Andes (Duellman & Venegas 2005, 2016, Duellman 2015, Venegas et al. 2021), where many species were discovered during herpetological expeditions to poorly explored areas (e.g., Duellman & Vene-

gas 2005, 2016, Venegas et al. 2021) or the study of specimens from scientific collections (e.g., Lehr & Catenazzi 2011, Duellman 2013).

In this study, we further contribute to the knowledge of the species diversity of marsupial frogs. We examined a series of specimens from Amazonas and La Libertad departments, in northern Peru, including those flagged as candidate new species by Echevarría et al. (2021) based on phylogenetic analyses. Our detailed comparisons of the external and internal phenotypic variation, including 3D models of the skeleton generated from computed tomography (CT) scanning, and phylogenetic analysis of DNA sequences support the recognition of two new species that we herein describe and name.

Material and methods
Field surveys

Specimens of the two new *Gastrotheca* species described herein were collected during herpetological surveys carried out between 2015 and 2019 by Centro de Ornitología y Biodiversidad (CORBIDI) researchers. Specimens of one of the new species were collected in December 2015 during an expedition led by one of the co-authors (PJV) to the grasslands and montane forest on the summits of the Cordillera Central in the Utcubamba River basin, Amazonas department. Between 2018 and 2019, another co-author (RP) carried out expeditions to the Abiseo River headwaters in La Libertad department, discovering new species of amphibians and reptiles, including the other new species of *Gastrotheca* that we describe herein. All specimens were euthanized with 20% benzocaine gel, and after extraction of a tissue sample, fixed in 10% formalin for 24 hours and stored permanently in 70% ethanol. Voucher specimens are deposited in the herpetological collection of CORBIDI in Lima, Peru. Specimens were collected under permit RDG Nº 179-2017-SERFOR-DGGSPFFS granted by the Servicio Nacional Foestal y de Fauna Silvestre (SERFOR).

Morphology

We follow Trueb & Duellman (1978), Duellman & Hillis (1987), and Duellman (2015) for external morphological characters and description format. When describing discrete, meristic, and continuous phenotypic characters we always refer to adult specimens unless otherwise stated. Likewise, coloration features included in the diagnosis always refer to live specimens unless otherwise stated. We identified sex and maturity of specimens by the presence of brood pouches, nuptial pads or vocal sac; when these structures were not present, we inspected the gonads through a longitudinal incision on the flank of the specimen. One of the co-authors (LYE) used a digital calliper to measure the following morphometric traits to the nearest 0.1 mm: snout–vent length (SVL), tibia length (TIBL) – distance from the knee to the distal end of the tibia, foot length (FL) – distance from the proximal edge of the inner metatarsal tubercle to the tip of the fourth toe, head length (HL) – straight-line distance from the posterior edge of the jaw to the tip of the snout, head width (HW) – greatest width across the maxillary arch, usually at the level of the angle of the jaws, interorbital distance (IOD) – straight-line distance between the inner edges of the upper eyelid, eyelid width (EW) – the greatest width of the upper eyelid, measured from its medial-most edge to its outer margin, internarial distance (IND) – straight-line distance between the inner edges of the narial openings, eye diameter (ED) – horizontal length of the orbit, eye–nostril distance (EN) – straight-line distance from the posterior edge of the opening of the nostril to the anterior corner of the orbit, tympanum diameter (TD) – horizontal distance between the peripheral borders of the tympanic annulus, first finger length (FFL) – straight-line distance between the proximal edge of the prepollical tubercle and the end of Finger I, Finger III length (TFL) – straight-line distance between the proximal edge of the palmar tubercle and the end of Finger III, and width of disc on third finger (TFD) – horizontal distance between the external borders of the finger pad. We assessed the relative lengths of Fingers I and II by adpressing them (Duellman 2015). We follow Savage & Heyer (1967, 1997) with the modifications of Myers & Duellman (1982) for the webbing description. For comparisons, we examined the specimens listed in Appendix I, including photographs of the type series of *Gastrotheca ossilaginis* in life. We based our comparisons with other species not listed in Appendix I on their original descriptions (Duellman et al. 2014, Duellman & Venegas 2005, 2016) and Duellman's (2015) species accounts. Characters of compared species included in the Diagnosis sections are enclosed in parentheses, unless otherwise stated.

We scanned the holotypes of the two new species, a brooding female (CORBIDI 16614) and an adult male (CORBIDI 18840) on a SkyScan 1173 Micro-CT scanner at the Instituto do Petróleo e dos Recursos Naturais (IPR) of PUCRS, Brazil. We set tube voltage and current at 60 kV and 75 µA, respectively, and image resolution was 19.1 µm and 13.8 µm, respectively. We visualized images using VG StudioMax (Volume Graphics, ver. 3.4.0). Cranial terminology follows Trueb (2015) and postcranial terminology follows Duellman & Trueb (1986) and Trueb (1973), that of manus and pes follows Fabrezi (1992, 1993, 2001), and ilium terminology follows Gómez & Turazzini (2016).

Molecular laboratory protocols and phylogenetic analyses

We performed phylogenetic analyses based on DNA sequences. While Echevarría et al. (2021) generated DNA sequences of specimen CORBIDI 16614, we generated a sequence of specimen CORBIDI 18840 for the first time. We extracted genomic DNA from a piece of muscle tissue preserved in pure ethanol using a commercial extraction kit

following the manufacturer's protocol (IBI Scientific, Peosta, USA). Using the polymerase chain reaction (PCR), we amplified a fragment of the mitochondrial gene 16S rRNA (16S) with the primers 16Sar (forward, 5'–3' sequence: CGCCTGTTTATCAAAAACAT) and 16Sbr (reverse, 5'–3' sequence: CCGGTCTGAACTCAGATCACGT) under the following thermocycling conditions: 1 cycle at 96°C/3 min; 35 cycles at 95°C/30 s, 55°C/45 s, 72°C/1.5 min; 1 cycle at 72°C/7 min (Palumbi et al. 2002). We purified the PCR products with Exosap-IT Express (Affymetrix, Santa Clara, CA) and sequenced the purified products at MCLAB (South San Francisco, CA). We deposited the 16S sequence of CORBIDI 18840 in GenBank.

We downloaded homologous DNA sequences from GenBank as well as sequences of the following genes: 12S rRNA (12S), NADH dehydrogenase subunit 1 (ND1), proopiomelanocortin A (POMC), and the recombination activating gene 1 (RAG1). We included terminals from all supraspecific taxa currently considered for *Gastrotheca* (Echevarría et al. 2021). We used *Hemiphractus proboscideus* to root the tree. All terminals and GenBank accession numbers of DNA sequences are listed in Appendix II. Terminals composed from sequences of different specimens are labelled without voucher numbers, and detailed information is included in Appendix II.

We aligned sequences of each gene in Aliview 1.17.1 (Larsson 2014), using Muscle (Edgar 2004) with default parameters. We concatenated alignments into a single matrix and exported them in Nexus format using Sequence-Matrix 1.7.8 (Vaidya et al. 2011). We assessed the best-fit partition scheme and models of evolution in Partition-Finder2 (Lanfear et al. 2017) using the corrected Akaike information criterion (AICc), as incorporated in the Cipres Science Gateway (Miller et al. 2010). We evaluated the following partition schemes: (i) unpartitioned, (ii) two partitions (mitochondrial and nuclear genes), and (iii) five partitions (by gene). We set branch lengths as linked. We conducted maximum likelihood (ML) analyses using Garli v2.01 (Zwickl 2006) as incorporated in the Cipres Science Gateway. We performed 200 independent tree searches and 1,000 bootstrap pseudoreplicates using the best models and partitions selected by PartitionFinder2. We set the parameter genthreshfortopoterm (run termination threshold of generations without significant improvement in likelihood) at 100,000, and all other parameters with default values. We used SumTrees 4.3.0 in DendroPy 4.3.0 (Sukumaran & Holder 2010) to summarize bootstrap pseudoreplicates upon the ML tree. We used MEGA 10.2.4 (Kumar et al. 2018) to compute intraspecific uncorrected p-distances for the longest (446 bp) 16S fragment without missing data. To describe the results, we follow the taxonomy proposed by Echevarría et al. (2021).

Species concept

We here follow the evolutionary species concept (Simpson 1951, Wiley 1978, de Queiroz 1998, 2007). We used characters from the integument and skeleton to diagnose and describe the two new species as identified through phylogenetic analyses of DNA sequences. Although neither species has been demonstrated to be monophyletic in our phylogenetic analysis, both are genetically and morphologically diagnosable from their more closely related species.

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: 18E1FCB3-3D8B-469F-A854-C40A0B9C7401. 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.salamandra-journal.com and zenodo.org.

Results
Phylogenetics

The molecular dataset includes 77 terminals, 63 of which represent described species of *Gastrotheca*, and 5,008 aligned positions (data matrix available from https://doi.org/10.5281/zenodo.5636357). According to the Partition-Finder results, we considered the five loci independently and applied the GTR+I+G model to each. The ML optimal tree has a log likelihood score of -40463.728785 (Fig. 1). Most clades have bootstrap (BS) values ≥ 75. However, the three most basal clades and several groups within the *Gastrotheca marsupiata* species group have BS < 50.

Among the *Gastrotheca* species groups, only the *G. fissipes* species group was recovered as non-monophyletic, although we only included one terminal of the *G. walkeri* species group. We recovered the two new species of *Gastrotheca* within the *G. marsupiata* species group, as part of a clade (BS = 87) of other north Andean species: *G. gemma*, *G. oresbios*, *G. psychrophila*, *G. spectabilis*, *G. stictopleura*, and *Gastrotheca* sp. I (CORBIDI 11776), an undescribed species. Uncorrected p-distances for the 16S fragment are 4.5–6.7 and 5.0–6.7% between the two new species and their most closely related congeners (Table 1).

Phenotypic data

We provide detailed descriptions of the integument and skeleton in each species account (illustrated in Figs 2–6 and 8–13, respectively), and summarize morphometric data in Table 2 and the main text.
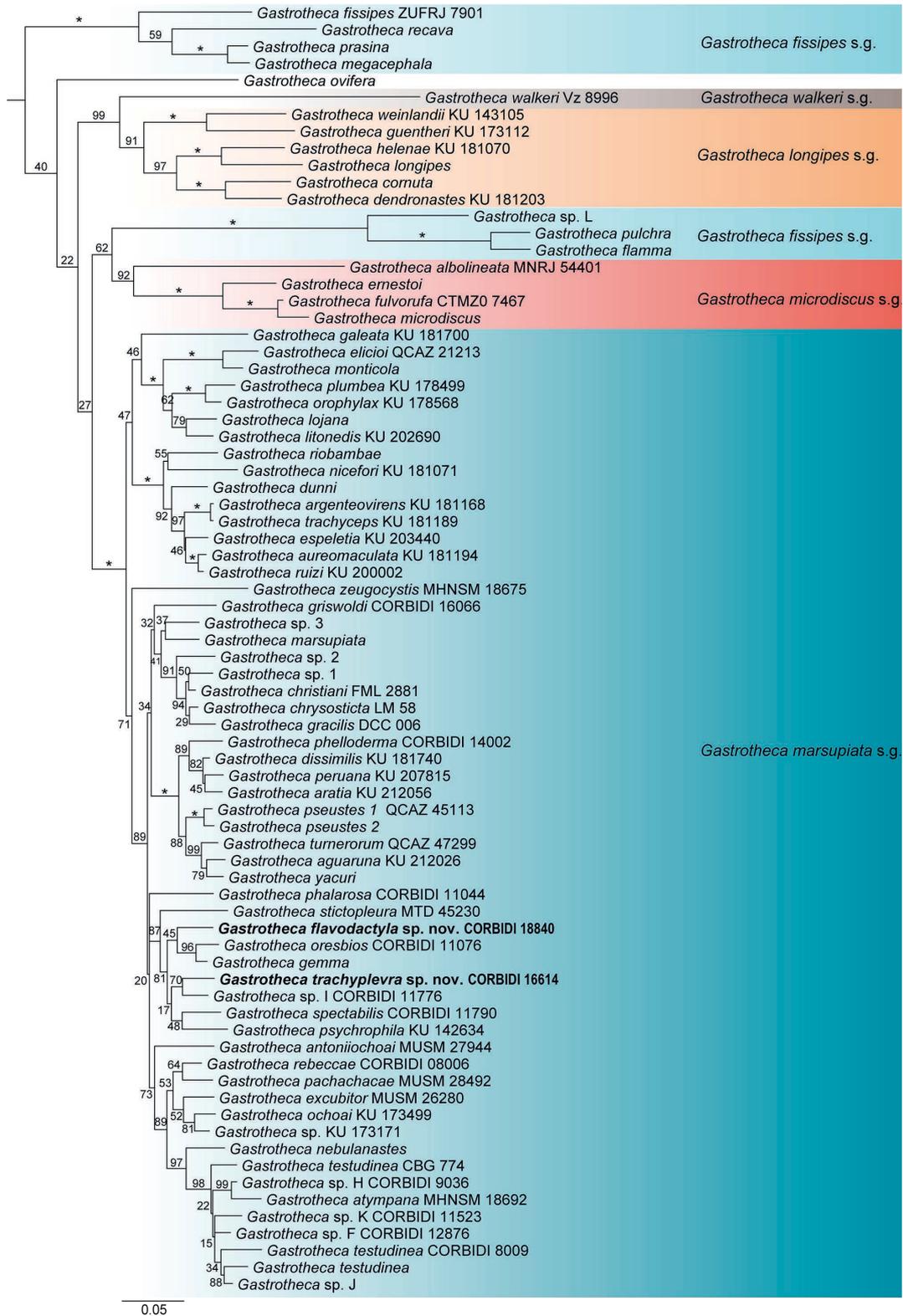
Figure 1. Maximum likelihood optimal tree of *Gastrotheca* (log likelihood = -40463.728785) inferred from 5008 bp of mitochondrial (12S rRNA, 16S rRNA, and ND1) and nuclear (POMC and RAG1) gene sequences. Numbers above branches are bootstrap support values, with an asterisk denoting 100%. Terminals composed from sequences of different specimens of the same species are labelled without voucher numbers; detailed information is included in Appendix II. Species groups are abbreviated as s.g., and *Hemiphractus proboscideus* was used to root the tree.

