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Getting back to name-bearing types: archival DNA and morphology clarify the identity of *Hyla splendens* Schmidt, 1857 and challenge the taxonomy of Bolivian populations of *Gastrotheca* (Anura: Hemiphractidae)

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Abstract. Currently, the name *Gastrotheca splendens* is applied to Bolivian montane forest populations of marsupial frogs that have been associated with *G. marsupiata* and its allies in the past. Because its comparatively large size evoked taxonomic doubts, we re-examined the holotype of *Hyla splendens* Schmidt, 1857 and extracted and sequenced archival DNA to clarify its identity. Morphological and molecular data revealed *H. splendens* as being conspecific with *Gastrotheca monticola* from northwestern Peru. We place *Gastrotheca monticola* Barbour & Noble, 1920 as a junior synonym of *Hyla splendens* Schmidt, 1857, regarding the latter a valid species, *Gastrotheca splendens* (Schmidt, 1857). We furthermore correct its type locality to 'northwestern Peru'. As a result of these findings and the morphological differences observed among the name-bearing types, the Bolivian taxa *Gastrotheca lauzuricae* De la Riva, 1992 and *G. piperata* Duellman & Köhler, 2005 are removed from the synonymy of *Hyla splendens*. Examination of the external morphology and osteology (inferred from micro-CT images) of the holotypes of *G. lauzuricae* and *G. piperata* revealed several differences. However, with the data currently available, we are unable to judge whether these differences represent species-specific diagnostic characters or intraspecific variation. We consider *G. lauzuricae* a valid species and, applying a principle of parsimony of taxonomic changes, provisionally regard *G. piperata* as its junior synonym pending future investigations. Furthermore, pending further studies, we tentatively continue to consider *Gastrotheca coeruleomaculata* (Werner, 1899) a valid species occurring in montane forests of the Departamento La Paz, Bolivia. Finally, *Leptodactylus andicola* Boettger, 1891 is removed from the synonymy of *Gastrotheca marsupiata* (Duméril & Bibron, 1841) and regarded a nomen dubium based on the morphological characters mentioned in its original description, which are in disagreement with *Gastrotheca* and argue for affinities with the genus *Yunganastes* (Strabomantidae). The results of this study highlight the importance of referring to name-bearing type specimens when taxonomically revising complex and species-rich groups of organisms.

Key words. Amphibia, micro-computed tomography (micro-CT), molecular genetics, museomics, osteology, revalidation, synonymy, systematics, type specimens, Bolivia, Peru.

Introduction

Hemiphractid frogs have received considerable scientific attention recently, mainly aimed at resolving their phylogenetic relationships (e.g., Duellman 2015, Castroviejo-Fisher et al. 2015, Echevarría et al. 2021) or the taxonomic problems affecting some of the species of marsupial frogs within the genus *Gastrotheca* (e.g., Carvajal-Endara et al. 2019, Rodríguez et al. 2019, Venegas et al. 2021, Echevarría et al. 2022). Among the six recognized hemiphractid genera, *Gastrotheca* is the most species-rich, being distributed from southern Central America southward to northern Argentina and southeastern Brazil (Frost 2024).

In Bolivia, populations of *Gastrotheca* occur in the high Andes region dominated by puna (highland grasslands), as well as in cloud forests and montane forests along the eastern Andean slopes (e.g., De la Riva et al. 2000). Apart from *G. testudinea*, Bolivian *Gastrotheca* populations were considered *G. marsupiata* and close allies in the past (see De la Riva 1992, Köhler et al. 1995, De la Riva et al. 2000, Köhler 2000a). While the status of *G. marsupiata* from puna habitats evoked little controversy, the cloud and montane forest populations experienced a complex history of taxonomic changes, including new species descriptions (De la Riva 1992, Duellman & Köhler 2005), rediscoveries (Duellman & De la Riva 1999), a resurrection from synonymy (Duellman 2015), and new synonymizations (Duellman 2015, Lansac et al. 2021). The taxonomic history of these Bolivian forest *Gastrotheca* has been comprehensively summarized by Lansac et al. (2021).

The following scientific names (nomina) are potentially available for the considered Bolivian *Gastrotheca* populations (in order of their year of description): (1) *Hyla marsupiata* Duméril & Bibron, 1841 (type locality: "Cuzco, au Pérou"), considered a valid species distributed at high altitudes in Bolivia and Peru; (2) *Hyla splendens* Schmidt, 1857 (type locality: "Chiriquiflusse unweit Bocca del toro"), a taxon currently considered a valid species endemic to Bolivia (Duellman & De la Riva 1999, Lansac et al. 2021); (3) *Leptodactylus andicola* Boettger, 1891 (Type locality: "Umgebung von Sorata, Bolivia"), a taxon currently considered a junior synonym of *G. marsupiata* (Frost 2024); (4) *Nototrema bolivianum* Steindachner, 1892 (type locality: "Bolivia, Provinz Yuracares, bei Puerto de S. Mateo am oberen Chaparé"), a taxon currently considered a junior synonym of *G. marsupiata* (Duellman & Fritts 1972); (5) *Hylodes coeruleomaculatus* Werner, 1899 (type locality: "Bolivia (Chaco)"), tentatively considered a valid species occurring in the Yungas de La Paz forests, Bolivia (Lansac et al. 2021); (6) *Gastrotheca lauzuricae* De la Riva, 1992 (type locality: "La Siberia, a 40 Km de Comarapa en dirección a Poho, 17°48' S/64°46' O, provincia Carrasco, departamento de Cochabamba, 2800 m"), currently considered a junior synonym of *G. splendens* (Lansac et al. 2021); and (7) *Gastrotheca piperata* Duellman & Köhler, 2005 (type locality: "Sehuencas, 17°29' S, 65°17' W, 2150 m a.s.l., Provincia Carrasco, Departamento de Cochabamba, Bolivia"), currently considered a junior synonym of *G. splendens* (Lansac et al. 2021).

At the current state, *Gastrotheca splendens* is considered the valid name for Bolivian *Gastrotheca* populations occurring in the montane forests of the Departamentos Cochabamba and Santa Cruz formerly considered allies of *G. marsupiata*. The nomen *Hyla splendens* was coined by Schmidt (1857) based on a single male specimen collected by J. Warszewicz purportedly at "Chiriquiflusse unweit Bocca del toro", a locality in Panama. Savage & Heyer (1969) examined the holotype and concluded that the species is not part of the Central American fauna and suggested that the type locality is in error and that the type may actually originate from Colombia, Peru or Bolivia, countries also visited by the collector (see also Jungfer 2017). Later, Duellman (1970), who also examined the type specimen in 1968 (Duellman & De la Riva 1999), associated the nomen with the genus *Gastrotheca*. The origin and identity of *Gastrotheca splendens* remained enigmatic for decades until Duellman & De la Riva (1999) reported its rediscovery in Bolivia. These authors described a single female specimen (MNK 1988) from Amboró National Park, Departamento Santa Cruz, which they identified as *G. splendens* mainly based on coossification of the skin and sculpturing on the head, a character noted by W. E. Duellman during his examination of the *H. splendens* holotype. Subsequently, Lansac et al. (2021) studied the external morphology and osteology of Bolivian *Gastrotheca* considered to represent *G. lauzuricae* (at that time placed as a junior synonym of *G. coeruleomaculata* by Duellman 2015), *G. splendens* and *G. piperata* and came to the conclusion that the differences observed among specimens, populations and nominal species represent variation in a single species. Consequently, they placed *G. lauzuricae* and *G. piperata* in the synonymy of the oldest available name, *G. splendens*.

Despite these efforts to clarify the status of various forest populations, the taxonomy of Bolivian *Gastrotheca* as currently recognized still suffers from missing data (i.e., imprecise or apparently wrong type localities), missing specimens (i.e., lost holotype of *Leptodactylus andicola*), as well as partly ambiguous results from morphology, osteology, and molecular genetics (see Castroviejo-Fisher et al. 2015, Lansac et al. 2021). While reviewing the published knowledge, we realized that the body size of the male *Hyla splendens* holotype is larger than any of these Bolivian forest *Gastrotheca* that have been collected by ourselves and colleagues during the past decades. This fact triggered us to re-examine the *H. splendens* holotype morphologically, and by archival DNA sequencing. We herein report on our findings and revise the identity of *H. splendens*, and comment on the identity and taxonomy of Bolivian *Gastrotheca*.

Material and methods

Museum abbreviations used throughout the text are as follows: Centro de Biodiversidad y Genética, Universidad Mayor de San Simón, Cochabamba, Bolivia (CBG); Nature Education Centre of the Jagiellonian University, Kraków, Poland (CEPUJ); Estación Biológica de Doñana-CSIC, Sevilla, Spain (EBD); University of Kansas, Museum of Natural History, Division of Herpetology, Lawrence, Kansas, USA (KU); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (MCZ); Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain (MNCN); Museo de Historia Natural "Noel Kempff Mercado", Santa Cruz de la Sierra, Bolivia (MNK, MNKA); Naturhistorisches Museum Wien, Austria (NHMW); Zoologisches Forschungsmuseum A. Koenig, Bonn, Germany (ZFMK).

Morphological measurements were taken with vernier callipers to the nearest 0.1 mm. The morphometric variables considered are: SVL, snout–vent length (from the tip of the snout to the posterior margin of the vent); HL, head length (from the angle of jaws to the tip of the snout); HW, head width (greatest width of the head); ED, eye diameter (greatest length of the orbit); TD, tympanum diameter (greatest horizontal distance between the edges of the tympanic annulus); TL, tibia length (from femur–tibia articulation to tibiotarsal articulation); and FL, foot length (from the proximal edge of the inner metatarsal tubercle to the tip of the fourth toe). Sex and maturity of specimens were determined either by the presence/absence of fully developed brood pouches, or dissection and direct observation of gonads. Photographs of preserved specimens were taken with different types of digital cameras, using metric scales. Unless otherwise mentioned, all photographs are by the authors. Description and classification of external morphological characters follow the definitions of Duellman (2015). These include, for example, skin texture, dermal folds and ridges, snout shape in dorsal and lateral view, and co-ossification of the skin on the head.

To infer osteological characters of the skull of the holotype of *Gastrotheca lauzuricae* (EBD 37379H; formerly CET 501), images based on micro-computed tomography (micro-CT) scanning were used as produced by Lansac et al. (2021). For comparison, five type specimens of *G. piperata* (ZFMK 60287, 60291, 66838, 66839, 66893) were scanned using a high-resolution micro-CT desktop scanner device (Bruker SkyScan 1173, Kontich, Belgium). To avoid movement during the scanning process, the material was placed in a small plastic container and fixed in the vessel with styrofoam. Acquisition parameters comprised: an X-ray beam (source voltage 45–60 kV and current 114–120 µA) without the use of a filter; 800 projections of 700–800 ms exposure time each with a frame averaging of 3 recorded over 180° using rotation steps of 0.3 degrees, resulting in a scan duration of 47–54 min; a magnification setup generating data with an isotropic voxel size of 7.09 µm (ZFMK 60291, 66839), 8.15 µm (ZFMK 60287), 9.58 µm (ZFMK 66893), and 18.10 µm (ZFMK 66838), respectively. The CT-dataset was reconstructed with N-Recon software (Bruker MicroCT, Kontich, Belgium) and rendered in three dimensions using CTVox for Windows 64 bits v.2.6 (Bruker MicroCT, Kontich, Belgium). Descriptive terminology of osteological characters follows that of Duellman (2015).

To clarify the identity of the *Hyla splendens* holotype based on molecular data, we sampled the specimen in 2024 for a small piece of skin with underlying tissue taken from the left side of the abdomen. The sample was stored in a vial with pure ethanol. The sample was first weighed and incubated in a Guanidine Thiocyanate (GuSCN) based extraction buffer solution at 37°C overnight. The next day, we extracted a total volume of 25 µl genomic DNA following the protocol of Rohland et al. (2004), in several consecutive steps as described in Straube et al. (2021). The yield of DNA was quantified based on 1 µl DNA extract using the Qubit dsDNA HS Assay Kit 0.2–100 ng/µl (Life Technologies, Carlsbad, California, US) according to the instructions of the manufacturer. Subsequently, we used 13 ng DNA as input for single-stranded library preparation according to the protocol of Gansauge et al. (2017). All lab work prior to qPCR was conducted in a dedicated DNA facility at the University of Potsdam, Germany, which meets all requirements to work with historical samples (see Fulton & Shapiro 2019) and where no *Gastrotheca* samples had been studied before. Extraction and library blanks were run alongside all samples to check for contamination. Final library concentrations and fragment length distributions were assessed using a 2200 TapeStation (Aligent Technologies) assay. The library was then shotgun-sequenced for approximately five million 75-bp single-end reads on an Illumina Nextseq 500/550 sequencing platform at the University of Potsdam, following the procedure described in Paijmans et al. (2017). The quality of the obtained reads was visualized twice using FastQC (https://www.bioinformatics.babraham.ac.uk), both before and after trimming of Illumina adapter sequences and discarding reads shorter than 30 base pairs (bp) with cutadapt v1.12 (Martin 2011).

To assemble a sequence of the *H. splendens* type from the shotgun sequencing reads fully avoiding reference bias, we applied a procedure consisting of multiple steps. In a first exploratory analysis, we used local Blast (Blast+; Camacho et al. 2009) against a library of sequences of the mitochondrial 16S rRNA gene (16S) from representatives of different families of frogs to verify that (by far) the largest numbers of hits were retrieved against a reference sequence of *Gastrotheca*. We then compiled a library of 16S sequences of six species of *Gastrotheca* representing most of the major clades within the genus (*G. excubitor, G. litonedis, G. monticola, G. pseustes, G. riobambae, G. testudinea*), transformed the sequences into a Blast reference database, blast-searched the *H. splendens* reads against it, and collected all matching reads > 90% sequence identity to any of the reference sequences. All matching reads were collected in a fasta file and CodonCode Aligner v 3.7.1 (CodonCode Corporation) was used to map the matching reads separately to 16S reference sequences of the various *Gastrotheca* sequences (option: "align to reference"). We verified that the resulting assemblies were congruent (thus, no reference bias was introduced), and used the consensus sequence obtained by aligning reads to *G. monticola* for downstream analysis, with missing sections in-between contigs coded by the letter "N". The sequence has been deposited in GenBank (accession number PQ436978).

Molecular phylogenetic analysis was then performed to analyze the phylogenetic placement and genetic divergence of the *Hyla splendens* holotype. To gather sequences from a representative set of taxa, we followed the approach of Köhler et al. (2023). We used BLAST searches (Altschul et al. 1990) of newly generated 16S rRNA sequences of *H. splendens* against the GenBank nucleotide archive for a check of plausibility, and to identify and download comparative sequences of greatest similarity to be included in the analysis. In addition, following indications of the

BLAST results, we searched manually for sequences of apparently closely related taxa, namely species in the *Gastrotheca marsupiata* species group (sensu Echevarría et al. 2021) to add them to the analysis. Sequences of *G. helenae* (*G. longipes* species group) and *G. walkeri* (*G. walkeri* species group) were added as representatives of respective sister groups (see Echevarría et al. 2022). A sequence of *Hemiphractus proboscideus* was used to root the tree. A table with metadata and sequences used has been deposited, along with assemblies, alignments and treefiles, in the Zenodo repository under DOI: 10.5281/zenodo.13903301.

We used MAFFT (Katoh & Standley 2013) with the G-INS-i algorithm as implemented in Concatenator (Vences et al. 2022) to align sequences. After trimming the start and end of some of the sequences retrieved from GenBank for approximately equal lengths, and using GBLOCKS (Castresana 2000) in its Python implementation in Concatenator (with settings: IS = 0.5, FS = 0.85, GT = 0.7) to remove unalignable, highly variable sequence stretches, we obtained an alignment of 737 bp and 77 terminals. We used these data to infer the best model (TIM2+F+I+G4) under the Bayesian Information Criterion in Model Finder (Kalyaanamoorthy et al. 2017), as well as a Maximum Likelihood (ML) tree, using IQ-TREE 2.2.0 (Nguyen et al. 2015, Minh et al. 2020) with default settings. Branch support was assessed from 2000 standard non-parametric bootstrap replicates calculated in IQ-TREE. Uncorrected pairwise genetic distances (p-distances) between sequences were calculated in MEGA v7 (Kumar et al. 2016) with the 'pairwise exclusion' setting.

Results and discussion

Identity of *Hyla splendens*

The original description by Schmidt (1857) is rather short and apart from some basic morphological characters provided in Latin only mentions the locality information "Chiriquiflusse unweit Bocca del toro" and three morphometric measurements (body length from tip of snout to anus, 48 mm; forelimbs from axilla to tip of longest finger, 33 mm; hindlimbs from anus to tip of fourth toe, 80 mm). Later, Schmidt (1858) provided more details and a drawing of the palmar surface of the left foot.

The holotype (CEPUJ 1008/1340; formerly KM 1008/1340 and recently renumbered CEP-DZ-51716-N; Figs 1–2) is an adult male that according to its external morphology is allocable to the genus *Gastrotheca*, as already stated by Duellman (1970, 1977) and Duellman & De la Riva (1999). The type specimen, initially preserved in alcohol, now stored in formalin, is in rather poor condition as of our examination in February 2024. Colors have almost completely faded, the body is rather soft, and the head appears to be dorsoventrally compressed. Furthermore, the anterior part of the head and distal parts of toes probably suffered from past desiccation (see Köhler et al. 2022 for explanation of similar preservation artifacts). We here describe its morphology as far as accessible in its current state: Adult male; body robust; head slightly wider than long, as wide as body; HW ca. 36% of SVL; HL ca. 31% of SVL; snout rounded in dorsal view, inclined to bluntly rounded from nostrils to upper lip in lateral profile; canthus rostralis angular in cross-section; loreal region concave; lips slightly flared; top of head flat; trace of an occipital ridge recognizable; internarial area flat; nostrils directed anterolaterally; eyes shrunken, their diameter not measurable; tympanum distinct, round, separated from the eye by a distance equalling its diameter; tympanic annulus distinct; supratympanic fold prominent, barely obscuring upper edge of tympanic annulus, and extending from the posterior corner of the orbit onto the flanks to level of midbody. Arm moderately robust, lacking tubercles; hand moderately sized; discs moderately large, round, width of the disc on third finger about 1.5 width of finger; relative length of fingers I = II < IV < III; fingers basally with a rudiment of webbing, bearing distinct lateral fringes; subarticular tubercles large, round; supernumerary tubercles present; palmar tubercle low, bifid; prepollical tubercle prominent, elliptical. Hind limb moderately slender; TL 49.9% of SVL; FL 42.9% of SVL; inner tarsal fold distinct, low, stretching over almost the entire tarsus; outer metatarsal tubercle absent; inner metatarsal tubercle prominent, elliptical; relative length of toes I < II < III < V < IV; toes about two-thirds webbed, bearing distinct lateral fringes; subarticular tubercles distinct, round; supernumerary tubercles present on proximal segments. Skin on head, snout and upper lips rugose, indicating dermal sculpturing; skin on dorsum shagreen to finely granular; skin on throat, chest, belly and ventral surfaces of thighs coarsely granular; skin on flanks granular; dentigerous processes of vomers in two separated transverse patches, between choanae (Schmidt 1858, Savage & Heyer 1969; not re-examined by us to avoid damage); single subgular vocal sac.

Measurements (in mm): SVL 51.3; TL 25.6; FL 22.0; HW 18.6; HL 16.1; TD 2.6; ED and IOD not measurable due to deformed and shrunken eyes and upper eyelids.

After more than 170 years in preservative, color pattern almost completely faded. Ground color of all surfaces pale cream; dorsal surfaces of limbs with traces of brown transverse cross-bars; dorsum with some faded irregular brown blotches, flecks, and spots, most obvious in the scapular region; posterior surfaces of thighs with some faded dark flecking; flanks with sole brown spots in inguinal region; ventral surfaces uniformly cream.

Schmidt (1858) described the dorsum to exhibit remnants of metallic greenish patches with some yellowish-green glance and the posterior surfaces of thighs being covered by dense blackish-blue marbling. He also mentioned dark transversal stripes on arms and legs. Savage & Heyer (1969), who examined the holotype, also stated "upper limb surfaces with a series of transverse bars" and mentioned the presence of a light labial stripe, which is barely evident today.

In exploratory analyses, despite very minor sequence differences, the 16S sequence assemblies obtained from the shotgun sequencing reads of the *Hyla splendens* holotype, obtained using different reference sequences, all clustered