Table 1. Uncorrected p-distances of the mitochondrial 16S rRNA gene between *Gastrotheca flavodactyla* sp. n., *G. trachyplevra* sp. n. and closely related *Gastrotheca* species.

	1	2	3	4	5	6
1. *Gastrotheca flavodactyla* CORBIDI 18840						
2. *Gastrotheca gemma* CORBIDI 21238	5.0					
3. *Gastrotheca oresbios* CORBIDI 11076	5.2	2.5				
4. *Gastrotheca psychrophila* KU 142634	5.7	5.5	5.7			
5. *Gastrotheca stictopleura* MTD 45230	5.4	5.7	6.2	5.7		
6. *Gastrotheca trachyplevra* CORBIDI 16614	6.7	6.5	6.2	6.5	6.5	
7. *Gastrotheca* sp. I CORBIDI 11776	6.7	5.7	6.4	6.0	6.2	4.5

Table 2. Variation in measurements (mm) and proportions in *Gastrotheca flavodactyla* sp. n.

Character	CORBIDI 18840	CORBIDI 18841	CORBIDI 20470
Snout–vent length	40.8	33.3	41.9
Tibia length	21.6	18.3	22.4
Foot length	20.8	16.2	21.8
Head length	15.3	12.5	14.7
Head width	16.2	13.7	16.3
Interorbital distance	6.3	5.3	6.3
Eyelid width	3.6	2.9	3.8
Internarial distance	2.6	2.3	2.3
Eye diameter	4.5	3.1	4.0
Eye–nostril distance	4.0	3.6	3.8
Tympanum diameter	2.3	1.6	1.9
First finger length	13.0	5.9	8.3
Third finger length	14.6	11.2	14.5
Width of disc on third finger	2.3	1.9	2.5
TL/SVL	52.9	54.9	53.4

Gastrotheca flavodactyla sp. n.
Figs 2–6

ZooBank LSID: urn:lsid:zoobank.org:act: 747CE698-5699-4836-B165-47875FA08B22

Holotype. CORBIDI 18840, an adult male, from Cruz Grande, latitude 8.175510° S, longitude 77.231355° W, 3298 m a.s.l., Ongón District, Pataz province, La Libertad department, Peru, collected on 18 January 2018 by R. Pradel.

Paratypes (3). CORBIDI 18841–42 adult male and juvenile, respectively, collected with the holotype. CORBIDI 20470 an adult male, from Laguna Secseragra, latitude 8.176819° S, longitude 77.233592° W, 3336 m a.s.l., Ongón District, Pataz province, La Libertad department, Peru, collected on 19 February 2019 by R. Pradel.

Diagnosis. Assigned to the genus *Gastrotheca* due to its phylogenetic placement in our results. The two unambiguous phenotypic synapomorphies proposed for the genus (Castroviejo-Fisher et al. 2015) – the presence of an enclosed pouch with a posterior opening in adult females, and two fused pairs of bell-shaped gills derived from Branchial arches I and II in embryos – correspond to semaphoronts not available for this study. A moderately small species (SVL between 33.3 and 41.9 mm in adult males) with: (1) snout acutely rounded and rounded in dorsal and lateral views, respectively; (2) canthus rostralis slightly concave; (3) loreal region concave; (4) tibia length 53–55% of SVL, slightly longer than foot; (5) interorbital distance almost twice the width of the upper eyelid; (6) skin on dorsum smooth with low granules, skull not co-ossified, but adherent with it above, lacking transverse ridges; (7) supraciliary processes absent; (8) tubercles on heel present, low; (9) tympanic annulus smooth; (10) nuptial pad present, oval; (11) vocal sac not evident externally; (12) Finger I slightly shorter than Finger II, discs wider than digits; (13) webbing between fingers basal; (14) foot webbing basal, extending to penultimate subarticular tubercle on the postaxial side of Toes II (2) and III (2⁺) and on the preaxial side of Toe V (2⁺); (15) dorsum green or brown with spots, blotches or wide dorsolateral stripes, dorsal surface of finger and toe pads yellow; (16) dark brown or black blotches

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(melanophores) forming a broad and discontinuous vertebral stripe extending from interorbital region to above the cloaca, more evident in preserved specimens; (17) dorsolateral stripe absent; (18) flanks green with or without black or brown blotches, or golden spots; (19) gular region yellow with dense black reticulation or uniformly black; venter yellow with a diffuse light green spot and melanophores in the middle or greyish cream; ventral surface of thighs black or dark grey; palms and soles black or dark grey due to abundant melanophores, which extend to all ventral surfaces of fingers and toes but are more abundant on Fingers III and IV, and Toes III and IV; (20) iris copper-red or yellow with black reticulation. Females unknown, for which reason the brood pouch opening and reproduction mode, two characters often used in *Gastrotheca* species diagnosis, are unknown as well.

Comparisons. According to our phylogenetic results, *Gastrotheca flavodactyla* is more closely related to *G. gemma*, *G. oresbios*, *G. psychrophila*, *G. spectabilis*, *G. stictopleura*, the new species described below, and one undescribed species than to all other sampled species of the genus. The smaller size of adult males of *G. flavodactyla* SVL = 33.3–41.9 mm, N = 3, distinguishes this species from adult males of *G. gemma* (SVL = 56.9–59.5, N = 2) and *G. psychrophila* (SVL = 45.8–49.9 mm, N = 3). It can be further distinguished from *G. psychrophila* by having a bifid palmar tubercle (trifid); dorsum with dark brown or black blotches forming a broad and discontinuous middle stripe that extends from the interorbital region to above the cloaca (dorsum and dorsal surface of head without markings). The smooth skin with low granules on the dorsum of *G. flavodactyla* differentiates it from *G. gemma* (uniformly granular in males) and *G. oresbios* (shagreen with scattered tubercles). A smooth tympanic annulus distinguishes *G. flavodactyla* from *G. gemma* (wrinkled or tuberculate) and *G. oresbios* (granular). A smooth supratympanic fold distinguishes *G. flavodactyla* from *G. oresbios* (tuberculate). Furthermore, *G. flavodactyla* differs from *G. gemma* by having the iris copper-red or yellow with black reticulation (silvery with a light blue hue or turquoise with thin black reticulation with or without an orange ring); labial stripe absent (chocolate or yellowish green labial stripe). It differs from *G. spectabilis* by having the gular region yellow with dense black reticulation or black (dull greyish brown). Finally, the absence of a dorsolateral stripe and small white spots in the posterior portion of the flanks distinguish *G. flavodactyla* from *G. stictopleura* (present).

Among the *Gastrotheca* from the Andes of northern Peru, *G. aguaruna*, *G. dysprosita*, *G. monticola*, and *G. ossilaginis* are similar to some specimens of *G. flavodactyla* in having a green dorsal coloration. An acutely rounded snout in dorsal view differentiates *G. flavodactyla* from *G. aguaruna, G. dysprosita*, and *G. monticola* (rounded). Furthermore, *G. flavodactyla* can be differentiated from *G. aguaruna* by having an interorbital distance that is greater than the width of the upper eyelid (about equal); black or dark grey ventral surface of thighs (cream). The moderately small size of *G. flavodactyla*, adult males SVL = 33.3–41.9 mm, N = 3, differentiates it from the moderately large *G. dysprosita* (adult males SVL = 45.9–60.5 mm, N = 2) and *G. monticola* (adult males SVL = 48.0–57.7 mm, N = 11). The absence of middorsal and dorsolateral stripes, and of black spots on the flanks and thighs distinguish *G. flavodactyla* from *G. dysprosita* and *G. monticola*, respectively. *Gastrotheca flavodactyla* differs from *G. ossilaginis* by having skin adherent to the skull, not co-ossified (skin co-ossified with underlying cranial elements); the skin on the throat smooth (coarsely areolate); dark brown specks over the lips (absent); dorsal surface of digital discs yellow (green or tan).
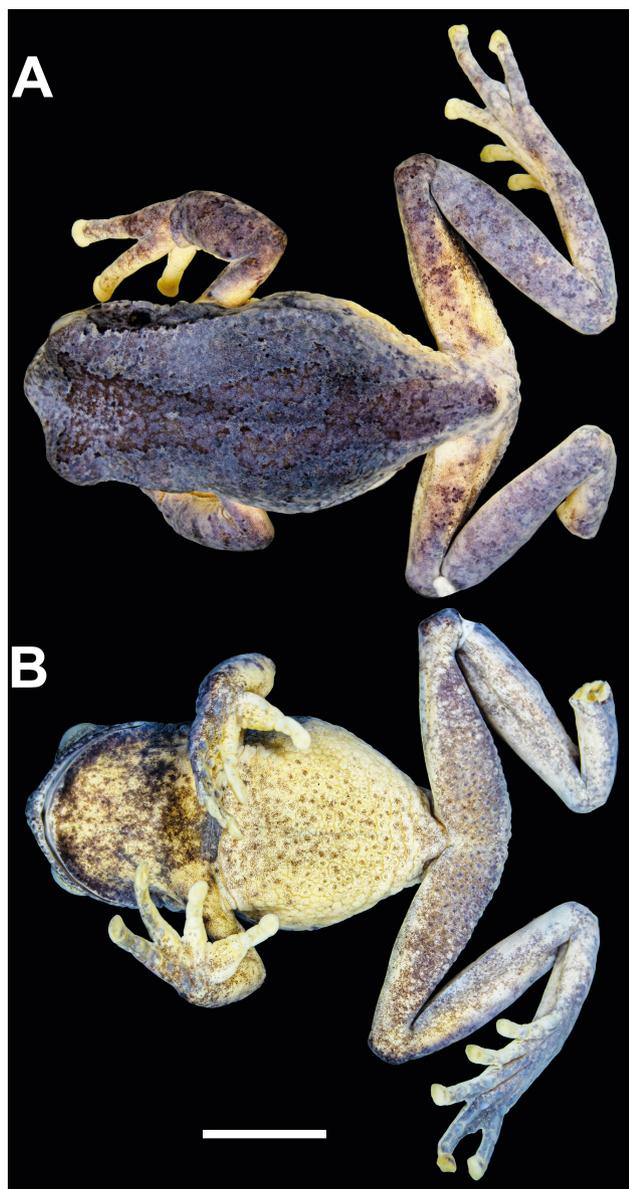
Figure 2. Preserved holotype of *Gastrotheca flavodactyla* sp. n. (CORBIDI 18840; male, SVL = 40.8 mm) in dorsal (A) and ventral (B) views. Scale bar = 10 mm. Photographs by L. A. García-Ayachi.

Other *Gastrotheca* species from northern Peru with a general shape similar to *G. flavodactyla* are *G. dissimilis, G. peruana, G. phalarosa,* and *G. phelloderma.* However, the absence of pustules on the dorsum distinguishes *G. flavodactyla* from all these species. *Gastrotheca flavodactyla* is similar in size and general shape to *G. rebeccae* from the eastern slopes of the Cordillera Oriental in southern Peru. It differs from *G. rebeccae* by having tubercles on its heels (absent); and dorsal surface of digital discs yellow (green or tan). Green or tanned individuals of the widely distributed *G. testudinea* may be confused with *G. flavodactyla.* The new species can be differentiated from *G. testudinea* by being of moderately small size, adult males SVL = 33.3–41.9 mm, N = 3 (large size, adult males SVL = 49.8–61.1 mm, N = 8); snout acutely rounded in dorsal view (rounded); smooth tympanic annulus (granular); foot webbing extending to penultimate subarticular tubercle on the preaxial side of Toe V (extending above the penultimate subarticular tubercle of Toe V).

Description of the holotype. An adult male in a good state of preservation, with the left foot removed and preserved as a tissue sample for molecular analyses (Figs 2–4A, B); SVL = 40.8 mm; head wider than long; snout acutely rounded in dorsal view, and rounded in profile; canthus rostralis slightly concave; loreal region concave; lips rounded, broad; skin on the head smooth and adherent to skull, granular on eyelids; width of upper eyelid 57% of interorbital distance; internarial area flat; nostrils not protuberant, directed anterolaterally, to the level of anterior margin of lower jaw; diameter of eye greater than its distance from nostril; tympanum round, separated from the eye by
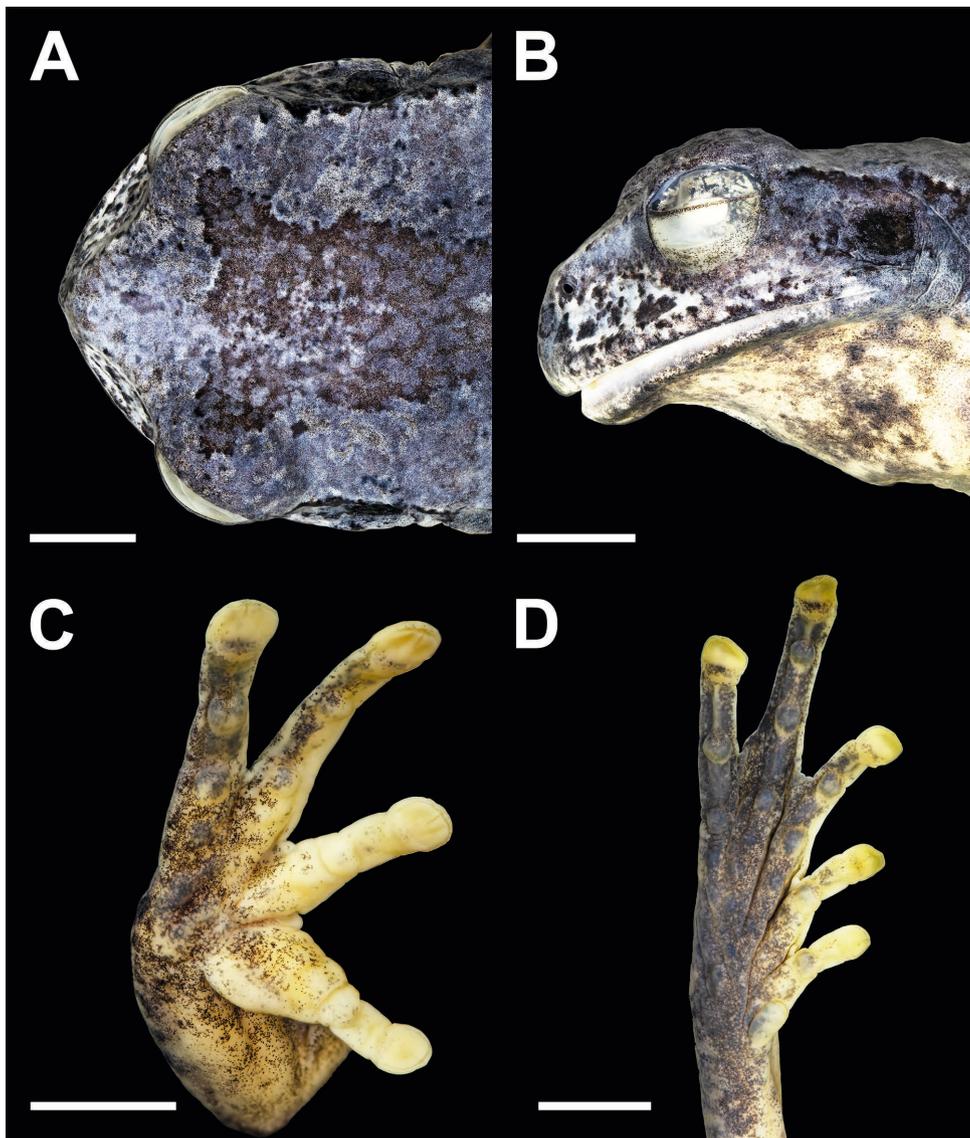
Figure 3. Dorsal (A) and lateral (B) views of the head, and views of the palm (C) and sole (D) of the preserved holotype of *Gastrotheca flavodactyla* sp. n. (CORBIDI 18840). Scale bar = 5 mm. Photographs by L. A. García-Ayachi.

a distance larger than the diameter of tympanum; tympanic annulus distinct, smooth; supratympanic fold distinct, smooth, extending from the top edge of the tympanum to the insertion of the forelimb. Dentigerous vomerine processes narrowly separated medially, bearing five attached teeth.

Arm robust; ulnar tubercles absent; hand and fingers moderately large (TFL 36% of SVL); fingers with basal webbings between all fingers; discs rounded, wider than digits, width of disc of Finger III slightly greater than diameter of tympanum; relative lengths of fingers: I<II<IV<III; subarticular tubercles prominent, round in dorsal and profile views, nonbifid; supernumerary tubercles, round; palmar tubercle barely visible, bifid; prepollical tubercle large, oval. Nuptial pad present, oval, same colour as palm. Vocal sac not evident externally. Hind limb slender; tibia length 53% of SVL; foot length 51% of SVL; calcar and tarsal tubercles absent; inner tarsal fold present; outer metatarsal tubercle absent; inner metatarsal tubercle oval, prominent; toes moderately long; relative length of toes: I<II<III<V<IV; webbing basal between toes, extending to penultimate

subarticular tubercle on postaxial side of Toes II (2) and III (2^+) and on preaxial side of Toe V (2^+); subarticular tubercles moderately large, rounded; supernumerary tubercles, numerous and rounded.

Skin on dorsum smooth with low granules; skin adherent to skull on dorsal surface of head; skin on flanks covered by low, round granules; skin on throat and chest smooth; skin on ventral surface of forelimbs smooth; skin on venter granular; ventral surface of thighs granular; posterior surface of thighs smooth with round granules on the base; ventral surface of shanks smooth; no enlarged tubercles below the cloacal opening.

In life (Figs 4A–B): all dorsal surfaces, except forelimbs, green. Dense dark brown reticulations on head and shanks, and lighter brown reticulations on dorsum and tarsus. Dorsal surfaces of forelimbs and feet light green with few dark brown blotches. Dorsally, finger and toe pads yellow. Lateral surface of head green with dark brown specks, present all over the lips. Tympanum almost completely black. Ventrolateral region and dorsal surface of thighs green. Throat yellow with dense black reticulation. Chest yel-
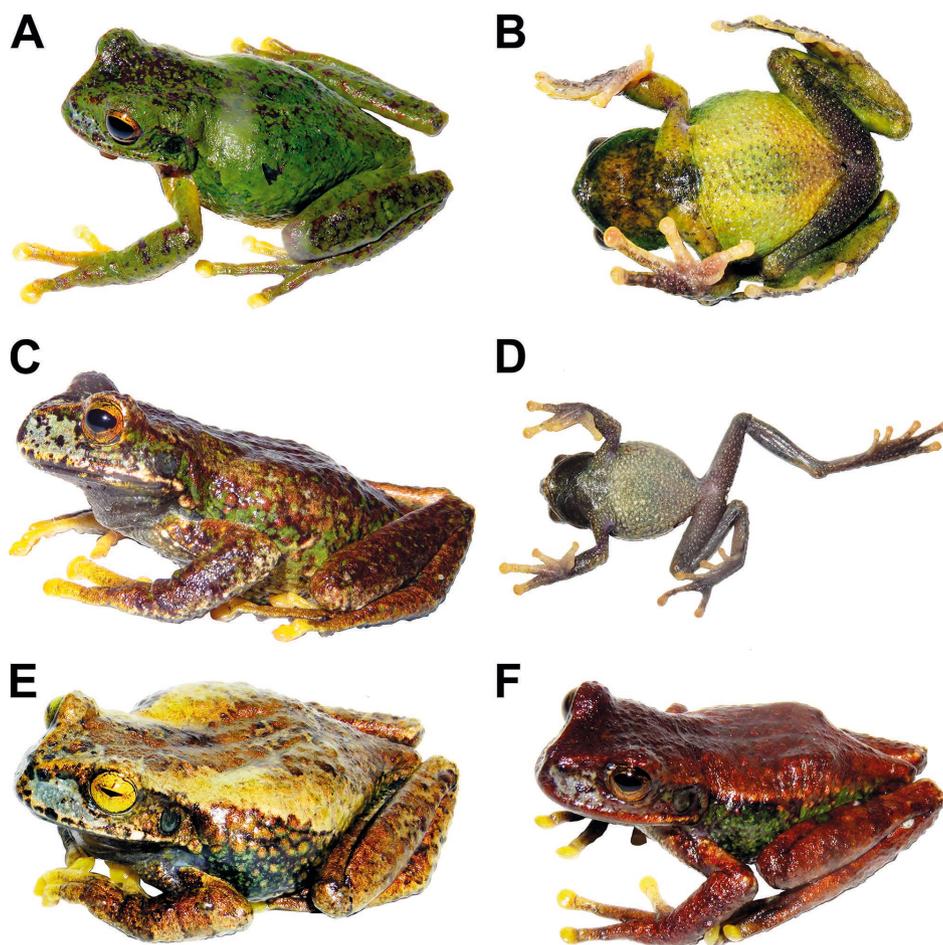
Figure 4. *Gastrotheca flavodactyla* sp. n. in life. Dorsolateral (A) and ventral (B) views of the male holotype (CORBIDI 18840), 40.8 mm SVL. Lateral (C) and ventral (D) views of a male paratype (CORBIDI 18841), 33.3 mm SVL. Dorsolateral (E) views of a male paratype (CORBIDI 20470) and of a juvenile paratype (CORBIDI 18842). Photographs by R. Pradel.

low with a black stain, continuous with throat coloration. Venter yellow with a diffuse light green spot and melanophores in the middle. Ventral surface of forelimbs yellow; palmar surface half black and half cream with black scattered melanophores, Fingers I and II pale yellow, Fingers III and IV black due to abundant melanophores. Thighs black, shanks green and partially covered with black melanophores, tarsus light green. Iris copper-red with black reticulation.

In preservative (Figs 2–3): dorsal surfaces greyish blue, dorsal inner half and posterior surface of thighs cream with a greyish blue hue and specks. All yellow coloured regions turned cream.

Measurements of the holotype (in mm): SVL: 40.8, TIBL: 21.6, FL: 20.8, HL: 15.3, HW: 16.2, IOD: 6.3, EW: 3.6, IND: 2.6, ED: 4.5, EN: 4.0, TD: 2.3, FFL: 13.0, TFL: 14.6, TFD: 2.3.

Intraspecific variation. The variation in measurements and proportions in adult specimens is presented in Table 2. The two adult male paratypes differ in coloration from the holotype. Specimen CORBIDI 18841 (Figs 4C–D) has a brown dorsum with green spots; flanks and ventrolateral region green with brown blotches; gular region black; chest grey; venter greyish cream; ventral surfaces of thighs and tarsi grey. Specimen CORBIDI 20470 (Fig. 4E) has a brown dorsum with broad pale yellow dorsolateral stripes; flanks golden with black reticulation and small green spots; ventrolateral region green with black reticulation and golden spots. Paratype CORBIDI 20470 has a yellow iris with a few black reticulations.

The juvenile CORBIDI 18842 (Fig. 4F) has a uniformly reddish brown dorsal coloration; flanks and ventrolateral region green with small black blotches. Gular region golden with a faded light brown coloration; chest golden; upper half of the venter golden and lower half dark brown; ventral surfaces of forelimbs and hind limbs dark brown; ventral surface of pads on fingers and toes yellow. Iris light brown with golden glints.

Osteology. This description is based on the reconstructed 3D model of the skeleton of the adult male holotype of *Gastrotheca flavodactyla* (CORBIDI 18840, SVL = 40.8 mm).

Cranial osteology. The skull of *Gastrotheca flavodactyla* is wider than long and measures 13.3 mm in length from the jaw joint to the tip of the snout and 15.9 mm in width at the level of the quadratojugal. The skull is hyperossified, with irregular pit and ridge dermal sculpturing on the frontoparietals, squamosals, maxillae, nasals, and the exposed sphenethmoid (Fig. 5A). The frontoparietals have a complete medial articulation with one another. A wide supraorbital and otic flange is present, but does not contact the head of the squamosal and a temporal arcade is therefore absent. The frontoparietal covers the anterior epiotic eminence of the prootic, and the carotid canal is partially closed. The skull roof is wide at the point of articulation between the frontoparietals and sphenethmoid, and the articulation surface of the sphenethmoid is convex and rounded. The nasals are expanded and broadly articulate with the pars facialis of the maxilla, forming a bony anterior orbital margin. The nasals overlap the anterior margin of the sphenethmoid, extend posteriorly, and contact the anterior edges of the frontoparietals. In lateral view (Fig. 5C), the dorsoanterior extent of the nasals is extended to the level of the alary processes of the premaxilla. The maxillary arcade is complete. The quadratojugal is overlapped laterally by the maxilla. The short postorbital process of the maxilla articulates with the elongated zygomatic ramus of the squamosal via a broad, nearly horizontal articulation, forming the posterior margin of the orbit. The head of the squamosal has a moderately wide crest, and the otic plate of the squamosal covers 20% of the width of the crista parotica. The anterior ramus of the pterygoid bifurcates distally, articulating with the zygomatic ramus of the squamosal via a high dorsal process and the pars palatina of the maxilla. The premaxillae are broad and bear alary processes that are deflected posteriorly at an 80° angle, forming a high and nearly square snout in lateral profile. The neopalatines are widely separated from one another and form a posterior margin to the choana (Fig. 5B). The vomers are widely separated from the medial ends of the neopalatines and from the anterior tip of the parasphenoid. The dentigerous processes of the vomers are located at the level between the middle quadrant of the choanae. The prechoanal processes of the vomers nearly contact the lingual surface of the pars facialis of the maxilla, supporting the anterior margin of the choana. The postchoanal processes of the vomers are short and support one third of the medial choanal margin. The parasphenoid is synostosed to the overlying prootics and exoccipitals. The cultriform process narrows abruptly anterior to the optic fenestra and terminates as a tapered point just posterior to the level of the neopalatines. The posterior extent of the bony sphenethmoid does not contact the prootic. There are 45 tooth loci (25–28 attached, pedicellate teeth) on each maxilla, 10 tooth loci (8–9 attached teeth) on each premaxilla, and 7 tooth loci (5 attached teeth) on each vomer. The dentary is edentate (Fig. 5D).

Vertebral column. Eight nonimbricated presacral vertebrae (Fig. 6A). The atlas lacks transverse processes, Presacrals III and IV bear thicker and longer processes than other presacral vertebrae. Transverse processes of Presacrals II–V are uniform in width. Transverse processes of Presacrals VI–VIII are slightly narrower distally. Transverse processes of Presacral II are anteriorly directed, transverse processes on Presacrals III and VI–VIII are perpendicular to the notochordal axis, and transverse processes on Presacrals IV–V are posteriorly directed. Relative lengths of transverse processes of presacrals and sacral diapophyses (SD): SD>III>IV>II>V–VIII. The anterior margin of the sacral diapophyses is perpendicular to the longitudinal axis of the vertebral column. The distal ends of the sacral diapophyses are approximately twice the width of the base. Both the anterior and posterior margins of the sacral diapophyses are straight. The lateral margins are convex. The urostyle is shorter than the presacral portion of the vertebral column and has a bicondylar articula-

tion with the sacrum. The shaft of the urostyle is dorsoventrally compressed in cross section. The width of the shaft is uniform along its length. The urostyle bears a dorsal crest along half of the bone shaft, the crest is higher anteriorly and gradually diminishes in height posteriorly.