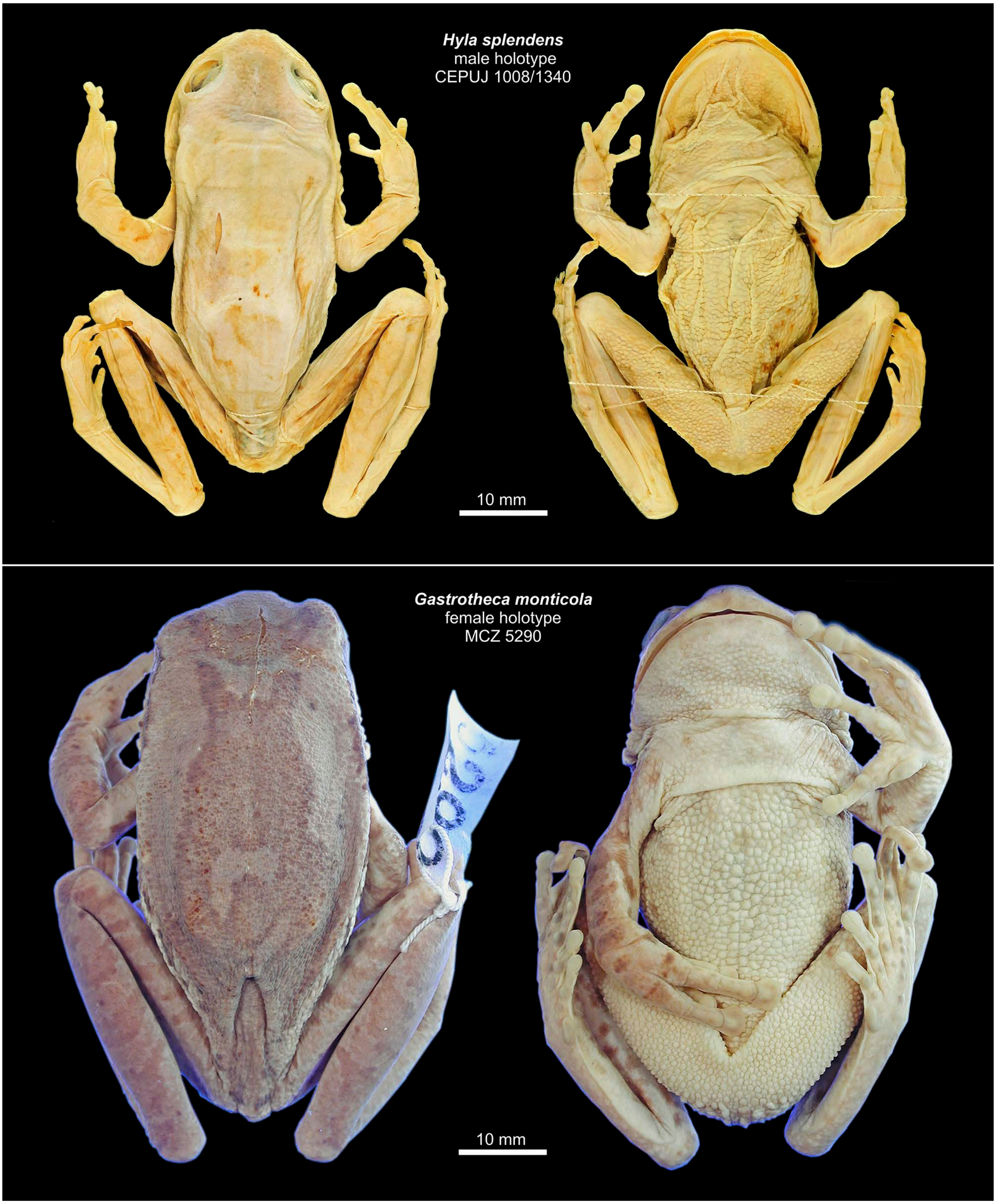

Figure 1. Dorsal (left) and ventral (right) views of the preserved holotypes of *Hyla splendens* (top row) and *Gastrotheca monticola* (bottom row) shown at the same scale. Photographs of MCZ 5290 from Museum of Comparative Zoology, Harvard University, USA, used according to license CC BY-NC-SA 4.0.

with *Gastrotheca monticola*. Visual inspection of the assembly only in a few cases revealed single nucleotide differences among overlapping reads, suggesting that all or most of the extracted reads came from the target sample. We therefore used the assembly of the reads against the *G. monticola* reference for phylogenetic analysis (742 nucleotides, with two stretches of missing data of 3 and 37 nt in length). In the resulting ML tree, the holotype sample of *H. splendens* is revealed as part of the *Gastrotheca marsupiata* species group (sensu Echevarría et al. 2021), clustering with samples of *G. monticola* from the vicinity of Huancabamba, Departamento Piura, northwestern Peru (KU 219767, 219768, 219770, MUSM 15418, 15419) and Departamento Amazonas, northern Peru (CORBIDI 15891, KU 212034–212036) (Fig. 3). Bootstrap support (BS) for the monophyly of the cluster of *G. monticola* and the *H. splendens* type is low (BS = 58%), probably due to missing data in the sequence assembly of the *H. splendens* type but the clustering of these sequences is unambiguous due to the very low genetic divergence between them (see below). All *G. monticola* + *Hyla splendens* are sister to *G. elicioi*. The *G. monticola*/*H. splendens*/*G. elicioi* clade (BS = 100%) is sister to a clade containing *G. cuencana*, *G. litonedis*, and *G. lojana* (BS = 74%) and the clade containing all these taxa received strong support as well (BS = 72%). The tree topology revealed by our analysis is in general agreement with formerly published phylogenies (Castroviejo-Fisher et al. 2015, Carvajal-Endara et al. 2019, Echevarría et al. 2021, 2022, Venegas et al. 2021), except for a different position of samples of *G. galeata*, *G. orophylax* and *G. plumbea*, which do not cluster with samples of *G. monticola*, *G. elicioi*, *G. litonedis* and *G. lojana*. Using the full sequences (pre-GBLOCKS trimming), the *H. splendens* sequence was fully identical to sequences of *G. monticola* from Huancabamba, Departamento Piura (0.0% uncorrected pairwise distance), and only minimally divergent from *G. monticola* sequences from other sites (0.1–1.0%). It differed by 4.4–4.7% from the phylogenetically next closest relative, *G. elicioi*.

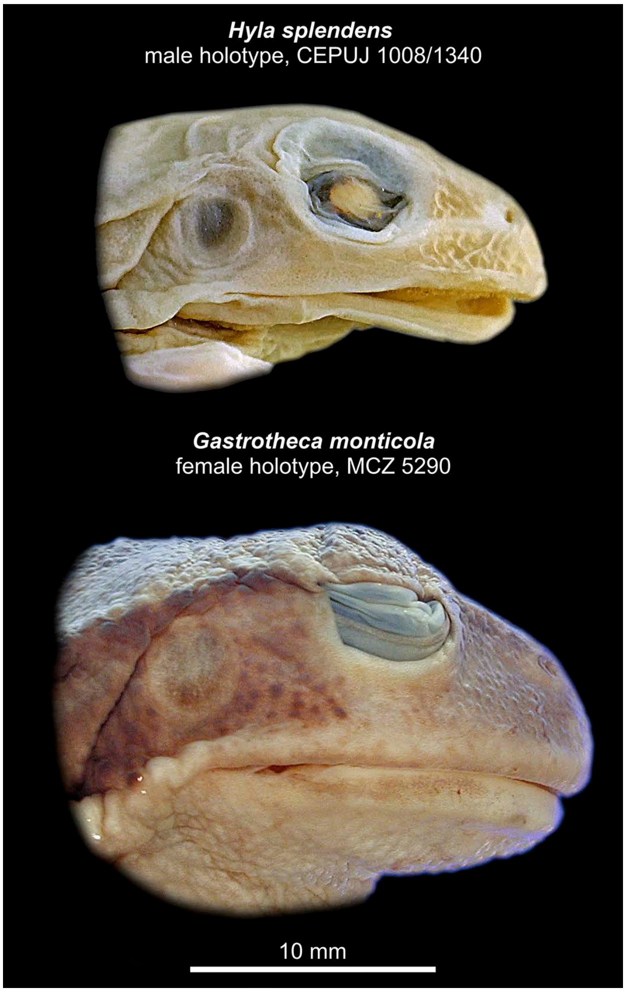

Figure 2. Comparative views of heads of preserved holotypes of *Hyla splendens* (top) and *Gastrotheca monticola* (bottom; mirrored) in lateral profile at the same scale. Photograph of MCZ 5290 from Museum of Comparative Zoology, Harvard University, USA, used according to license CC BY-NC-SA 4.0.

Given that the type locality of *G. monticola* was mentioned as "Huancabamba, northwestern Peru" by Barbour & Noble (1920), which is clearly in the department of Piura, and that the sequence of *Hyla splendens* clusters with those of *G. monticola* samples from close to its type locality, molecular genetic data strongly imply that *Hyla splendens* is conspecific with populations currently referred to as *Gastrotheca monticola*. This is further corroborated by comparison of the morphology of the *H. splendens* holotype with that of *G. monticola* (MCZ 5290, adult female; Figs 1–2). The respective key characters shared among both name-bearing types are: (1) snout inclined to bluntly rounded from nostrils to upper lip in lateral profile; (2) distinct round tympanum, separated from eye by a distance roughly equalling its diameter; (3) prominent supratympanic fold extending from posterior orbit posteriorly to the flanks; (4) fingers I and II about equal in length; (5) fingers with a basal rudiment of webbing; (6) toes about two-thirds webbed; (7) fingers and toes bearing lateral fringes; (8) inner metatarsal tubercle prominent, elliptical; outer metatarsal tubercle absent; (9) inner tarsal fold distinct, stretching along the inner side of the tarsus; (10) skin on throat, chest, belly and ventral surfaces of thighs coarsely granular; skin on flanks granular; (11) dark transverse crossbars on dorsal surfaces of limbs. Furthermore, the size of the male *H. splendens* holotype is perfectly within the range documented for *G. monticola* (male SVL 49.0–55.7 mm; Duellman 2015). Schmidt (1858) described a yellowish-green dorsal coloration in the alcohol preserved holotype, which also would be in agreement with predominantly green colored individuals of *G. monticola* (see Duellman 2015; Fig. 4).

In contrast to the morphological agreement of the *H. splendens* holotype with *G. monticola*, it disagrees with the morphology of the *Gastrotheca* female MNK 1988 from Amboró National Park, Bolivia, used by Duellman & De la Riva (1999) to redescribe *Gastrotheca splendens*.

We here only list those characters of MNK 1988 mentioned by Duellman & De la Riva (1999) that are most obviously not congruent with the type of *H. splendens* (characters of the latter in parentheses): snout bluntly rounded in profile (inclined from nostrils to bluntly rounded towards lips); canthus rostralis barely angular in cross-section (angular); supratympanic fold weak, not extending onto flank (prominent, extending onto flank); lateral fringes absent on digits (present); TL 42.5% of SVL (49.9%); inner tarsal fold absent (distinct, long); skin on belly and proximal posteroventral surfaces of thighs weakly granular (coarsely granular); other ventral surfaces smooth (coarsely gran-