Pectoral girdle. Arciferal pectoral girdle (Fig. 6C). Clavicles curved, concave, and with the lateral region wider. Clavicles well developed posterolaterally, in contact with the glenoid head of the humerus. Medial tips of clavicles not in contact, reaching beyond the level of the anterolateral end of each clavicle. In ventral view, the sternal and glenoid ends of the coracoids have the same width and the midshaft has two thirds the width of the lateral ends. The sternal end is concave and the glenoid end is flattened. The sternal ends of the coracoids are not in contact. The scapula is stout, longer than the coracoid. The scapula bears a prominent acromion processes. The pars glenoidalis is narrower than the pars acromialis. The suprascapular end is narrower than the zonal end. The clavicle, coracoid and scapula form the margins of the glenoid fossa. Cleithrum and ossified portion of the suprascapula fused.

Pelvic girdle. In dorsal view, the ilial shafts have a V-shaped configuration. The ilial shaft does not bear a dorsal crest (Fig. 6D). The dorsal prominence is conspicuous; the dorsal protuberance is elongate and positioned above the dorsal margin of the acetabular fossa. The anterior margin of the ventral acetabular expansion is straight and forms an obtuse angle with the ilial shaft. The articulations of the ilium with the ischium and pubis are evident, but not the articulation of the pubis and the ilium.

Forelimb and manus. The humerus has a prominent ventral crest, extending along more than half the length of the bone, higher at the proximal end of the humerus and gradually diminishing in height distally. The distal head (eminentia capitata) is expanded and it is wider than the glenoid head (caput humeri). The radioulna is flattened and distinctly wide distally; the sulcus intermedius is indicated by a distinct groove on the distal half of the bone. The carpus is composed of radial, ulnar, distal carpal 3-4-5, Element Y fused to distal Carpal 2, and elements of the prepollex (Fig. 6B). The phalangeal formula is 2-2-3-3. The terminal phalanges have a rounded proximal base, and be-
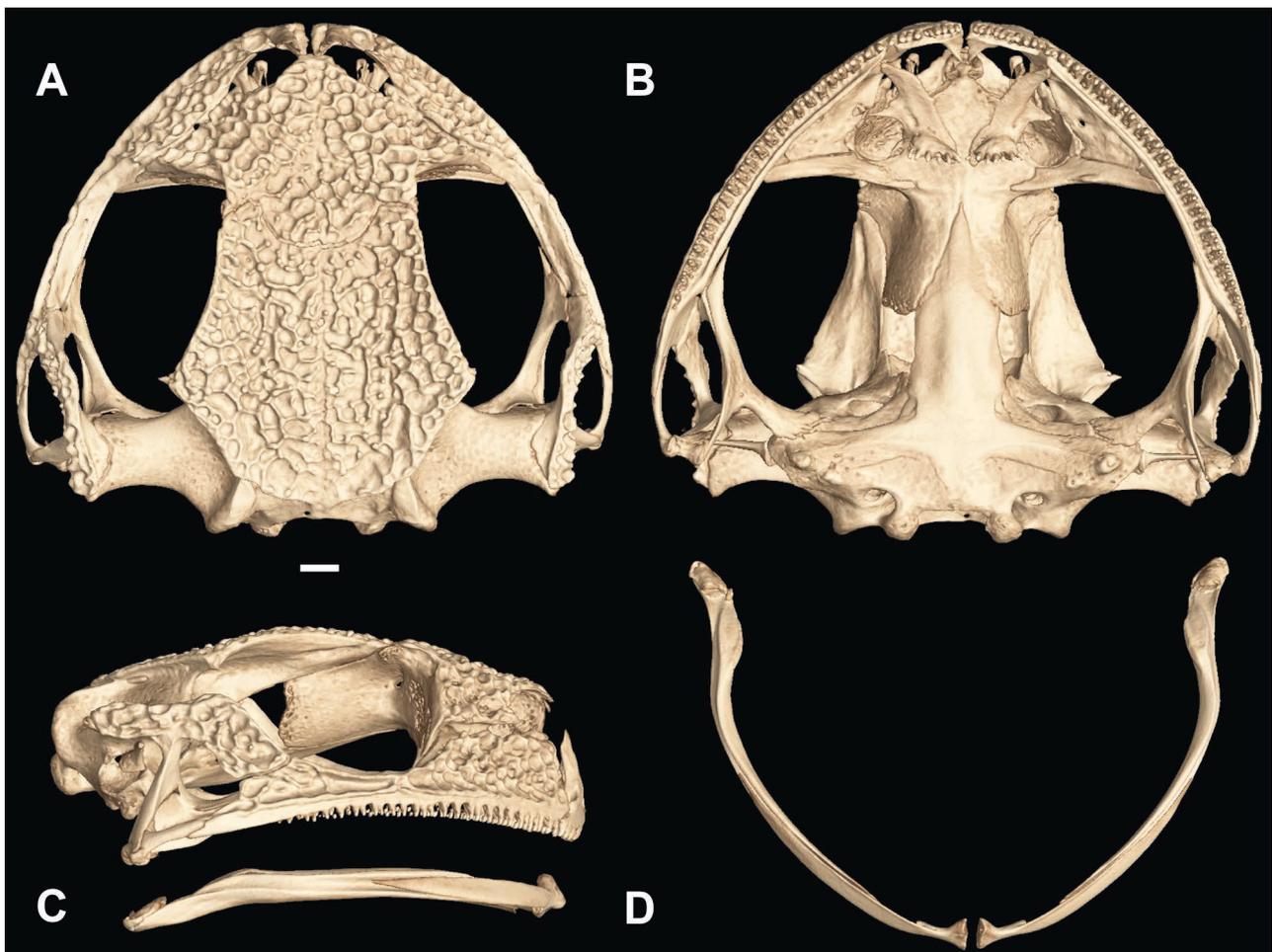
Figure 5. Skull of *Gastrotheca flavodactyla* sp. n. (CORBIDI 18840) as visualized via Micro-CT scanning in dorsal (A), ventral (B), and right lateral (C) views. D) Mandible in dorsal view. Scale bar = 1 mm.

come gradually narrower from the base towards the tip. The prepollex has two elements.

Hindlimb and pes. The femur is slightly sigmoid, shorter than the tibiofibula. The sulcus intermedius of the tibiofibula is shallow. Tibia and fibula are separated medially and fused at the proximal and distal ends. The tarsal elements are: Element Y, two distal tarsals, and the prehallux (Fig. 6B). The phalangeal formula is 2-2-3-4-3. The terminal phalanges have a rounded proximal base, and become gradually narrower from the base towards the tip.

Distribution and natural history. *Gastrotheca flavodactyla* is known so far only from Cruz Grande and Laguna Secseragra, at 3298 and 3336 m a.s.l. respectively, in La Libertad department. These localities are less than 1 km apart and lie in the humid montane forest of the headwaters of the Abiseo River, Cordillera Central Páramo ecoregion (Olson et al. 2001), in the northern portion of the Central Andes (Fig. 7). All specimens were found inactive under stones along the edge of a road at the transition between elfin forest and grassland between 14:20 and 17:00 hours, where they seemed to be resting.

Etymology. The specific epithet combines the Latin word *flavo*, an adjective meaning "yellow", and the Greek word *dáchtyla*, a noun meaning "fingers". This specific name is used in apposition and refers to the yellow finger and toe pads of the new species in life.
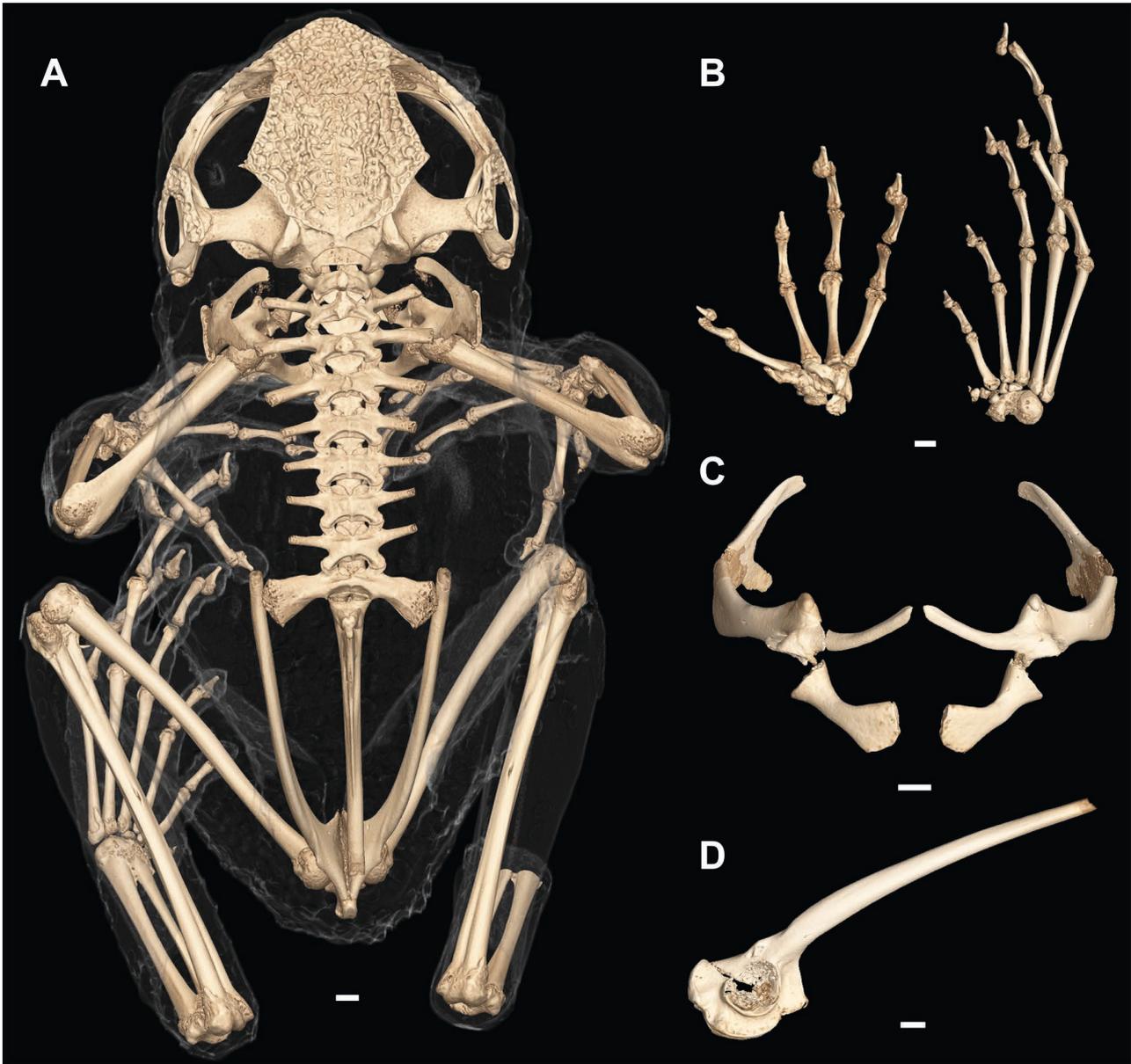
Figure 6. Skeleton of *Gastrotheca flavodactyla* sp. n. (CORBIDI 18840) as visualized via Micro-CT scanning in dorsal view (A). (B) Left manus and pes in ventral view, (C) pectoral girdle in ventral view, and (D) ilium in right lateral view. Scale bar = 1 mm.

Gastrotheca trachyplevra sp. n.
Figs 8–10, 11F, 12–13

Gastrotheca sp. G (Echevarría et al. 2021)

ZooBank LSID: urn:lsid:zoobank.org:pub: 7DAC8CA4-ECFC-41B3-9B56-4D5F58A9B404

Holotype. CORBIDI 16614, a brooding female, from María, latitude 6.335803° S, longitude 78.0132069° W, 3434 m a.s.l., Colcamar District, Luya province, Amazonas department, Peru, collected on 4 December 2015 by P. J. Venegas.