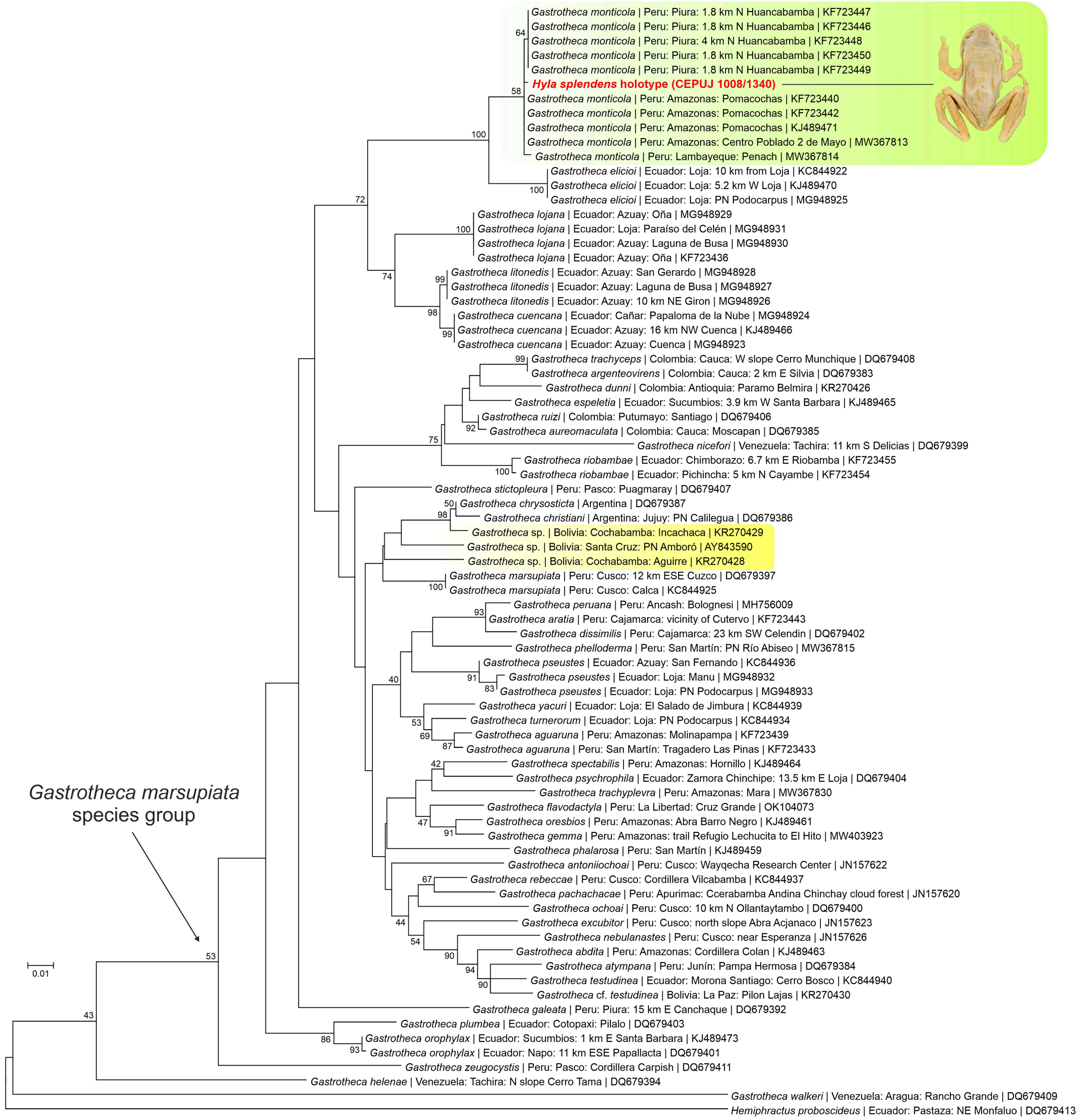

Figure 3. Maximum Likelihood phylogenetic tree of the mitochondrial 16S rRNA gene of samples of *Gastrotheca* representing the *G. marsupiata* species group. Numbers at nodes are bootstrap values in percent (2000 standard non-parametric replicates; not shown if < 40). The clade highlighted in green refers to samples of *G. monticola* and the *Hyla splendens* holotype. Samples highlighted in yellow refer to samples from Bolivian populations of uncertain taxonomic status referred to in the text. The inset photo depicts the preserved holotype of *Hyla splendens* (CEPUJ 1008/1340).

ular). Furthermore, the authors describe the coossification of the skin on the head and provide a respective drawing (Duellman & De la Riva 1999: Fig. 1). A dorsal photo of the head of the same specimen is provided by Lansac et al. (2021: Fig. 1c). In both, the drawing and the photo, the extent of coossification on the head is clearly recognizable. It differs from the structures observed in the *H. splendens* holotype by a different fine scale structure and a different extent. Whereas in MNK 1988 the coossification comprises a narrow area reaching from the tip of the snout to the interorbital area and beyond, being equally broad over its entire length, the sculpturing in *H. splendens* broadens posteriorly to the upper eyelids, thus covering a much larger area of the head. Moreover, in the *H. splendens* holotype the sculpturing assessed from the present skin structure is not congruent with coossification in a strict sense, but more likely the result of the skin on the head being adherent to underlying bones (see Duellman 2015). Given these distinct differences in morphology, we conclude that the *Gastrotheca* specimen MNK 1988 is not conspecific with *H. splendens*.

As Lansac et al. (2021), in their analysis of morphological and osteological variation of Bolivian montane forest *Gastrotheca*, considered MNK 1988 and morphologically similar specimens (mainly based on the presence of coossification on the head) to represent *G. splendens*, their analyses and the taxonomic conclusions derived from them were influenced by these misidentifications. In fact, given our results presented above, none of the specimens considered by Lansac et al. (2021) is referable to the name *splendens*.

As a result of our findings, in morphology and molecular genetics, we conclude that the name *Hyla splendens* Schmidt, 1857 is applicable to populations referred to in the current literature as *Gastrotheca monticola* (e.g., Duellman et al. 2014, Duellman 2015, Carvajal-Endara et al. 2019, Echevarría et al. 2021). Consequently, we consider *Gastrotheca monticola* Barbour & Noble, 1920 a junior synonym of *Hyla splendens* Schmidt, 1857, which is regarded a valid species, *Gastrotheca splendens* (Schmidt, 1857).

We furthermore corroborate former statements that the type locality of *Hyla splendens* is in error (Savage & Heyer 1969, Duellman 1970) and that the type specimen, as revealed by our molecular analysis, most likely originates from northwestern Peru, probably from the area known as the Huancabamba depression. Such an origin is furthermore plausible, as its collector J. Warszewicz travelled and collected in that area and the nearby Río Marañon

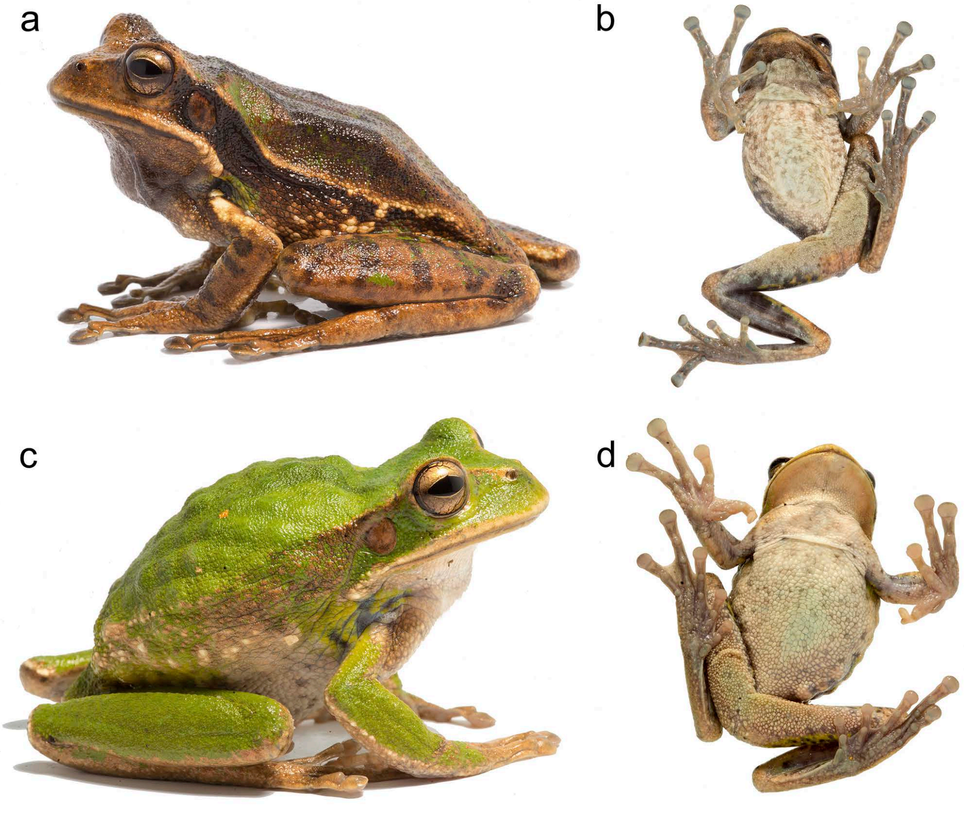

Figure 4. Adult *Gastrotheca splendens* in life, showing skin texture and variation in color pattern; dorsolateral and ventral views: (a, b) male CORBIDI 24012, from La Florida, Provincia de Cutervo, Departamento Cajamarca, 2412 m a.s.l.; (c, d) female CORBIDI 24210, from San Andres de Cutervo, Provincia de Cutervo, Departamento Cajamarca, 2067 m a.s.l. These populations have been formerly referred to *Gastrotheca monticola*. Not to scale. Photographs by E. Quispe.

valley (see Brzeziński et al. 1927, Savage 1970, Yearsley 2004, Jungfer 2017). Following the recommendation 76A.2. of the Code (ICZN 1999), we correct the type locality of *Hyla splendens* Schmidt, 1857 to 'northwestern Peru'.

Concurrently, we reject the proposal of Lansac et al. (2021) that *Gastrotheca splendens* is the name applicable to any of the Bolivian montane forest *Gastrotheca* that have been associated with *G. marsupiata* and allies in the past.

Status of *Gastrotheca lauzuricae*

Gastrotheca lauzuricae was described by De la Riva (1992) based on a female from a Bolivian cloud forest locality at the border of the Departamentos Cochabamba and Santa Cruz called La Siberia (2800 m a.s.l.). Among the diagnostic characters mentioned by De la Riva (1992) were most importantly the presence of bright blue spots on dorsum and flanks in life, and a head being notably wider than long with a HL/HW ratio of 0.79. For a long period, the holotype was considered to be the sole representative of this species, until Duellman (2015) concluded that it is more widespread in the Bolivian Yungas and that the name *Hylodes coeruleomaculatus* Werner, 1899 is applicable for the respective populations. His conclusion was based on comparison of the respective type specimens, highlighting the shared character of blue spots, as mentioned in the description of *H. coeruleomaculatus* by Werner (1899) for one of the specimens, and similar morphometric proportions. However, Lansac et al. (2021) doubted these conclusions, as morphological proportions used by Duellman (2015) to differentiate *G. coeruleomaculata* from *G. marsupiata* (both taxa had formerly been suggested to be synonymous; Duellman & Fritts 1972) were demonstrated to be highly variable in the latter. Moreover, the blue spots (bordered with black margins) mentioned by Werner (1899) for one preserved syntype of *G. coeruleomaculata* (apparently NHMW 16496:1; Fig. 10) are of completely different appearance and outline, resembling dorsal color patterns described in the variation of *G. marsupiata* (Duellman 2015) and thus differing from those exhibited by the living holotype of *G. lauzuricae* (Fig. 7; blue spots absent in preservative, Fig. 6). This raises further doubt on the somewhat arbitrary allocation of additional preserved specimens to *G. coeruleomaculata* by Duellman (2015) as mentioned already by Lansac et al. (2021). Comparison of the syntypes of *Hylodes coeruleomaculatus* with the *G. lauzuricae* holotype reveals additional differences, mainly with respect to snout shape and skin texture. We therefore conclude that *G. lauzuricae* is not conspecific with *G. coeruleomaculata* as suggested by Duellman (2015).

In their study of morphological and osteological variation of *Gastrotheca* frogs from the montane forest of central Bolivia, Lansac et al. (2021) concluded that *G. lauzuricae* is not distinct from other populations occurring in such region. They interpreted observed differences in morphometry and osteology to represent intra-specific variation. Consequently, the authors considered *G. lauzuricae* as a junior synonym of the putative oldest available name for these populations, i.e., *Hyla splendens*. This conclusion was based on the assumption that *G. splendens* occurs in Bolivia and is present in the same general area, exhibiting the morphological characters described by Duellman & De la Riva (1999) based on the female MNK 1988.

As demonstrated above, Duellman & De la Riva (1999) did not rediscover *G. splendens* and neither the specimen MNK 1988, nor other specimens referred to as *G. splendens* by Lansac et al (2021) actually correspond to this species. We thus conclude that *G. lauzuricae* is not conspecific with *G. splendens*. Comparison of the *G. lauzuricae* holotype (Figs 4, 5) with the *H. splendens* holotype revealed at least the following differences (characters of *H. splendens* holotype in parentheses): snout rounded in profile, with a distinct indentation below nostrils (inclined from nostrils to bluntly rounded towards upper lip); canthus rostralis acutely rounded in cross-section (angular); supratympanic fold moderately heavy (prominent, extending onto flank); relative length of fingers I < II < IV < III (I = II < IV < III); lateral fringes on digits absent (present); toes about one-fourth webbed (two-thirds webbed); skin on throat and chest smooth (coarsely granular).

Given that *G. lauzuricae* is properly diagnosable against *G. marsupiata* (see De la Riva 1992, Lansac et al. 2021) and is neither conspecific with *G. splendens*, nor with *G. coeruleomaculata*, we consider it a valid species. At the current state of knowledge, we can allocate this name with absolute certainty to the holotype only, as its conspecifity with other Bolivian montane forest populations of *Gastrotheca* remains somewhat ambiguous (see below). However, it is highly probable that *G. lauzuricae* is the name applicable to populations occurring in the upper Bolivian montane forests of the Departamentos Cochabamba and Santa Cruz, at least in the wider surroundings of its type locality.

Status of *Gastrotheca piperata*

Gastrotheca piperata was described by Duellman & Köhler (2005) based on a series of specimens from central Bolivian upper montane forests. Its type locality is Sehuencas, 2150 m a.s.l., in the Carrasco National Park, Provincia Carrasco, Departamento Cochabamba, but the type series also comprises three localities in the Provincia Caballero, Departamento Santa Cruz. Populations partly referable to *G. piperata* had formerly been referred to as cloud forest populations of *G. marsupiata* (De la Riva 1992, De la Riva et al. 1995, 2000, Köhler et al. 1995) or a distinct undescribed species (*G.* sp. A; Köhler 2000a). In their diagnosis of *G. piperata*, Duellman & Köhler (2005) provided several qualitative morphological differences to high-Andean *G. marsupiata* and emphasised the differences in life history between both species (number of eggs in the brood pouch, developmental stage and size of tadpoles at time of release). The character these authors mentioned to distinguish *G. piperata* from *G. lauzuricae* was far less convincing and refers only to the presence of dark spots on dorsum and flanks in *G. lauzuricae* versus fine black flecks in *G. piperata*. Later, Duellman (2015) added that *G. piperata* has comparatively narrower discs when compared to *G. coeruleomaculata* (at that time including *G. lauzuricae* as a junior synonym). Currently, *G. piperata* is considered a junior synonym of *G. splendens*, based on the study of morphological and osteological variation of central Bolivian montane forest *Gastrotheca* (Lansac et al. 2021). However, Lansac et al. (2021) did neither include *G. splendens* (see above), nor type specimens of *G. piperata* in their analyses.

Based on our findings described above, we conclude that *G. piperata* is not conspecific with *G. splendens*. Comparison of the *G. piperata* type specimens (Figs 4, 5) with the holotype of *H. splendens* (Figs 1, 5) revealed at least the following differences (characters of *H. splendens* holotype in parentheses): maximum male SVL 36.3 mm (51.3 mm); snout bluntly rounded in profile (inclined from nostrils to bluntly rounded towards upper lip); canthus rostralis acutely rounded in cross-section (angular); supratympanic fold moderately heavy, not extending onto flank (prominent, extending onto flank); relative length of fingers I < II < IV < III (I = II < IV < III); lateral fringes on digits absent (present, distinct); toes about one-fourth webbed (two-thirds webbed); skin on proximal posteroventral surfaces of thighs granular (skin on entire ventral surfaces of thighs granular).

Although specific distinctness of *G. piperata* with respect to *G. splendens* is pretty obvious, it is far less so with respect to *G. lauzuricae*. Both species are generally similar in external morphology and share a similar body size. In the following comparison of both taxa, we refer to the characters of the name-bearing *G. lauzuricae* holotype and topotypic *G. piperata* (n = 16) only, as the identity of additional specimens considered to represent either of both species by Lansac et al. (2021) remains questionable to some extent (see below). Comparing external morphology, the following differences between *G. piperata* topotypes and the *G. lauzuricae* holotype (characters in parentheses) are evident (Figs 5–6): snout rounded to truncate in dorsal view (acutely rounded); snout bluntly rounded in profile (rounded, with distinct indentation below nostrils); canthus rostralis straight in dorsal view (slightly concave); loreal region slightly concave (distinctly concave); HW/SVL ratio 0.326–0.359 (0.420); supratympanic fold almost straight (distinctly curving downward, reaching level of jaw articulation); skin on throat and chest granular (smooth); and dorsum and flanks lacking bright blue spots or flecks in life (present) (Fig. 7).

Cranial osteology inferred from micro CT-scanning of both holotypes revealed further differences (Fig. 8): In the skull of the *G. piperata* holotype, the dermal bones (frontoparietals, sphenethmoid, nasals, maxillae, and zygomatic rami of squamosals) barely exhibit exostosis, thus being barely hyperossified and bones are not fused. The lateral edges of frontoparietals are only very slightly elevated and there is no distinct pit-and-ridge sculpturing covering the entire surfaces of dermal bones, i.e., frontoparietals and sphenethmoid are smooth in the centre and exhibit some shallow pits at outer edges only; the maxillae and zygomatic rami of squamosals are entirely smooth. In contrast, exostosis is distinctly evident in the skull of the *G. lauzuricae* holotype. The lateral edges of frontoparietals are distinctly elevated and frontoparietals, nasals and sphenethmoid are entirely synostosed, being completely covered by a distinct pit-and-ridge sculpturing, as are the maxillae and zygomatic rami of squamosals. Furthermore, in lateral view of the skulls it is evident that in *G. lauzuricae* the sphenethmoid extends farther posteriorly, leaving only a small optic fenestra, whereas in the *G. piperata* holotype the optic fenestra is distinctly larger (at least 4 × the relative size of that of *G. lauzuricae*). In lateral view, the shape of the maxilla is far more slender, i.e less expanded in the dorsoventral dimension, in *G. piperata* when compared to *G. lauzuricae*. The outline of the maxilla is distinctly curved in lateral view (from the quadratojugal to the premaxilla) in *G. piperata*, whereas in *G. lauzuricae* the outline is straight. The position of the choanae in *G. lauzuricae* is more central, whereas the choanae in *G. piperata* are positioned more distally, closer to the maxillary arch. Finally, differences in snout shape described for the preserved holotype specimens are also reflected by respective differences in the shape of skull bones.

To infer the degree of variation in cranial osteology in nominal *G. piperata*, we in addition obtained CT-scans from four paratypes, two males and two females (Fig. 9). We can generally confirm the cranial characters found in the holotype for two paratopotypes (ZFMK 60291, 66839), namely the dermal bones of the skull barely exhibiting any sculpturing. However, the skull of the female paratopotype ZFMK 60287 exhibits a shallow pit-and-ridge sculpturing covering the dermal bones, squamosals and maxillae. All three mentioned specimens from the type locality, however, agree in other cranial characters, as, for example, the relatively large size of the optic fenestra, as present in the *G. piperata* holotype. In contrast, in the male *G. piperata* paratype ZFMK 66893, originating from La Siberia, 2800 m a.s.l. (the type locality of *G. lauzuricae*), cranial osteological traits appear more similar to those described for the *G. lauzuricae* holotype, namely frontoparietals, nasals and sphenethmoid completely covered by a distinct pit-and-ridge sculpturing, as are the maxillae and zygomatic rami of squamosals, but in contrast to the *G. lauzuricae* holotype dermal skull bones are not completely synostosed. Also, like in *G. lauzuricae*, the optic fenestra is distinctly smaller when compared to *G. piperata* topotypes (Figs 6, 7), but the slender maxilla in lateral view is in agreement with *G. piperata* topotypes and in contrast to the *G. lauzuricae* holotype.

Referring to the data provided by Lansac et al. (2021) on variation in cranial osteology of Bolivian *Gastrotheca*, the skull of the specimen MNKA 7157 from La Yunga de Mairana (2300 m a.s.l.), Provincia Florida, Departamento Santa Cruz, used and figured to infer the cranial osteology of *G. piperata*, differs osteologically from topotypic *G. piperata* by exhibiting a very distinct coarse pit-and-ridge sculpturing of frontoparietals, sphenethmoid, nasals and maxillae (Lansac et al. 2021: Fig. 6), a dorsoventrally expanded maxilla in lateral view, and a small optic fenestra. The same is true for the skull of CBG 1034 from La Siberia, 2750 m a.s.l. (allocated to *G. splendens* by Lansac et al. 2021), which is rather similar to the skull of MNKA 7157. Both mentioned skulls (CBG 1034, MNKA 7157) are similar to that of the *G. lauzuricae* holotype in sharing a distinct pit-and-ridge sculpturing of frontoparietals, sphenethmoid, nasals and maxillae. However, only in

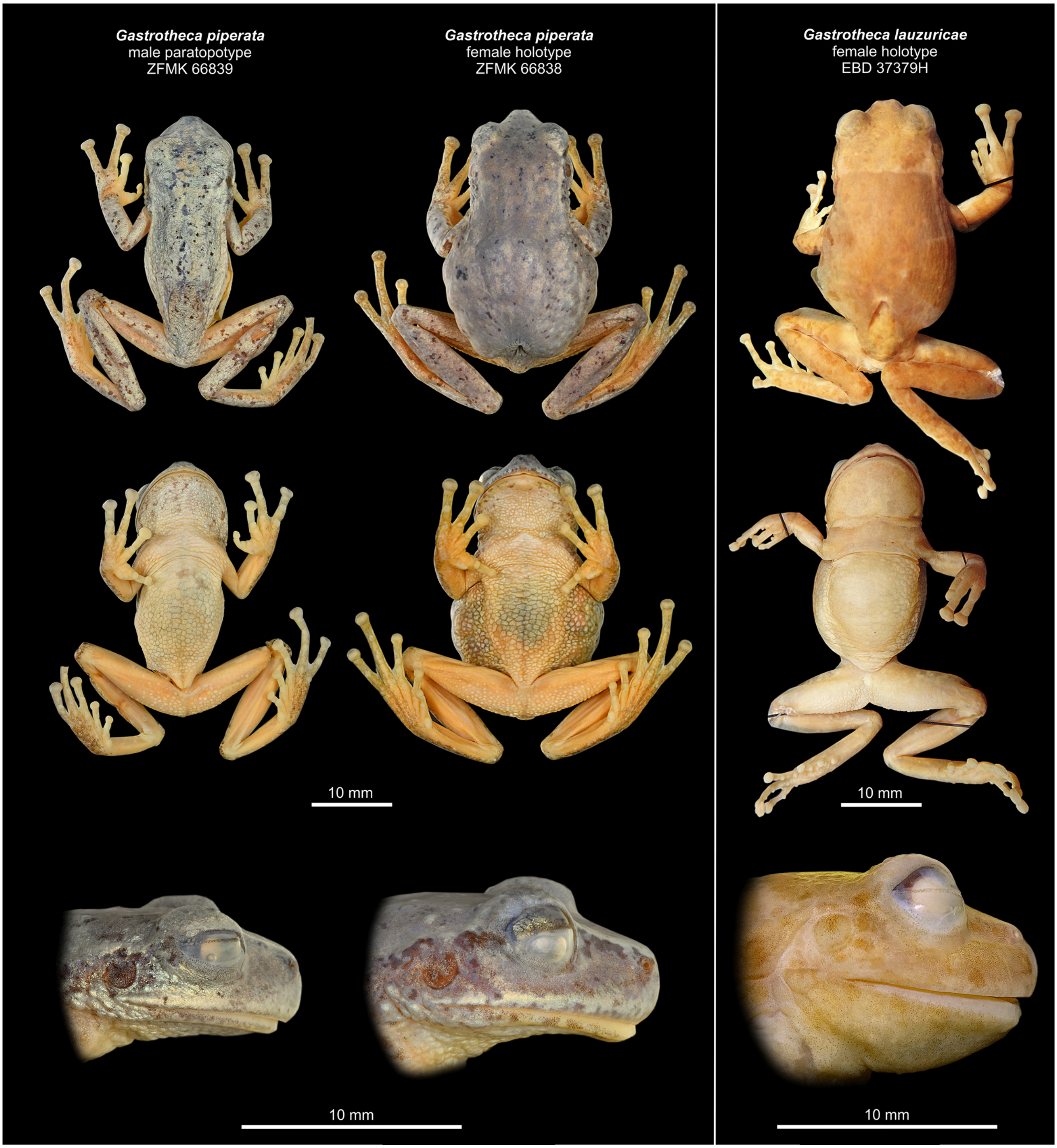

Figure 5. Dorsal (top row) and ventral (middle row) views, and lateral views of the heads (bottom row) of preserved type specimens of *Gastrotheca piperata* (left) and *Gastrotheca lauzuricae* (right) from Bolivian montane forest regions. Respective views figured at the same scale. Photographs of *G. lauzuricae* by J. C. Señaris.