Paratype. CORBIDI 16613, adult male, collected with the holotype.
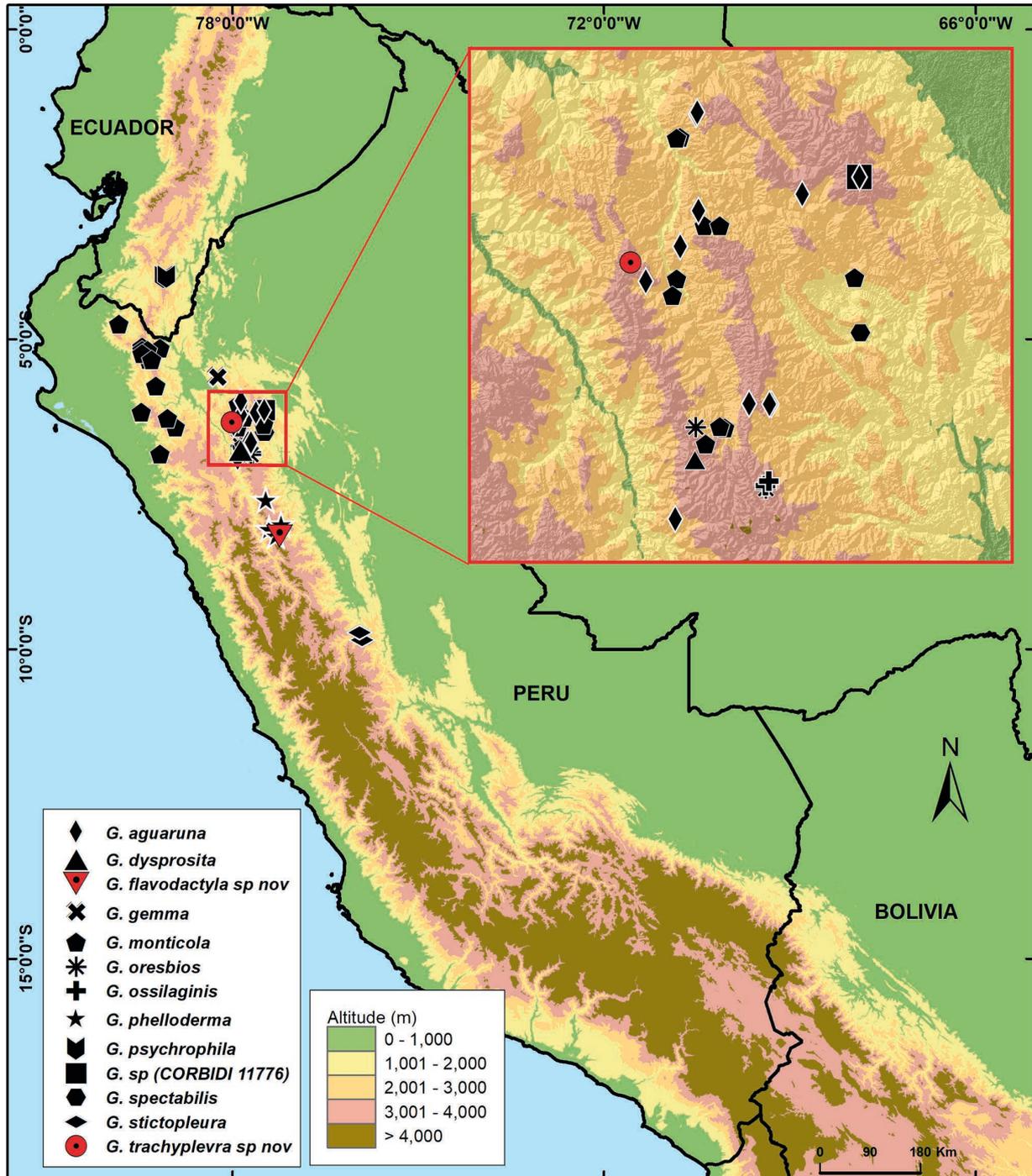
Figure 7. Map of western South America and inset map of the Cordillera del Colán, with symbols indicating the known localities of *Gastrotheca flavodactyla* sp. n., *G. trachyplevra* sp. n., and their closest and most similar Andean congeners.

Diagnosis. Assigned to the genus *Gastrotheca* by the presence of a closed brood pouch on the dorsum of the only known adult female, and its phylogenetic placement in the genus. A moderately small species (43.9 mm SVL in one female, 33.5 mm SVL in one male) with: (1) snout rounded and inclined anteroventrally in dorsal and lateral views, respectively; (2) canthus rostralis concave; (3) loreal region concave; (4) tibia length 40–41% of SVL, slightly shorter than foot; (5) interorbital distance less than twice the width of upper eyelid; (6) dorsum covered with large and closely packed rounded pustules and two prominent paravertebral longitudinal pustular ridges, skin not co-ossified with skull; (7) supraciliary processes absent; (8) small rounded tubercles on heel present; (9) tympanic annulus smooth; (10) nuptial pad present, oval; (11) vocal sac not evident externally; (12) Finger I longer than Finger II, discs barely wider than digits; (13) fingers unwebbed, basal webbing only between Fingers II and III; (14) toe webbing basal, extending to penultimate subarticular tubercle on preaxial (2$^+$) and postaxial (2–2$^-$) sides of Toe II, on postaxial side of Toe III (2$^+$), and on preaxial side of Toe V (2$^+$); (15) female dorsal coloration light brown with black and dark brown blotches; male dorsal coloration green with brown blotches; (16) male and female's head markings consisting of small brown blotches; (17) dorsolateral stripe absent; (18) flanks with the same coloration and pattern as the dorsum; (19) gular region dull white in female and golden in male, venter dull white with a pink or light orange hue over the posterior edge in female and male, respectively, ventral surface of thighs red, brighter in the female, and greyish towards the knee, palms and soles grey with reddish and yellowish hues in female and male, respectively; (20) iris dark brown with a few golden specks and a golden pupillary ring; (21) brood pouch single, dorsal, with a V-shaped opening; (22) direct development of embryos into froglets.

Comparisons. *Gastrotheca trachyplevra* differs from all other *Gastrotheca* species by its unique dorsal skin texture, with: (1) a distinctly thick and elevated supratympanic fold, extending from the top edge of tympanum to flank, continuous or fused with the dorsolateral row of elongated pustules; (2) dorsum covered with large and closely packed rounded pustules; (3) two prominent paravertebral longitudinal pustular ridges.

Gastrotheca trachyplevra is more closely related to *G. flavodactyla*, *G. gemma*, *G. oresbios*, *G. psychrophila*, *G. spectabilis*, *G. stictopleura*, and one undescribed species. Besides the aforementioned dorsal skin texture, having Finger I longer than Finger II distinguishes *G. trachyplevra* from *G. gemma*, *G. flavodactyla*, *G. oresbios*, and *G. psychrophila* (Finger I shorter than Finger II). A smooth tympanic annulus differentiates *G. trachyplevra* from *G. gemma* (wrinkled or tuberculate) and *G. oresbios* (granular). A distinct red blotch covering the inner half of the ventral surface of thighs distinguishes *G. trachyplevra* from *G. flavodactyla*, *G. psychrophila* and *G. spectabilis* (ventral surfaces of thighs dull, without bright coloration). Absence of a labial stripe (present), and a light brown or green dorsum with dark blotches (green with small flecks or dots) distinguish *G. trachyplevra* from *G. gemma*. Presence of tarsal fold differentiates *Gastrotheca trachyplevra* from *G. oresbios* (absent). *Gastrotheca trachyplevra* can be distinguished from *G. spectabilis* by having Finger I being longer than Finger II (equal); and by the absence of a middorsal marking (present). *Gastrotheca trachyplevra* can be distinguished from *G. stictopleura* by having a tibia length of 40–41% SVL (49–59%), and absence of dorsolateral stripe (present).

Other Peruvian *Gastrotheca* species with pustular dorsal skin are *G. aratia*, *G. dissimilis*, *G. peruana*, *G. phalarosa*, and *G. phelloderma* (Fig. 11). Among them, *G. phelloderma* is the only one with pustular longitudinal paravertebral
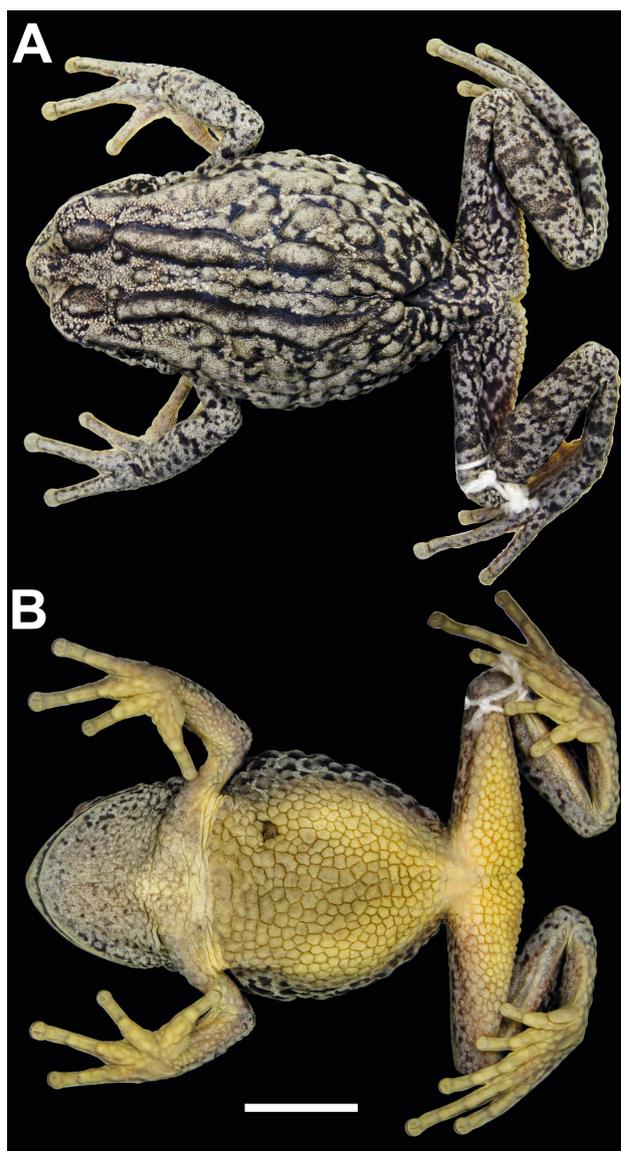
Figure 8. Preserved holotype of *Gastrotheca trachyplevra* sp. n. (CORBIDI 16614; female, SVL = 43.9 mm) in dorsal (A) and ventral (B) views. Scale bar = 10 mm. Photographs by L. A. García-Ayachi.

ridges and many scattered pustules. However, *G. phelloderma* can be differentiated from *G. trachyplevra* by having (character states of the latter in parentheses): paravertebral longitudinal pustular ridges thin and low (comparatively thicker and higher); thigh ventral surfaces cream (proximal half red); and reddish brown markings on dorsal and lateral surfaces (absent).

Description of the holotype. An adult brooding female in a good state of preservation, with a small portion of liver removed through a ventral cut on the left anterior side of the venter and preserved as a tissue sample for molecular analyses (Figs 8–10A, B); SVL = 43.9 mm; head wider than long; snout acutely rounded in dorsal view, inclined anteroventrally in profile; canthus rostralis concave; loreal region concave; lips rounded, broad; skin on the head finely granular; interorbital distance 66% of width of upper eyelid; internarial area slightly convex; nostrils protuberant, directed anterolaterally, behind the level of anterior margin of lower jaw; diameter of eye greater than its distance from nostril; tympanum ovoid, separated from the eye by a distance larger than the diameter of tympanum; tympanic annulus distinct, smooth; supratympanic fold distinct and thick, extending from top edge of the tympanum to the insertion of the forelimb and continuous with the thick warts of the ventrolateral surface of body. Dentigerous vomerine processes narrowly separated medially, bearing four attached teeth.

Arm robust; ulnar tubercles present; hand and fingers moderately large (TFL 31% of SVL); basal webbing between Fingers II and III; discs rounded, not much wider than digits, width of disc of Finger III smaller than diameter of
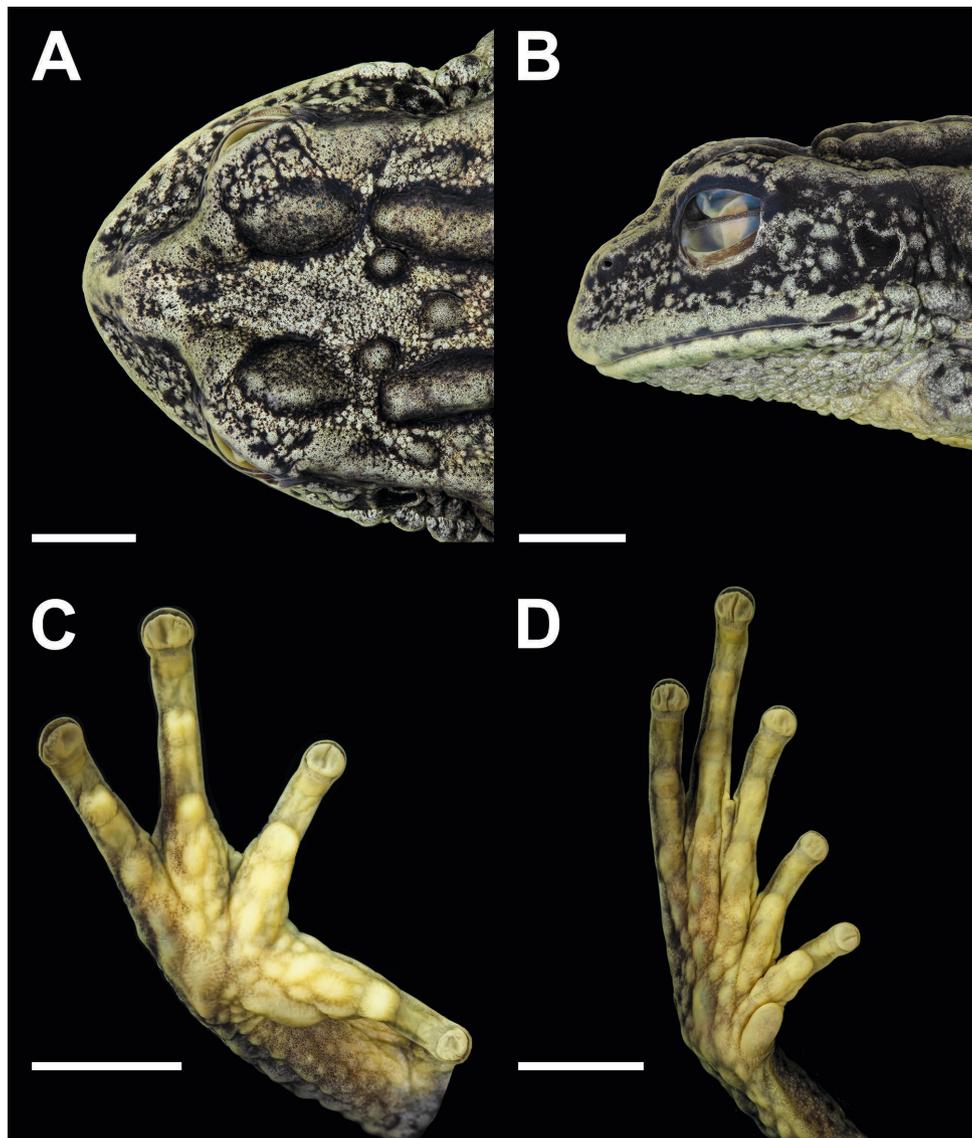
Figure 9. Dorsal (A) and lateral (B) views of the head, and views of the palm (C) and sole (D) of the preserved holotype of *Gastrotheca trachyplevra* sp. n. (CORBIDI 16614). Scale bar = 5 mm. Photographs by L. A. García-Ayachi.

tympanum; relative lengths of fingers: II<I<IV<III; subarticular tubercles prominent, round in dorsal and profile views, nonbifid; supernumerary tubercles, round; palmar tubercle barely visible, bifid, prepollical tubercle large, oval. Nuptial pad oval, same colour as palm. Hind limb robust; tibia length 40% of SVL; foot length 43% of SVL; calcar and tarsal tubercles absent; inner tarsal fold present; outer metatarsal tubercle present; inner metatarsal tubercle oval prominent; toes moderately long; relative length of toes: I<II<III<V<IV; toe webbing basal, except on postaxial side of Toe II (2), Toe III (2$^+$), and preaxial side of Toe V (2$^+$); subarticular tubercles moderately large, rounded; supernumerary tubercles, numerous, and rounded; outer edge of Toe V bears a short fringe.

Skin on dorsum covered with large and closely packed rounded pustules, with two prominent paravertebral longitudinal pustular ridges; two large and rounded pustules on each eyelid; rounded and large granules around tympanic annulus; skin on flanks covered by large ovoid pustules; skin on throat and chest granular; ventral surfaces of thighs and arms granular; skin on belly granular; ventral surface of shanks smooth; posterior surface of thighs granular; no enlarged tubercles below the cloacal opening. Pouch opening V-shaped with anterior border at the level of the posterior edge of sacrum.

In life (Figs 10A, B): dorsal surfaces light brown with dark brown speckles on the head; dark brown blotches between pustules on dorsum; fore and hind limbs with small dark brown spots; a dark brown stripe on the thighs, and two dark brown stripes on shanks; lateral surface of head light brown with dark brown blotches, tympanum almost completely dark brown; flanks dark cream with dark brown blotches; ventrolateral region dark cream with small dark brown blotches. Ventral surfaces of throat and chest dark cream with few brown flecks on the lower lateral edges of the throat; venter and ventral surfaces of forelimbs and hind limbs dull white; a pink hue over the posterior edge of venter; a red blotch over the proximal half of the ventral thigh. Iris dark brown with a few golden specks, golden pupillary ring present.

In preservative (Fig. 8): dorsum grey with black blotches and markings; gular region, chest, and shanks light grey, all other ventral surfaces pale yellow.

Measurements of the holotype (in mm): SVL: 43.9, TIBL: 17.7, FL: 18.7, HL: 14.4, HW: 16.5, IOD: 3.2, EW: 3.7, IND: 2.8, ED: 4.1, EN: 3.7, TD: 1.9, FFL: 10.0, TFL: 13.6, TFD: 1.7.

Colour of the holotype. In life (Figs 10A, B): dorsal surfaces light brown with dark brown speckles on the head; dark brown blotches between pustules on dorsum; forelimbs and hind limbs with small dark brown spots; a dark brown stripe on the thighs and two dark brown stripes on shanks; lateral surface of head light brown with dark brown blotches, tympanum almost completely dark brown; flanks dark cream with dark brown blotches; ventrolateral region dark cream with small dark brown blotches. Ventral surfaces of throat and chest dark cream with few brown flecks
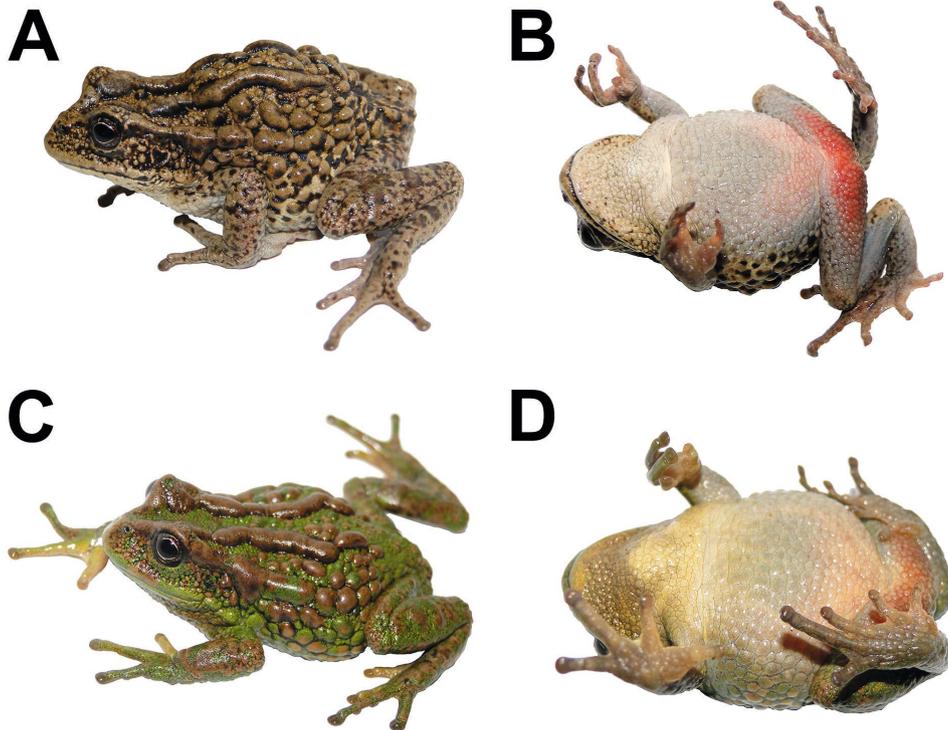
Figure 10. *Gastrotheca trachyplevra* sp. n. in life. Dorsolateral (A) and ventral (B) views of the female holotype (CORBIDI 16614), 43.9 mm SVL. Dorsolateral (C) and ventral (D) views of the male paratype (CORBIDI 16613), 33.5 mm SVL. Photographs by P. J. Venegas.

on the lower lateral edges of the throat; venter and ventral surfaces of fore and hind limbs dull white; a pink hue over the posterior edge of venter; a red blotch over the proximal half of the ventral thigh. Iris dark brown with a few golden specks, golden pupillary ring present.

In preservative (Fig. 8): dorsum grey with black blotches and markings; gular region, chest, and shanks light grey, all other ventral surfaces pale yellow.

Intraspecific variation. The smaller, male paratype (33.5 mm SVL vs. 43.9 mm SVL of the female holotype) has a different colour pattern (Figs 10C–D). The dorsal surfaces are green with few and small brown blotches on the head and brown blotches on dorsum, fore and hind limbs. The pustular paravertebral longitudinal ridges and supratympanic fold are brown as well. The brown coloration of snout, canthus rostralis and eyelids is continuous with that of the supratympanic folds. The lateral surfaces are green with few brown blotches on head and flanks. Ventrally it differs from the holotype by having a yellow throat, yellowish cream chest, a light orange hue over the lower portion of the venter, and a dull red blotch covering the inner half of the ventral surface of the thigh.

Osteology. This description is based on the reconstructed 3D model of the skeleton of the brooding female holotype of *Gastrotheca trachyplevra* (CORBIDI 16614, SVL = 43.9 mm).

Cranial osteology. The skull of *Gastrotheca trachyplevra* is wider than long and measures 14.0 mm in length from the jaw joint to the tip of the snout and 16.3 mm in width at the level of the quadratojugal. The skull is hyperossified, with low, irregular vermiform ridging (lack of clearly formed pits) on the frontoparietals, squamosals, maxillae, and nasals (Fig. 12A). The exposed sphenethmoid also has dermal sculpturing similar to the surrounding ele-
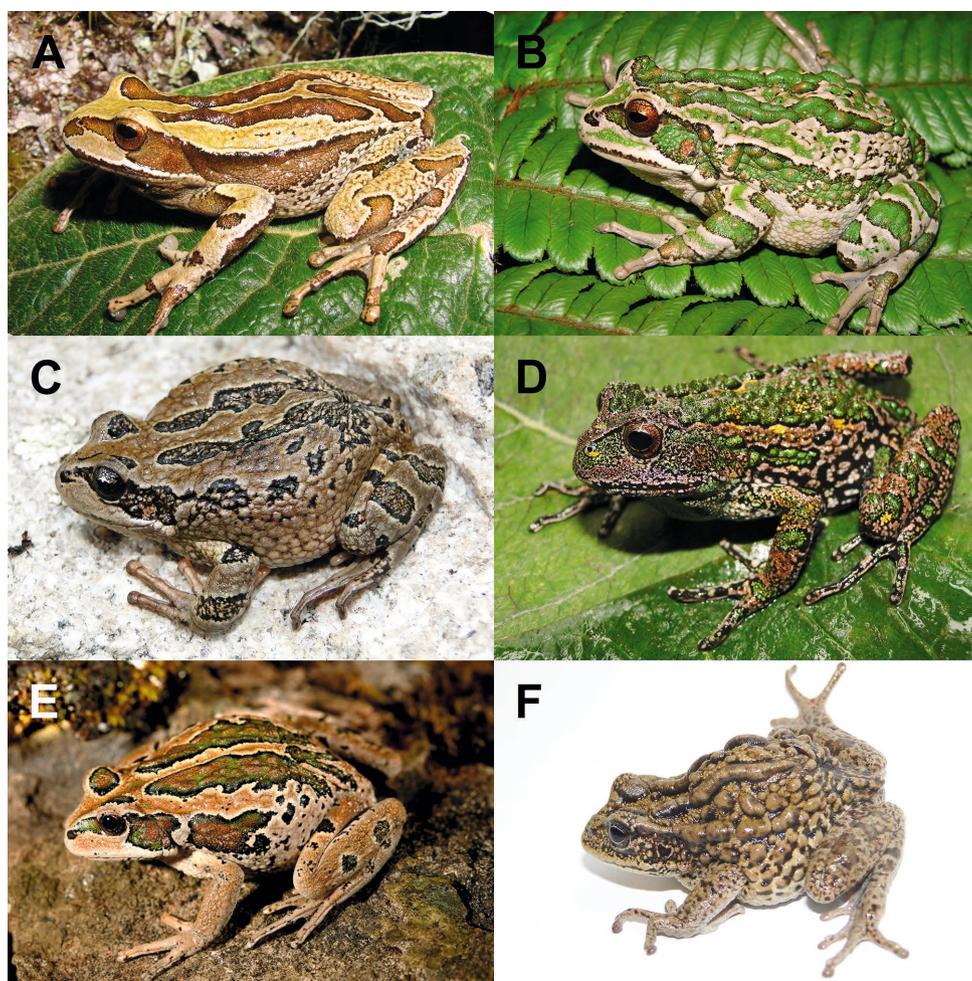
Figure 11. Species of *Gastrotheca* with pustular dorsal skin. (A) *Gastrotheca aratia* from Cañariaco at 2700 m a.s.l., Ferreñafe province, Lambayeque department, Peru; (B) *G. dissimilis* (CORBIDI 3635) from Laguna Norte, Chogur, at 3593 m a.s.l., Hualgayoc province, Cajamarca department, Peru; (C) *G. peruana* (CORBIDI 10447) from San Marcos at 4338 m a.s.l., Huari province, Ancash department, Peru; (D) *G. phalarosa* (CORBIDI 11771) from Hornillo at 3308 m a.s.l., Rodriguez de Mendoza province, Amazonas department, Peru; (E) *G. phelloderma* (CORBIDI 14002) from Porcoy at 4109 m a.s.l., Pataz province, La Libertad department, Peru; (F) *G. trachyplevra* holotype (CORBIDI 16614). Photographs A–D and F by P. J. Venegas and E by G. Chávez.

ments. The frontoparietals have a complete medial articulation with one another, a narrow supraorbital flange, and a moderately wide otic flange. There is no articulation between the frontoparietals and the heads of the squamosal. The frontoparietal covers the anterior epiotic eminence of the prootic, and the carotid canal is partially closed. The frontoparietal narrows anteriorly, and the articulation between the frontoparietals and the sphenethmoid is tapered to a point. The nasals are expanded, articulating with the pars facialis of the maxilla, and form a bony anterior orbital margin. The nasals overlap the anterior margin of the sphenethmoid, extend posteriorly, and nearly contact the anterior edge of the frontoparietal. The maxillary arcade is complete, and the quadratojugal is broadly overlapped by the maxilla. The postorbital process of the maxilla articulates with the zygomatic ramus of the squamosal via a broad, nearly horizontal articulation (Fig. 12C). The head of the squamosal has a wide crest, and the otic plate of the squamosal covers 35% of the width of the crista parotica. The anterior ramus of the pterygoid bifurcates distally. The high dorsal process of the anterior ramus articulates with both the zygomatic ramus of the squamosal and the pos-