Figure 6. Straight dorsal views of the heads of the preserved holotype specimens of *Hyla splendens*, *Gastrotheca lauzuricae* and *G. piperata*. Note rugose skin on head and snout of *H. splendens*, and slight differences between *G. lauzuricae* and *G. piperata* in relative snout length and outline of the canthus rostralis. Not to scale. Photograph of *G. lauzuricae* by J. C. Señaris.

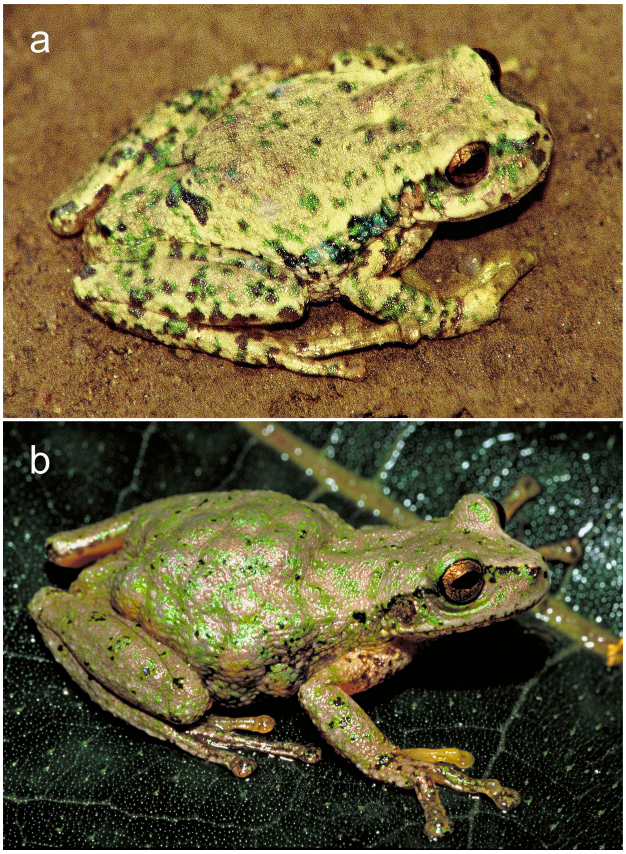

Figure 7. Dorsolateral views of adult female holotypes of (a) *Gastrotheca lauzuricae* (EBD 37379H; SVL 35.8 mm) and (b) *Gastrotheca piperata* (ZFMK 66838; SVL 36.5 mm) in life.

G. lauzuricae these dermal bones are entirely synostosed. Slight differences are also obvious in differently shaped frontoparietals, sphenetmoid, and vomers. However, with the current data at hand we are unable to provide any conclusive interpretation of the observed variation.

In summary, skulls from *Gastrotheca* specimens used by Lansac et al. (2021) and originating from Bolivian montane forests of the Departamento Santa Cruz and the easternmost Departamento Cochabamba, and including the holotype of *G. lauzuricae*, are all rather similar in characters and share a distinct sculpturing of dermal bones, a relatively small size of the optic fenestra and a dorsoventrally expanded maxilla. The male *G. piperata* paratype ZFMK 66893, originating from the same area, is also in respective agreement, but differs slightly by a slender maxilla. Skulls of *G. piperata* from its type locality Sehuencas, Carrasco National Park, Departamento Cochabamba, show some variation with respect to the degree of dermal sculpturing, ranging from sculpturing being completely absent (ZFMK 66839) to presence of a shallow pit-and-ridge sculpturing entirely covering the dermal bones (ZFMK 60287). However, all osteologically studied topotypes of *G. piperata* agree in the relatively large size of the optic fenestra and a slender maxilla, and thus differ in these character states from studied specimens with a more eastern origin (except for the slender maxilla in ZFMK 66893).

Although we pointed to certain differences in external morphology and osteology between the name-bearing types of *G. lauzuricae* and *G. piperata*, when taking into account available information for other Bolivian montane forest specimens and populations, data are hardly conclusive with respect to the specific distinctness of both nominal taxa. At the current state, we are unable to judge whether the observed differences display variation in a single species occupying most of the Bolivian montane forests of the Departamentos Cochabamba and Santa Cruz as proposed by Lansac et al. (2021), or represent species-specific differences, indicating the existence of more than one species in this respective region. Although widespread species of *Gastrotheca* are known, in most cases these refer to species occurring in high-altitude puna habitats, like for example *G. marsupiata*, *G. peruana* or *G. pseustes*. When referring to Andean montane forest inhabiting species of *Gastrotheca*, ranges are usually much smaller (e.g., Duellman

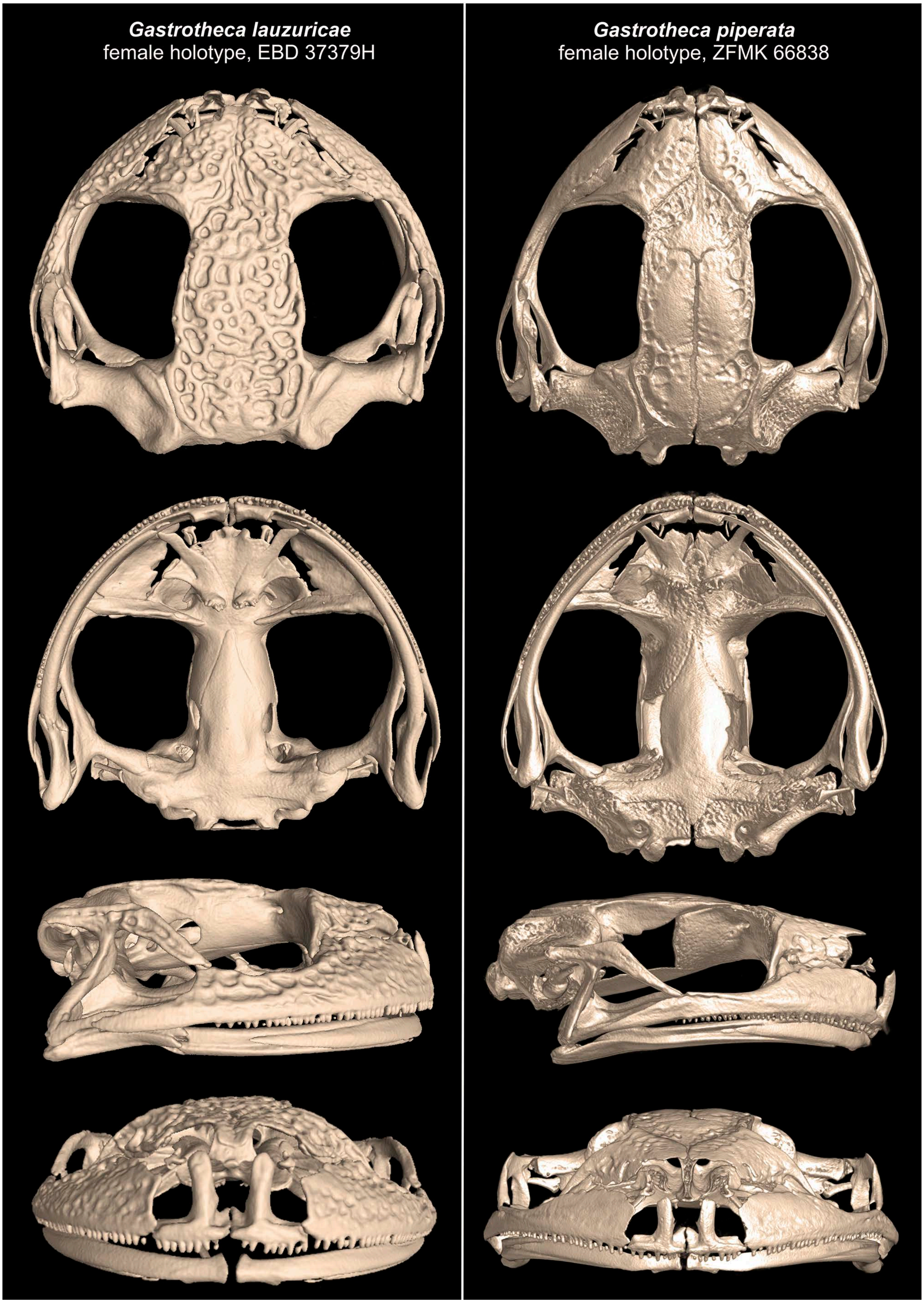

Figure 8. Images produced from micro CT-scanning showing comparative cranial osteology of the female holotypes of *Gastrotheca lauzuricae* (left column) and *Gastrotheca piperata* (right column). From top to bottom, skulls in dorsal, ventral, lateral and frontal views. Not to scale.

2015). An exception is *G. testudinea*, currently considered to occur along the eastern Andean slopes from northern Ecuador south to central Bolivia (Duellman 2015, Frost 2024). However, Köhler (2000a) already suspected that nominal *G. testudinea* likely constitute a complex of species, a view later corroborated by a phylogenetic study revealing the paraphyly of this nominal taxon (Echevarría et al. 2021). Other studies demonstrated the presence of species-level lineages within nominal species of *Gastrotheca* distinguished by only subtle morphological differences (e.g., Duellman et al. 2014, Carvajal-Endara et al. 2019). Taking into account such results and given the current knowledge for other anuran genera occurring in Bolivian montane forests along the eastern Andean slopes, like, for example, *Boana*, *Oreobates*, and *Yunganastes* (Köhler et al. 2010, Köhler & Padial 2016, Padial et al. 2007), a parallel scenario of multiple species occurring largely in sympatry and/or close parapatry seems also possible for Bolivian montane forest *Gastrotheca*. A faint indication for such a situation is some genetic diversification among the Bolivian montane forest populations in question revealed by phylogenetic studies (Castroviejo-Fisher et al. 2015, Echevarría et al. 2021; but see below).

Although we are unable to exclude the possibility that *G. piperata* is specifically distinct from *G. lauzuricae* and represents a valid taxon, due to a lack of unambiguously conclusive data, we here provisionally continue to consider *Gastrotheca piperata* Duellman & Köhler, 2005 a junior synonym of *Gastrotheca lauzuricae* De la Riva, 1992, as implied by Lansac et al. (2021). With this decision, we follow the proposed principle of 'parsimony of taxonomic changes' (see Scherz et al. 2017).