torbital process of the maxilla. The distal extent of the anterior ramus articulates with the pars palatina of the maxilla. The premaxillae are broad and bear alary processes that are deflected posteriorly at a 65° angle, forming an inclined snout in lateral profile. The neopalatines are widely separated from one another and form a posterior margin to the choana (Fig. 12B). The prechoanal processes of the vomers are short and do not contact the lingual surface of the pars facialis of the maxilla, forming an incomplete anterior margin of the choana. The postchoanal processes of the vomers support two thirds of the medial choanal margin. The dentigerous processes of the vomers are located at the level between the posterior quadrant of the choanae. The parasphenoid is synostosed to the overlying prootics and exoccipitals. The cultriform process narrows abruptly anterior to the optic fenestra and terminates considerably posterior to the level of the neopalatines. The bony sphenethmoid does not contact the prootic. There are 36–40 tooth loci (18–20 attached, pedicellate teeth) on each maxilla, 9 tooth loci (3–4 attached teeth) on each premaxilla, and 5 tooth loci (4 attached teeth) on each vomer. The dentary is edentate (Fig. 12D).
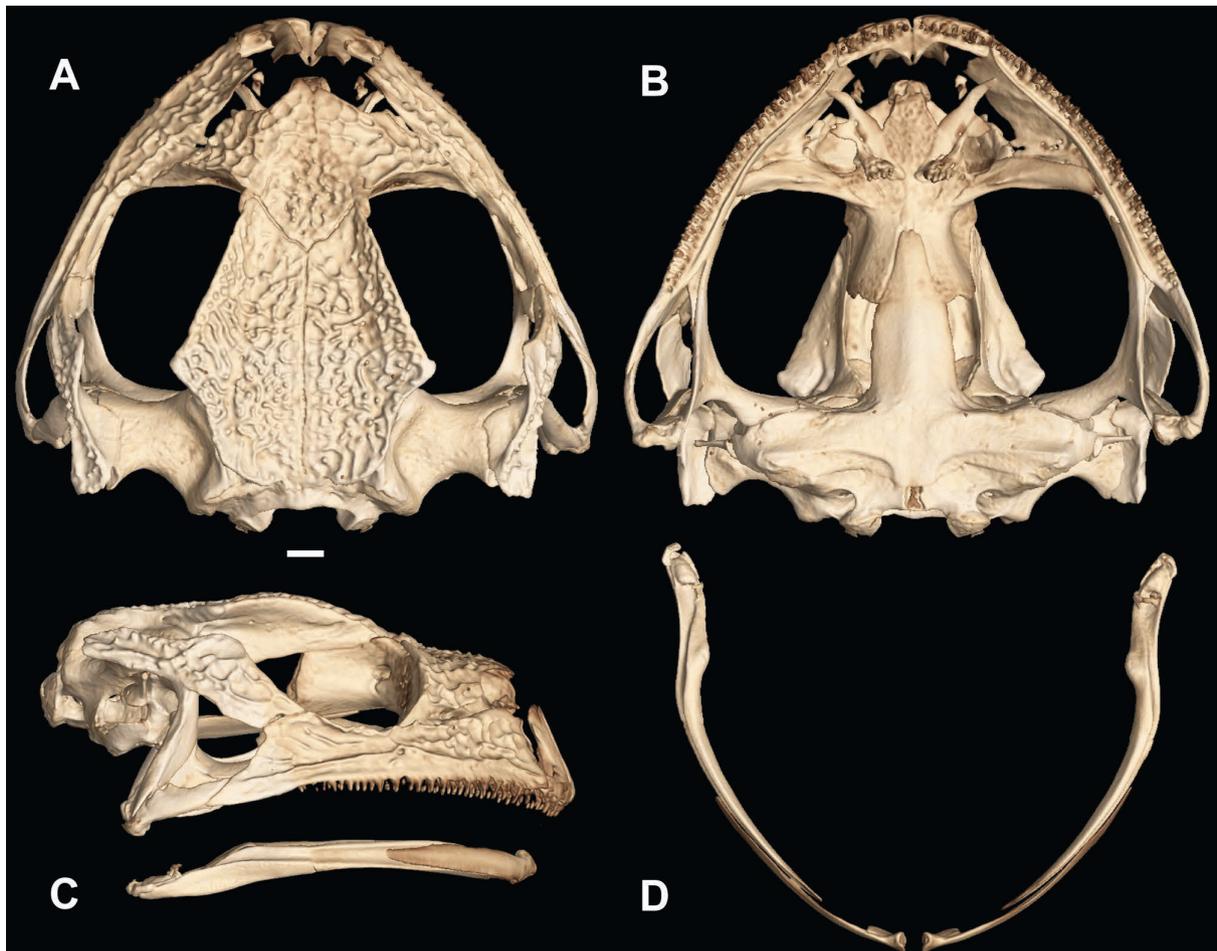
Figure 12. Skull of *Gastrotheca trachyplevra* sp. n. (CORBIDI 16614) as visualized via Micro–CT scanning in dorsal (A), ventral (B), and right lateral (C) views. (D) Mandible in dorsal view. Scale bar = 1 mm.

Vertebral column. Eight nonimbricated presacral vertebrae (Fig. 13A). Transverse processes of Presacrals II–VIII uniform in width. Transverse processes of Presacral II anteriorly directed, transverse processes of Presacrals III and VI–VIII are perpendicular to the notochordal axis, transverse processes of Presacrals IV and V posteriorly directed. Relative lengths of transverse processes of presacrals and sacral diapophyses (SD): SD>III>IV>II, VI–VIII. The anterior margin of the sacral diapophyses is perpendicular to the long axis of the vertebral column. The distal ends of the sacral diapophyses are wider than the base. The anterior and posterior margins of the sacral diapophyses are straight. The lateral margins are concave. The urostyle is as long as the presacral portion of the vertebral column and has a bicondylar articulation with the sacrum. The shaft of the urostyle is dorsoventrally compressed in cross section. The width of the shaft of the urostyle is uniform through-out its length. The urostyle bears a dorsal crest along half the length of the bone shaft, the crest is higher anteriorly and gradually diminishes in height posteriorly.

Pectoral girdle. Arciferal pectoral girdle (Fig. 13C). Clavicles curved and concave, with the lateral region wider. Clavicles well developed posterolaterally, in contact with the glenoid head of the humerus. Medial tips of clavicles not in contact, reaching beyond the level of the anterolateral end of each clavicle. In ventral view, the sternal and glenoid ends of the coracoids have the same width and the midshaft has two thirds the width of the lateral ends. The sternal end is flattened and the glenoid end is concave. The sternal ends of the coracoids are not in contact. The scapula is stout, longer than the coracoid. The pars glenoidalis is narrower than the pars acromialis. The suprascapular end is slightly wider than the zonal end. The clavicle, coracoid and scapula form the margins of the gle-
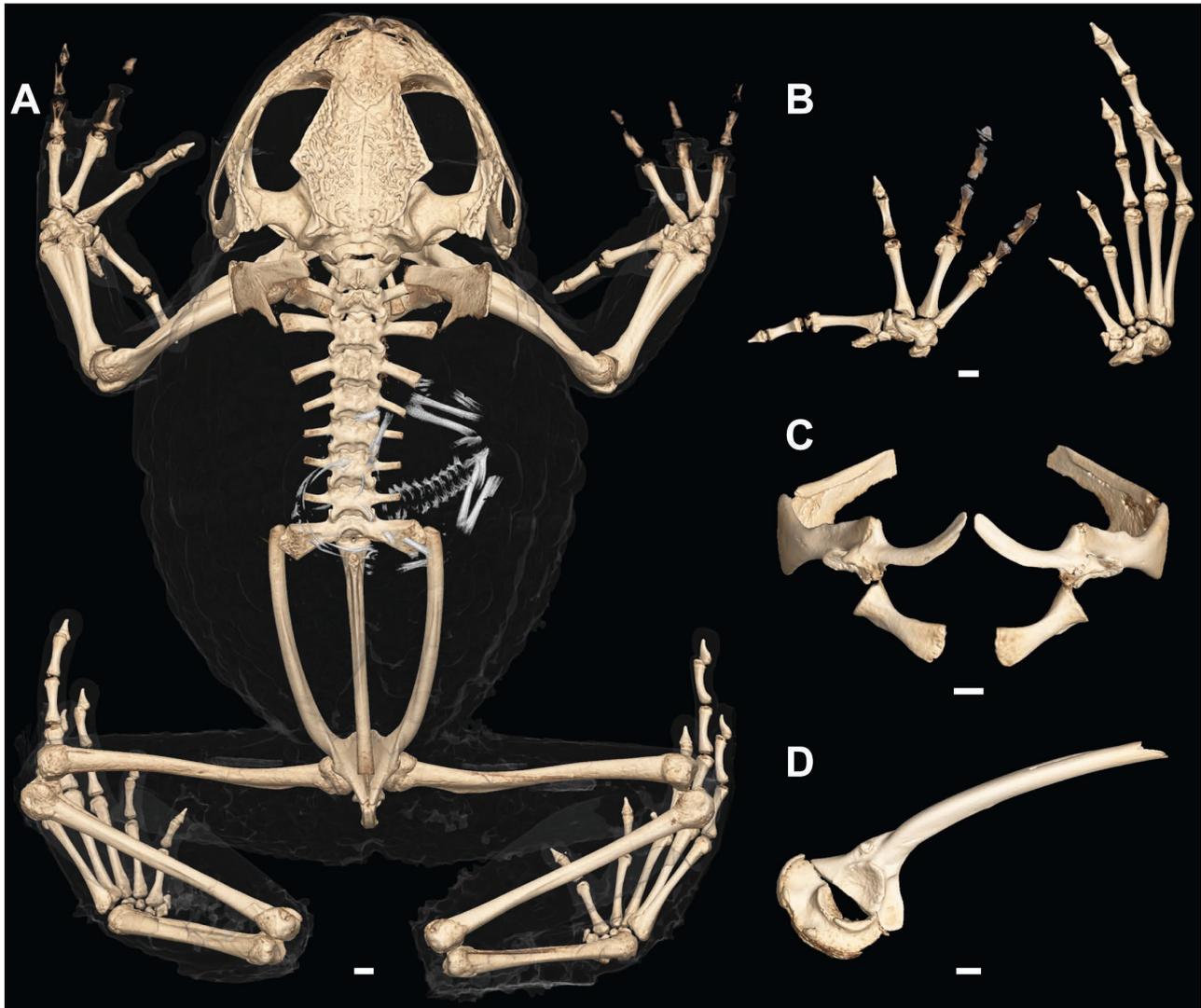
Figure 13. Skeleton of *Gastrotheca flavodactyla* sp. n. (CORBIDI 16614) with a single late stage froglet inside the pouch as visualized via Micro-CT scanning in dorsal view (A). (B) Left manus and pes in ventral views, (C) pectoral girdle in ventral view, and (D) ilium in right lateral view. Scale bar = 1 mm.

noid fossa. Cleithrum and ossified portion of the supras-capula fused.

Pelvic girdle. In dorsal view, the ilial shafts have a V-shaped configuration. The ilial shaft bears a very low crest (Fig. 13D). The dorsal prominence is low; the dorsal protu-berance is rounded and positioned above the dorsal mar-gin of the acetabular fossa. The anterior margin of the ven-tral acetabular expansion is straight and forms an obtuse angle with the ilial shaft. The articulations of the ilium with the ischium and pubis are evident, but not the articulation of the pubis and the ilium.

Forelimb and manus. The humerus has a prominent ventral crest, extending along more than half the length of the bone, higher at the proximal end of the humerus and gradually diminishing in height distally. The distal head (eminentia capitata) is expanded and wider than the gle-noid head (caput humeri). The radioulna is flattened and distinctly wide distally; the sulcus intermedius is indicated by a distinct groove on the distal half of the bone. The car-pus is composed by radial, ulna, distal carpal 3-4-5, Ele-ment Y fused to distal Carpal 2, and elements of the pre-pollex (Fig. 13B). The phalangeal formula is 2-2-3-3. The terminal phalanges have rounded proximal bases, and be-come gradually narrower from the base towards the tip. The prepollex has one element.

Hindlimb and pes. The femur is slightly sigmoid, slight-ly shorter than the tibiofibula. The sulcus intermedius of the tibiofibula is shallow. The tibia and fibula are separat-ed medially and fused at the proximal and distal ends. The tarsal elements are: Element Y, two distal tarsals, and the prehallux (Fig. 13B). The phalangeal formula is 2-2-3-4-3. The terminal phalanges have rounded proximal bases, and become gradually narrower from the base towards the tip.

Distribution and natural history. *Gastrotheca trachyplevra* is known from one locality at 3434 m a.s.l. in the grass-lands of the northern portion of the Central Peruvian An-des in the Utcubamba river basin in Amazonas department (Fig. 7). The type locality of *G. trachyplevra* is located in the Peruvian Yungas ecoregion (OLSON et al. 2001).

The two type specimens were found approximately 30 cm apart from each other, on a cloudy morning, when the male was heard vocalizing at 11:00 hours. Both spec-imens were perched on moss at the base of bunch grass (Poaceae). The holotype is a brooding female with a single late-stage froglet inside her pouch (Fig. 13A).

Etymology. The specific epithet results from combining the Greek words *trachýs*, an adjective meaning "rugose", and plevrá, a noun meaning "flank". This specific name is used in apposition and refers to a distinctive feature of the new species, the rugose flanks full of pustules.

Discussion

Gastrotheca flavodactyla and *G. trachyplevra* are nested within the *Gastrotheca marsupiata* species group, the most species-rich supraspecific unit of *Gastrotheca*. Although the monophyly of this clade is overall stable to different analytical factors, such as optimization criterion, align-ment strategy, and indel coding (ECHEVARRÍA et al. 2021), support values are very low for many clades within the group (CASTROVIEJO-FISHER et al. 2015, DUELLMAN 2015, ECHEVARRÍA et al. 2021, this study). In our study, there is a clear connection between BS and branch length within the *G. marsupiata* species group, with all BS < 50 correspond-ing to short branches. Some of these very short branches with low support are shallow clades, involving sister species relationships such as *G. chrysosticta* and *G. gracilis* (BS = 29) or *G. aratia* and *G. peruana* (BS = 45), while others in-volve more basal relationships, often with several consecu-tive short branches with low BS, such as the most exclusive clade containing *G. gracilis* and *G. griswoldi* (BS = 32) or the most exclusive clade including *G.* sp. H and *G.* sp. J (BS = 22). This pattern is compatible with a scenario of rapid spe-ciation following the accelerated orogeny of the tropical Andes during the last 5 million years or so (HOOGHIEMS-TRA & VAN DER HAMMEN 2004, MADRIÑÁN et al. 2013; HUTTER et al. 2017), as most species of the *G. marsupiata* species group are highland Andean species. If rapid and consecutive speciation is the cause of the observed short branches with low support within the *G. marsupiata* spe-cies group, resolving their evolutionary relationships may prove very challenging (BRYANT & HAHN 2020).