Status of *Hylodes coeruleomaculatus*

Hylodes coeruleomaculatus Werner, 1899 has been described based on two syntypes (NHMW 16496:1–2; Fig. 10), both of which appear to be non-adult male specimens. Currently, the species is tentatively considered val-

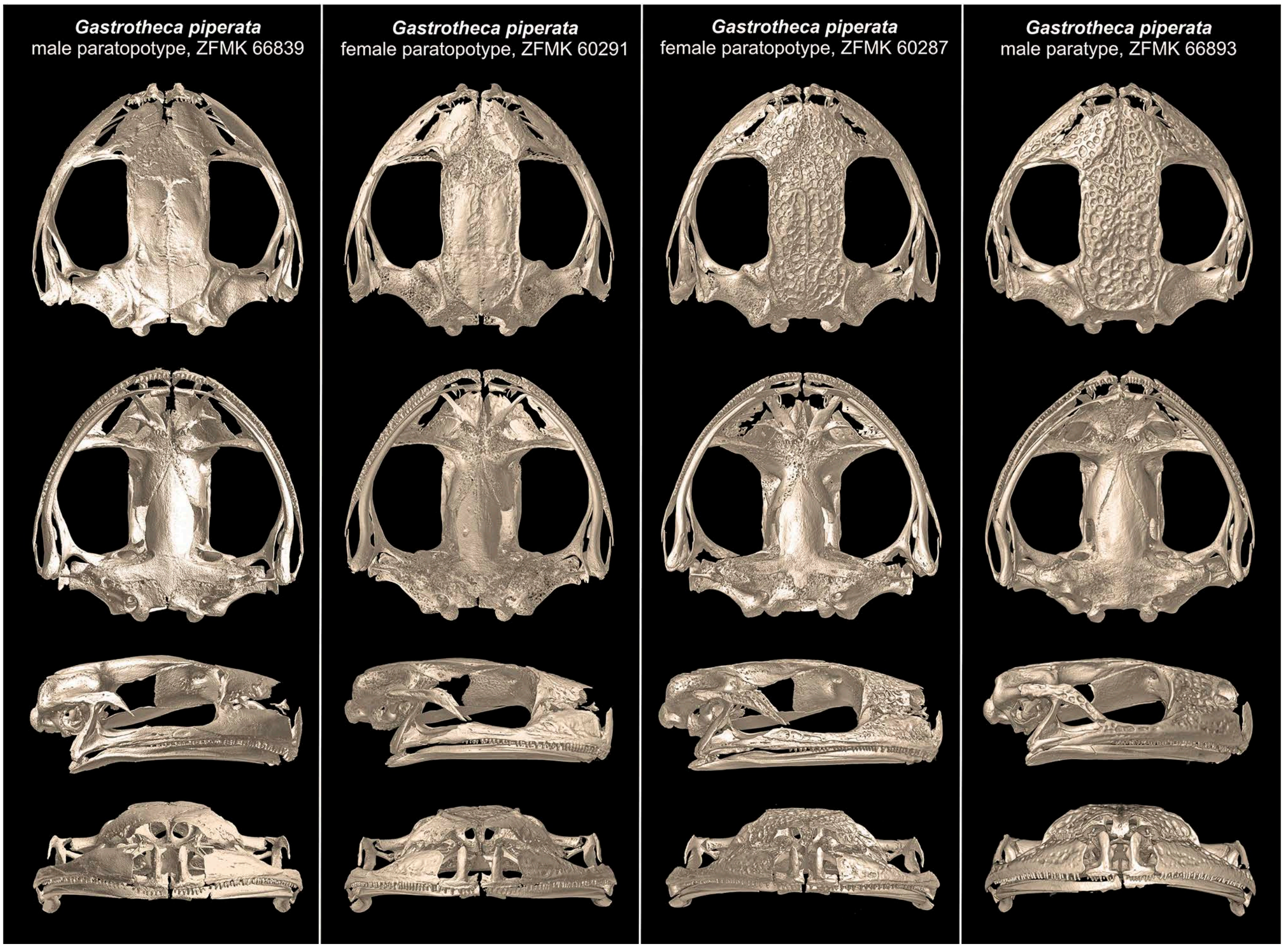

Figure 9. Images produced from micro-CT scanning showing comparative cranial osteology of *Gastrotheca piperata* paratypes. From top to bottom, skulls in dorsal, ventral, lateral and frontal views. Specimens ZFMK 60287, 60291 (adult females) and ZFMK 66839 (adult male) originate from the type locality Sehuencas, 2150 m a.s.l., Departamento Cochabamba, Bolivia, whereas the paratype ZFMK 66893 (adult male) originates from La Siberia, 2800 m a.s.l., Departamento Cochabamba, Bolivia. Not to scale.

id under the name *Gastrotheca coeruleomaculata* (erroneously spelled *G. coeruleomaculatus* in several publications; the gender of *Gastrotheca* is feminine; see Frost 2024) and considered to be the name applicable to populations occurring in the Yungas montane rainforests in Departamento La Paz, Bolivia (Lansac et al. 2021). This proposal was based on the fact that the type locality "Bolivia (Chaco)" (Werner 1899) most probably corresponds to a so-called locality situated at 16°20'55" S, 67°49'05" W, 2042 m a.s.l., in the Yungas de La Paz, Bolivia (see Lansac et al. 2021), a locality from which Werner (1899) also described *Telmatobius verrucosus* and *Hylodes gollmeri* var. *bisignata* (= *Yunganastes bisignatus*) (De la Riva 2005, Padial et al. 2007). Although the syntypes exhibit several characters that would also be in agreement with the external morphology documented for *G. marsupiata*, including the dorsal color pattern of NHMW 16496:1 (Fig. 10), we here tentatively continue to consider the name *G. coeruleomaculata* to correspond to a population originating from a montane forest location in the Yungas de La Paz, Bolivia, sensu Lansac et al. (2021), an area from where *G. marsupiata* is unknown. Lansac et al. (2021) pointed to a *Gastrotheca* population from the Yungas de La Paz reported by Pacheco (2015) and figured one living adult female of this

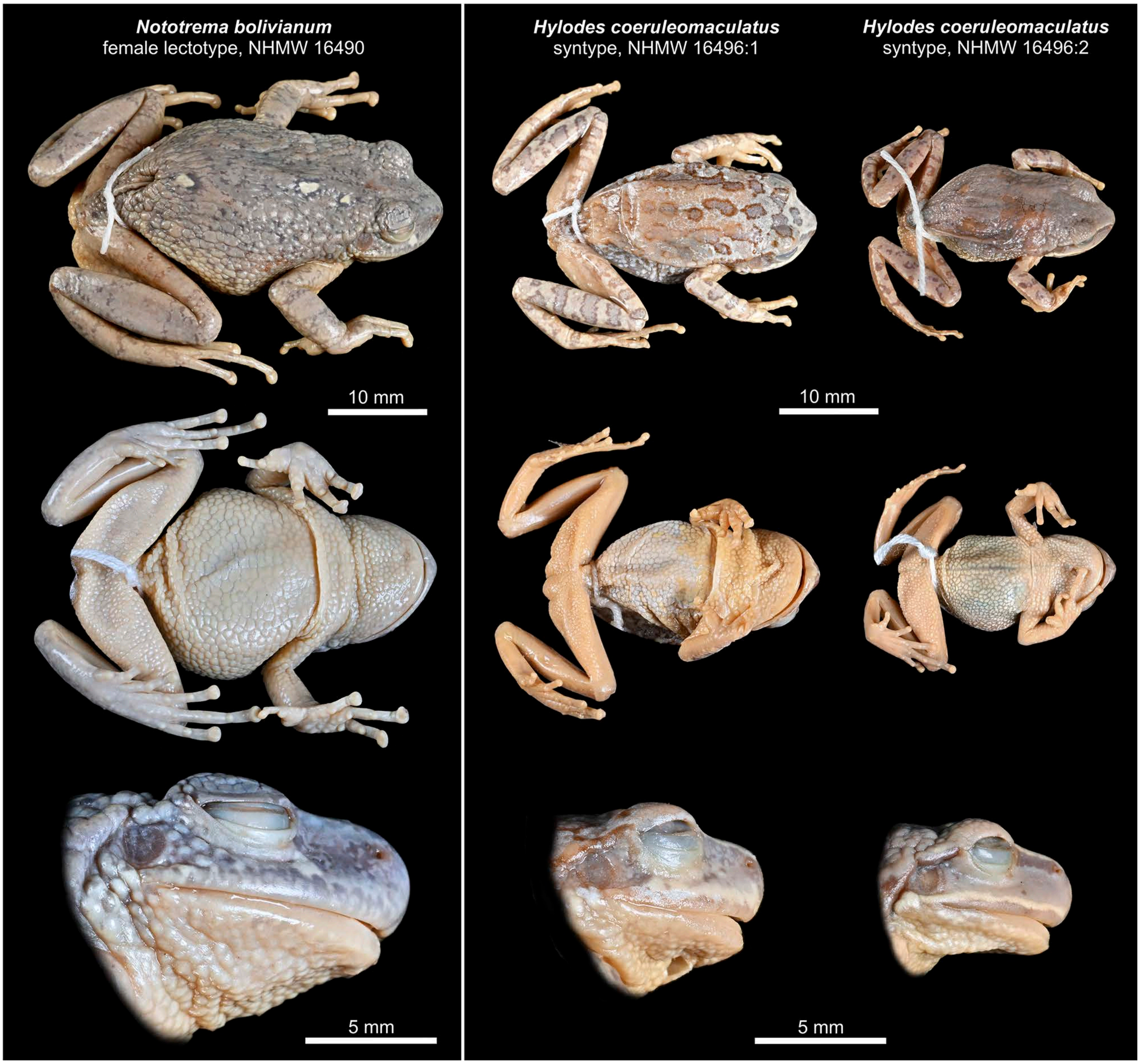

Figure 10. Preserved type specimens of nominal taxa associated with Bolivian *Gastrotheca* (*Nototrema bolivianum*, *Hylodes coeruleomaculatus*) in dorsolateral views (top row), ventral views (middle row), and lateral profile of the heads (bottom row). Respective views figured at the same scale. Photographs by C. Potter.

population in dorsolateral and ventral views (Lansac et al. 2021: Fig. 7). The ventral surfaces of the respective individual show a striking pattern of different colors, including a yellowish-cream throat, a belly with blue, green and yellow colors, and orange ventral surfaces of thighs. Remarkably, the syntype NHMW 16496:1 exhibits a distinctive pattern of colors on its ventral surfaces (Fig. 10), somehow reminding that of the individual photographed in life: throat and chest pale orange-tan, with some of this color extending to the anterior belly, belly greyish, and ventral surfaces of thighs orange-cream. This ventral color pattern may indeed argue for conspecifity of *G. coeruleomaculata* with the reported population, but further studies, once specimens from the Yungas de La Paz become available, are needed to confirm or reject this hypothesis (Lansac et al. 2021).

Status of *Nototrema bolivianum*

Nototrema bolivianum Steindachner, 1892 was placed in the synonymy of *Gastrotheca marsupiata* by Duellman & Fritts (1972), who also designated the specimen NHMW 16490 as lectotype. This view was later followed by Duellman & Köhler (2005) and Duellman (2015). Characteristics of the adult female lectotype (Fig. 10) are concordant with *G. marsupiata* as currently defined (sensu Duellman 2015), with a body size (SVL 42.8 mm) and dorsal color pattern falling into its documented intra-specific variation, the snout acutely rounded in dorsal view and rounded in profile, canthus rostralis rounded in cross-section, and dorsal skin densely covered by flat, rounded pustules (termed warts by Steindachner 1892). This combination of characters distinguishes *N. bolivianum* from *G. splendens*, *G. lauzuricae* and *G. piperata* and we thus here confirm its synonymy with *G. marsupiata*. As already stated by Duellman & Köhler (2005), the type locality of *N. bolivianum* "Bolivia, Provinz Yuracares, bei Puerto de S. Mateo am oberen Chaparé" (Steindachner 1892) most probably corresponds to a locality at the Andean foot in the Departamento Cochabamba, Bolivia, an area from where *G. marsupiata* is unknown, as it occurs at much higher elevations (2500–4360 m a.s.l.; Duellman 2015). Therefore, the type locality probably is in error (see Duellman & Köhler 2005).