Regardless of the diversification scenario within the *G. marsupiata* species group, this clade accumulates the highest species description rate within the Hemiphracti-dae, with the Peruvian Andes as a hotspot of new species (DUELLMAN & VENEGAS 2005, 2016, LEHR & CATENAZZI 2011, DUELLMAN 2013, DUELLMAN et al. 2014, CARVAJAL-ENDARA et al. 2019, ECHEVARRÍA et al. 2021, VENEGAS et al. 2021). Furthermore, we predict more discoveries of new species within the *G. marsupiata* species group, be-cause the herpetofauna of large and relevant areas within the Peruvian Andes remains scarcely studied (e.g., LEHR & CATENAZZI 2011, VENEGAS et al. 2021). Also, follow-up studies on the life history, ecology, and distribution of most northern Andean *Gastrotheca* are needed. For exam-ple, the *G. marsupiata* species group exhibits the highest variation of developmental strategies among hemiphrac-tids (and probably among all tetrapod clades of simi-lar age). We have here provided direct evidence that em-bryos of *G. trachyplevra* experience direct development (Fig. 13). Among its more closely related species for which this character is known (i.e., *G. gemma*, *G. psychrophila*, and *G. stictopleura*), only embryos of *G. gemma* are direct developers, while those of the other two species undergo a tadpole stage. With the evidence at hand and based on our optimal topology, the developmental strategy changed multiple times within this clade of just eight species. This pattern of multiple recent changes in developmental path-ways is also observed in the most exclusive clade including *G. gracilis* and *G. griswoldi*, flagging both groups as poten-tial models to study the genomic, phenotypic, and environ-mental causes of this astonishing diversity.

Gastrotheca flavodactyla is morphologically most similar to *G. ossilaginis*, a species with an unresolved phylogenetic position. They differ by the presence of skin co-ossification with underlying cranial elements in the latter, throat skin texture, and colour pattern. However, differences in skin co-ossification should be further evaluated because sample size is limited (three adult males of *G. flavodactyla* and one adult female and two adult males of *G. ossilaginis*) and the degree of co-ossification seems to be sexually dimorphic in *G. ossilaginis*, with males having less pronounced co-ossification (Duellman & Venegas 2005). Our description of the osteology of *G. flavodactyla* offers a new system for morphological comparisons with *G. ossilaginis*. However, the osteological information of the latter is limited to a cursory description of some cranial characteristics based on radiographs (Duellman & Venegas 2005), which does not allow for meaningful comparisons. We recommend expanding the comparisons between *G. flavodactyla* and *G. ossilaginis* to osteological characters, for example by generating non-destructive osteological models through computed tomography of *G. ossilaginis* specimens.

Acknowledgements

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Appendix I

Additional specimens examined. Museum acronyms follow Sabaj (2020).

Gastrotheca dissimilis – Peru: Cajamarca department: Cajamarca province: La Chorrera: MUSM 38445; 30 km NNW Cajamarca: UF 65784, Santa Cruz province: Quebrada Ojos: MUSM 38303, La Libertad department: Bolívar province: Condormarca: MUSM 9761. *Gastrotheca gemma* – Peru: Amazonas department: Utcubamba province: Cajaruro district: trail from Refugio Lechucita to El Hito: CORBIDI 21238, El Hito: CORBIDI 19396. *Gastrotheca monticola* – Peru: Amazonas department: Bongará province: Pamacochas: MUSM 6128, Chachapoyas province: Leimebamba: MUSM 24441, Cajamarca department: Celendin province: subcuenca Sendemal: MUSM 26244, Piura department: Huancabamba province: El Tambo: MUSM 7398. *Gastrotheca oresbios* – Peru: Amazonas department: Chachapoyas province: Abra Barro Negro: CORBIDI 11076. *Gastrotheca ossilaginis* – Peru: San Martín department: Huallaga province: Lago Quindecocha, 3100 m a.s.l.: KU 272293–94, Juanjui province: Lago Quindecocha: MUSM 19486. *Gastrotheca peruana* – Peru: Pasco department: Pasco province: Huchuyputahua: MUBI 11467, 13278, Riachuelo arriba de la laguna Panrum: MUSM 1594, Carhuamayo: MUSM 31244. *Gastrotheca phalarosa* – Peru: San Martín department: Mariscal Cáceres province: Quindecocha, 3119 m a.s.l.: CORBIDI 11044, Huallaga province: Esperanza, 3435 m a.s.l.: MUSM 19487. *Gastrotheca phelloderma* – Peru: San Martín department: Mariscal Cáceres province: Parque Nacional del Río Abiseo (ca 25 km NE Pataz, Los Chochos): KU 331040, Parque Nacional del Río Abiseo at Pampa del Cuy, 3400 m a.s.l.: MUSM 27739, La Libertad department: Pataz province: Quebrada Mush Mush: MUSM 33345, Quebrada Molinete: MUSM 33350, 33352. *Gastrotheca spectabilis* – Peru: Amazonas department: Rodríguez de Mendoza province: Vista Alegre district: Hornillo: CORBIDI 11790. *Gastrotheca stictopleura* – Peru: Huánuco department: Huánuco province: Achupampa, 3116 m a.s.l.: CORBIDI 16064, Pachitea province: Tranca Grande at Chaglla, 3090 m a.s.l.: MUSM 20319, Pasco department: Shalcayoc: MUSM 23548, La Florida: MUSM 23550. *Gastrotheca sp.* – Peru: Amazonas department: Rodríguez de Mendoza province: Vista Alegre district: Hornillo, 3308 m a.s.l.: CORBIDI 11768, 11775–78.

Appendix II

Taxa, vouchers, and GenBank accession codes for DNA sequences used in this study. Newly generated sequences are in bold face and markers correspond to those described in Echevarría et al. (2021). * Erroneously reported as MZUSP 17460 in GenBank by Duellman (2015).

Taxon	12S	16S (1)	ND1	POMC	RAG1 (1)
G. aguaruna KU 212026	–	KF723438	KF723462	KF723484	KF723505
G. albolineata MNRJ 54401	KR559919	KR270407 + KR270425	KC844949	KR270365	KR138423
G. antoniiochoai MUSM 27944	–	JN157622	KC844950	KC844972	KC844993
G. aratia KU 212056	–	KF723443	KF723467	KF723489	KF723510
G. argenteovirens KU 181168	DQ679233	DQ679383	DQ679342	DQ679311	–
G. atympana MHNSM 18692	DQ679234	DQ679384	DQ679343	DQ679312	DQ679276
G. aureomaculata KU 181194	DQ679235	DQ679385	DQ679344	–	DQ679277
G. christiani FML 2881	DQ679236	DQ679386	DQ679345	DQ679313	DQ679278
G. chrysosticta LM 58	DQ679237	DQ679387	DQ679346	–	DQ679279
G. cornuta USNM 572472 + AMNH 107251	AY843591	AY843591	DQ679347	DQ679314	DQ679280
G. dendronastes KU 181203	DQ679239	DQ679389	DQ679348	DQ679315	DQ679281
G. dissimilis KU 181740	DQ679253	DQ679402	DQ679361	–	–
G. dunni ICN 10059 + MHUA A 4800	DQ679240	KR270426	DQ679349	DQ679316	DQ679282
G. ernestoi MNRJ 57129 + MNRJ 64000	KR559920	KR270408 + KR270427	KC844952	KR270366	KR138424
G. espeletia KU 203440		KJ489465	KJ489514	KJ489555	
G. sp. KU 173171	DQ679241	DQ679391	DQ679350	DQ679317	DQ679283
G. excubitor MUSM 26280	–	JN157623	–	–	–
G. fissipes ZUFRJ 7901	–	–	JX262925	–	–
G. flamma MZUESC 21989 + MZUESC 21990	MW367865	MW367791	–	MW389824	MW389839
G. flavodactyla CORBIDI 18840	–	**OK104073**	–	–	–
G. fulvorufa CTMZ 07467	–	KC844929	KC844954	KC844977	KC844997
G. galeata KU 181700	DQ679242	DQ679392	DQ679351	DQ679318	DQ679284
G. gracilis DCC 006	DQ679243	–	–	DQ679319	–
G. griswoldi CORBIDI 16066	MW367877	MW367826	–	MW389828	MW389840
G. guentheri KU 173112	DQ679245	DQ679393	DQ679353	DQ679321	DQ679285
G. helenae KU 181070	DQ679246	DQ679394	DQ679354	DQ679322	DQ679286
G. litonedis KU 202690	DQ679247	DQ679395	DQ679355	DQ679323	DQ679287
G. lojana QCAZ 42725 + KU 203546	–	KC844938	KC844964	KC844988	KJ489595
G. longipes USNM 258905 + GGU 1634	DQ679248	DQ679396	DQ679356	DQ679324	DQ679288
G. marsupiata KU 214813 + KU 214814	AY819356	DQ679397	AY819487	AY819105	DQ679289
G. megacephala JLG 90 + CFBH T377	AY843592	AY843592	KC844953	KC844976	AY844381 + KC844996
G. microdiscus CFBH T 1250 + CFBH T 3068	–	KC844932	KC844958	KC844979	KC844999
G. monticola KU 212036 + CORBIDI 15891	AY819357	DQ679398	AY819488	AY819106	DQ679290
G. nebulanastes MUSM 27943 + MCZ 265218	–	JN157625	KC844959	KC844982	KC845001
G. nicefori KU 181071	DQ679249	DQ679399	DQ679357	DQ679325	DQ679291
G. ochoai KU 173499	DQ679250	DQ679400	DQ679358	DQ679326	DQ679292
G. oresbios CORBIDI 11076	–	KJ489461	KJ489509	KJ489552	KJ489588
G. orophylax KU 178568	DQ679251	DQ679401	DQ679359	DQ679327	DQ679293
G. ovifera KU 185758 + MHNLS 20979	DQ679252	MW367808	DQ679360	MW389826	MW401603
G. pachachacae MUSM 28492	–	JN157620	–	KC844983	KC845002
G. peruana KU 207815		KF723451	KF723475	KF723497	
G. phalarosa CORBIDI 11044	–	KJ489459	KJ489507	KJ489551	KJ489585
G. phelloderma CORBIDI 14002	MW367881	MW367815	–	MW389819	MW389841
G. plumbea KU 178499	DQ679254	DQ679403	DQ679362	DQ679328	DQ679294

Taxon	12S	16S (1)	ND1	POMC	RAG1 (1)
G. prasina MZUSP 147060 + MZUESC 21766	JX262891	KJ489476*	JX262922	MW389825	KJ489602*
G. pseustes 1 QCAZ 45113	–	KC844923	KC844948	KC844970	–
G. pseustes 2 QCAZ 42862 + TNHC 62492	AY326051	JX564866	KC844962	KC844986	KX208740
G. psychrophila KU 142634	DQ679255	DQ679404	DQ679363	DQ679329	DQ679295
G. pulchra MZUESC 14541 + MZUESC 21991	MW367866	MW367784	–	–	MW389842
G. rebeccae CORBIDI 08006	–	KC844937	KC844963	KC844987	–
G. recava MZUSP 147044 + MZUSP 147042	JX262890	KJ489497	JX262921	–	KJ489604
G. riobambae KU 178468 + KU 203516	DQ679256	DQ679405	DQ679364	KJ489580	DQ679296
G. ruizi KU 200002	DQ679257	DQ679406	DQ679365	–	DQ679297
G. sp. 1 IDLR 4073 (MNCN/ADN 566)	–	KR270428	–	–	–
G. sp. 2 MNK 5286 + CBG 1020	AY843590	AY843590	KC844955	–	AY844380
G. sp. 3 ZFMK 66954 + MNCN 43052	–	KR270429	–	–	–
G. yacuri QCAZ 21105 + CORBIDI 14194	MW367882	KC844939	KC844965	KC844989	MW389849
G. turnerorum QCAZ 47299	–	KC844934	KC844960	KC844984	–
G. elicioi QCAZ 21213	–	KC844922	KC844947	–	–
G. sp. F CORBIDI 12876	MW367875	MW367822	–	MW389822	MW389843
G. sp. H CORBIDI 9036	MW367871	MW367823	–	MW389831	MW389845
G. sp. I CORBIDI 11776	MW367880	KJ489475	KJ489525	KJ489563	MW389847
G. sp. J CORBIDI 862 + CORBIDI 15070	MW367876	MW367820	KJ489511	MW389821	KJ489590
G. sp. K CORBIDI 11523	MW367872	MW367819	–	–	–
G. sp. L MTR 16228 + MZUESC 8827	JX262894	MW367782	–	–	KJ489603
G. spectabilis CORBIDI 11790	–	KJ489464	KJ489513	KJ489554	KJ489592
G. stictopleura MTD 45230	DQ679258	DQ679407	DQ679366	DQ679330	DQ679298
G. testudinea CORBIDI 14824 + QCAZ 16444	MW367874	MW367821	KC844966	MW389830	MW389837
G. testudinea CBG 774	–	KR270430	–	–	–
G. testudinea CORBIDI 8009	MW367873	MW367818	–	MW389829	MW389836
G. trachyceps KU 181189	DQ679259	DQ679408	DQ679367	DQ679331	DQ679299
G. trachyplevra CORBIDI 16614	MW367879	MW367830	–	MW389823	MW389844
G. walkeri Vz 8996	DQ679260	DQ679409	DQ679368	DQ679332	DQ679300
G. weinlandii KU 143105	DQ679261	DQ679410	DQ679369	DQ679333	DQ679301
G. zeugocystis MHNSM 18675	DQ679262	DQ679411	–	DQ679334	DQ679302
Hemiphractus proboscideus KU 217513	AY819358	DQ679413	AY819489	AY819107	DQ679304