Comments on *Leptodactylus andicola*

Although not the focus of this contribution, the taxon *Leptodactylus* (*Plectromantis*) *andicola* Boettger, 1891 deserves some comments. The species, originating from the vicinity of Sorata (Departamento La Paz), Bolivia, was described by Boettger (1891) in a fairly detailed manner. However, as the type is apparently lost (Heyer 1978), its identity remains obscure. Heyer (1978) associated the name with the genus *Eleutherodactylus* without further explanation, but probably based on the fact that Boettger (1891) described well-developed and slightly triangular discs on fingers. Later, Lynch & McDiarmid (1987) noted some striking agreement of Boettger's (1891) description with *Gastrotheca marsupiata*. Although Lynch & McDiarmid (1987) did not formally place *L. andicola* as a junior synonym of *G. marsupiata*, it is since treated as such (see Frost 2024).

Reviewing Boettger's (1891) description again and taking into account current knowledge, we come to a different conclusion. Among the characters mentioned by Boettger (1891) are: first and second finger equal in length; fingers and toes bearing narrow lateral fringes; well-developed [expanded] somewhat triangular discs on fingers and toes; prominent whitish tarsal fold; two metatarsal tubercles, inner oval, outer round; skin on dorsum finely granular, some single larger warts on flanks; distinct supratympanic fold; tibiotarsal articulation reaching slightly beyond tip of snout [when hindlegs flexed perpendicular to body]; black frenal stripe, black supratympanic stripe; lips reddish-white with black flecks or cube-like bars; limbs with indistinct dark transversal bars; venter yellowish-brown with blackish marbling on throat, chest and inner side of shanks. These characters as well as the SVL of 48 mm are in agreement with species of *Yunganastes*, like e.g., *Y. bisignatus*, known from montane forests of the Departamento La Paz, Bolivia (see Köhler 2000a, Padial et al. 2007, Ocampo et al. 2020). The character of the first and second finger being equal in length is also covered by known species of *Yunganastes* with the first finger being only slightly longer than the second in *Y. ashkapara* and *Y. fraudator* (Köhler 2000b, Lynch & McDiarmid 1987), very slightly longer or equal in length in *Y. pluvicanorus* (De la Riva & Lynch 1997), or first finger being even slightly shorter than second in *Y. mercedesae* (Lynch & McDiarmid 1987). Although Boettger (1891) did not mention the presence of dorsolateral folds typically present in *Yunganastes*, these can be indistinct in some species or individuals in the genus (see Lynch & McDiarmid 1987, Ocampo et al. 2020).

In contrast, Boettger's (1891) diagnostic characters are not in agreement with *Gastrotheca marsupiata* as currently defined (Duellman 2015). The description of *L. andicola* differs in the following aspects from *G. marsupiata* (characters of the latter in parentheses): first and second finger equal in length (first finger shorter than second); well-developed triangular discs on fingers and toes (small round discs); fingers with narrow lateral fringes (absent); round outer metatarsal tubercle (absent); prominent tarsal fold along 1/3 of tarsus (weak tarsal fold on distal half of tarsus); lips with black flecks or bars (absent); and tibiotarsal articulation reaching beyond tip of snout (reaching level of eye).

Thus, we conclude that *Leptodactylus andicola* is not synonymous with *Gastrotheca marsupiata*, but probably assignable to a species of *Yunganastes*, some of which are known to occur close to the type locality of *L. andicola* in the montane forests of the Departamento La Paz, Bolivia (see Padial et al. 2007, Ocampo et al. 2020). However, as it is impossible to assign the name to a certain population based on Boettger's (1891) description alone and given that the type is lost, we consider *Leptodactylus* (*Plectromantis*) *andicola* Boettger, 1891 a nomen dubium, as already implied by De la Riva (1990).

Genetics of Bolivian montane forest populations

Samples of Bolivian montane forest *Gastrotheca* have so far been included in two major contributions on hemiphractid phylogeny (Castroviejo-Fisher et al. 2015, Echevarría et al. 2021). Both studies used the same sampling of Bolivian montane forest *Gastrotheca* which they referred to as *Gastrotheca* sp. 1–3 given the unsolved taxonomy of these populations. However, these studies did not aim at the clarification of alpha taxonomy, but focused on the relationships of genera and species groups. For their multigene phylogenetic approaches both contributions used gene sequences generated from multiple specimens for single terminals. Their *Gastrotheca* sp. 2 contained sequences of the specimen MNK 5286 (from PN Amboró, Prov. Caballero, Departamento Santa Cruz) and specimen CBG 1020 (from Karahuasi, Departamento Cochabamba). In an erroneous statement, Castroviejo-Fisher et al. (2015) claimed that MNK 5286 was redetermined as *G. piperata* by Duellman & Köhler (2005), whereas they flagged CBG 1020 as *G. lauzuricae*. Moreover, the terminal named *G.* sp. 3 by Castroviejo-Fisher et al. (2015) and Echevarría et al. (2021) is composed of sequences generated from ZFMK 66954, a juvenile of 17.7 mm SVL with a striped dorsum (from Incachaca, Departamento Cochabamba) and MNCN 43052 (from Camino de los tubos del Puente Penstock, Departamento Cochabamba). Apparently, this mixing of different specimens for single terminals was based on unpublished results of 27 samples and three genes of Bolivian *Gastrotheca* resulting in three non-sister lineages (see Castroviejo-Fisher et al. 2015), but the authors did not further explain their action. Later, Echevarría et al. (2021), using the same combined sampling for *G.* sp. 1–3, stated that they did not include samples of the nominal taxa *G. piperata* and *G. splendens*. In view of the problematic taxonomy of the considered Bolivian populations, the available phylogenetic data are thus inappropriate to provide insight at the species level.

Nevertheless, both phylogenetic analyses (Castroviejo-Fisher et al. 2015, Echevarría et al. 2021) basically revealed the same relationships of the respective Bolivian populations, with *Gastrotheca* sp. 1–3 included in a clade containing *G. marsupiata*, *G. christiani*, *G. chrysosticta* and *G. gracilis*. Differentiation among the lineages in this clade was moderate, but at a similar level when compared to other species-level lineages within the *G. marsupiata* species group (see also Fig. 3).

Given that available morphological and osteological data are partly inconclusive, the analysis of sequences from respective name-bearing type specimens, or at least topotypes, appears to be crucial to shed light on the relationships and species delimitation among Bolivian montane forest *Gastrotheca* and the potential nominal taxa involved. So far, no sample of *G. piperata* from the type locality or the type series has been included in any molecular genetic analysis, nor have been samples of specimens unequivocally identifiable as *G. lauzuricae* or *G. coeruleomaculata*. Future molecular approaches should take the effort of trying to extract and sequence archival DNA from these name-bearing types (e.g., Scherz et al. 2020), as otherwise sampling of multiple, potentially closely related species, partly occurring in sympatry, may result in even more obfuscation. Such future molecular analyses should also include a more comprehensive sampling of Bolivian montane forest populations whose identities are in question.

Conclusions

Although the present study is not completely conclusive with respect to the majority of populations and nominal taxa of Bolivian montane forest *Gastrotheca*, we here summarize our taxonomic conclusions derived from the investigation of crucial specimens:

(a) Morphological characters and molecular genetics of the holotype of *Hyla splendens* reveal it as part of the genus *Gastrotheca* (*G. marsupiata* species group) and as being conspecific with *Gastrotheca monticola*. Consequently, *Gastrotheca monticola* Barbour & Noble, 1920 is considered a junior synonym of *Hyla splendens* Schmidt, 1857, with the latter regarded a valid species, *Gastrotheca splendens* (Schmidt, 1857). Applying the recommendation 76A.2. of the Code (ICZN 1999), we correct its type locality to 'northwestern Peru'.

(b) The rediscovery of *Gastrotheca splendens* in Bolivia as reported by Duellman & De la Riva (1999) based on a Bolivian specimen collected in the 1990s (MNK 1988) is in error. None of the Bolivian *Gastrotheca* populations known is referable to the name *G. splendens*.

(c) *Gastrotheca lauzuricae* De la Riva, 1992 is not conspecific with *G. splendens* and is consequently removed from its synonymy where it has been placed by Lansac et al. (2021). It is furthermore not conspecific with *G. coeruleomaculata* (see Duellman 2015, Lansac et al. 2021) and regarded a valid species occurring (at least) in upper Bolivian montane forests at the border of the Departamentos Cochabamba and Santa Cruz.

(d) *Gastrotheca piperata* Duellman & Köhler, 2005 is not conspecific with *G. splendens* and is consequently removed from its synonymy where it had been placed by Lansac et al. (2021). Given the data available, its conspecifity with *G. lauzuricae* as implied by Lansac et al. (2021) is questionable, but remains a possible scenario. Due to this inconclusive situation, we apply a principle of parsimony of taxonomic changes at the current stage and provisionally regard *Gastrotheca piperata* Duellman & Köhler, 2005 representing a junior synonym of *Gastrotheca lauzuricae* De la Riva, 1992, pending future investigations.

(e) The taxonomic status and distribution of *Gastrotheca coeruleomaculata* (Werner, 1899) is not completely conclusive and partly remains obscure. However, we tentatively continue to consider it a valid species occurring in montane forests in the Yungas de La Paz, Bolivia, as proposed by Lansac et al. (2021).

(f) The taxonomic status of *Gastrotheca marsupiata* (Duméril & Bibron, 1841) in Bolivia is unquestioned when considering it representing populations from the high Andean puna habitats. In addition, it is common agreement that *G. marsupiata* may occur close to cloud forests or even enter those to a slight extent in some areas in Bolivia (e.g., Duellman 2015, Lansac et al. 2021). We furthermore support the synonymy of *Nototrema bolivianum* (whose type locality most probably is in error) and *G. marsupiata*, as the morphological characters of the *N. bolivianum* lectotype, as well as Steindachner's (1892) description and drawings, are in agreement with the morphology of *G. marsupiata* as currently defined.

(g) *Leptodactylus andicola* Boettger, 1891 is removed from the synonymy of *Gastrotheca marsupiata* (Duméril & Bibron, 1841) and considered a nomen dubium (lost type specimen). The characters provided in the original description (Boettger 1891) are in disagreement with *G. marsupiata* but in concordance with species of the genus *Yunganastes* and argue for respective affinities.

The results of our study highlight the importance of referring to name-bearing type specimens when taxonomically revising a certain group of organisms and the particularly high value of isolating and sequencing archival DNA from historical types. As practically demonstrated by recent studies on anuran systematics (Rancilhac et al. 2020, Scherz et al. 2020, Vences et al. 2021), obtaining DNA barcode sequences from old type specimens in many cases is an essential requirement to solve problems commonly connected to older taxon names, as, for example, uncertain or imprecise type localities, lack of recently collected topotypic material, poor state of preservation of name-bearing types, and/or morphological crypsis of phylogenetically identified species-level lineages. The complex taxonomic situation of Bolivian montane forest *Gastrotheca*, with variation in morphology and osteology that is currently hardly interpretable taxonomically, calls for such a future approach which hopefully will result in genotyped name-bearing types and decryption of their relationships within a comprehensive populational sampling.

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