Three new Bolivian species of *Psychrophrynella* (Anura: Craugastoridae), and comments on the amphibian fauna of the Cordillera de Apolobamba

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Abstract. Three new species of *Psychrophrynella* from the Bolivian section of the Cordillera de Apolobamba are described. The new species are distinguished from their closest relatives mainly by characters such as colour pattern, size, and skin texture. With the addition of these three new species, the diversity of the genus *Psychrophrynella* in Bolivia increases to 21 species. The protected Area Natural de Manejo Integrado Nacional (ANMIN) Apolobamba holds seven endemic species, and it is highly likely that more undescribed forms will be discovered when new surveys are conducted in this region, underscoring the need to preserve its rich endemic amphibian fauna.

Key words. Amphibia, Andes, endemism, new species, Psychrophrynella.

Introduction

Direct-developing frogs from the northern and central Andes that live in high-altitude cloud forests, elfin forests, and humid highland grasslands share a suite of morphological characteristics such as small to moderate adult size, short legs, robust body, and tips of digits not or scarcely expanded. LYNCH (1975) grouped most of these forms distributed from northern Colombia to central Bolivia in the genus Phrynopus PETERS, 1863. However, HEDGES et al. (2008) and PADIAL et al. (2012, 2014) demonstrated the nonmonophyly of Phrynopus sensu LYNCH (1975). These distinct Andean lineages have independently evolved similar morphologies, and their members are currently classified in several genera. Phrynopus is now restricted to central Peru, whereas all the species occurring in Bolivia were assigned to the genus Psychrophrynella Hedges, DUELLMAN & HEINICKE, 2008, where they represent an important proportion of the Andean anuran diversity. Eighteen species of Psychrophrynella, all of them endemic, are known thus far from Bolivia, and many more await description (DE LA RIVA 2007, DE LA RIVA & BURROWES 2014). The diversity of these frogs seems to be especially high in certain regions, among them the Cordillera de Apolobamba, which extends across de Bolivian-Peruvian border. So far, four species have been described from the Bolivian section of Apolobamba (DE LA RIVA 2007), while only one is known from the Peruvian section (P. boettgeri [LEHR, 2006]), and two more are currently being described (DE LA RIVA et al. unpubl. data). However, the large expanse of suitable areas that have remained unexplored, and the known high endemism within the genus, make it likely that many undescribed species of *Psychrophrynella* occur in the region. In this paper, we describe three additional Bolivian species of *Psychrophrynella* found during faunistic surveys in the protected Area Natural de Manejo Integrado Nacional (ANMIN) Apolobamba. At the same time, we discuss the conservation value of the rich, highly endemic amphibian fauna of this region.

Material and methods

Specimens were fixed in 10% formalin and preserved in 70% ethanol. They were deposited at the Museo Nacional de Historia Natural, Colección Boliviana de Fauna (CBF, La Paz, Bolivia). We considered nine morphometric variables as follows: snout-vent length (SVL), head length (HL, from rictus to tip of snout), head width (HW, at level of rictus), internarial distance (IND), distance from eye to nostril (END), eye diameter (ED), tympanum diameter (TD), tibia length (TL), and foot length (FL, from proximal border of inner metatarsal tubercle to tip of fourth toe). Lengths of digits were compared by adpressing them against each other. For measurements, we used a digital calliper to the nearest 0.01 mm, but rounded results to only one decimal

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to avoid pseudo-precision (HAYEK et al. 2001). Character definitions follow DUELLMAN & LEHR (2009), and diagnosis and descriptions the format suggested by DE LA RIVA (2007). When sex could not be identified by external characters (e.g., size, sexual dimorphism in colour pattern, eggs observable through the ventral skin, presence of vocal sac in adult males, etc.), gonads were examined. Descriptions of colour in life were based on field notes. Drawings were made under a stereomicroscope with the aid of a camera lucida.

Species of Psychrophrynella are highly endemic, with their distributions being often extremely restricted; thus, they are well characterized by geography, which always strongly supports species separation (DE LA RIVA 2007). Two species separated by, say, 200 km, can be remarkably similar in morphology and coloration, while species from adjacent valleys are usually easy to distinguish by external characteristics. In taxonomy, diagnoses are provided mostly for practical purposes, to facilitate telling apart (in the field or lab) closely related species, externally similar species, or species living in the same region. For this reason, and given the highly endemic distributions of species of Psychrophrynella, we herein emphasize diagnostic comparisons between the geographically closest species (i.e., those occurring in the Apolobamba range) and from those particularly similar ones, if any.

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: 1AADF552-DBAE-4765-A6E9-2B9673970FDA. The electronic edition of this work was published in a journal with an ISSN, has been archived and is available from the following digital repositories: www.salamandra-journal.com.

Psychrophrynella chaupi DE LA RIVA & APARICIO, sp. n. (Figs 1, 4C)

ZooBank LSID: urn:lsid:zoobank.org:act: 0119034A-00FB-4AB7-A334-AB92F95C5DCC

Holotype: CBF 5694, an adult female from Valle de Tojoloque, 14°44'19.5" S, 69°00'33.3" W, 3,940 m, Province Franz Tamayo, Department La Paz, Bolivia, collected on 24 October 1999 by J. APARICIO.

Paratypes: Nineteen specimens, CBF 5691, 5697–8, 5700, 5703, adult males; CBF 5695–96, 5704–05, 5708, adult females; CBF 5690, 5692–93, 5699, 5701–02, 5706–07, 6044, all of them collected with the holotype.

Diagnosis: 1) medium size (maximum SVL 22.2 mm), body moderately robust, legs moderately short (TL + FL = 78.1%SVL; range, 74.5-81.9%; N = 8); 2) tympanic membrane and tympanic annulus present and clearly visible; 3) first finger slightly shorter than second; 4) tips of digits slightly swollen, not expanded laterally; 5) no webbing of toes or lateral fringes; 6) two metatarsal tubercles, tarsal fold absent; 7) dorsal skin and flanks shagreen with scattered small warts; no dorsolateral folds; ventral skin finely granular; 8) snout rounded in dorsal view and in profile; 9) dorsum mostly uniformly brown; 10) venter greyish brown, chest and throat tan.

The new species is assigned to the genus Psychrophrynella as defined by HEDGES et al. (2008) and DUELLMAN & LEHR (2009). Frogs of the allied genus Bryophryne are morphologically similar to Psychrophrynella, but Bryophryne does not occur in Bolivia, being restricted to the Department of Cusco in southern Peru. Psychrophrynella chaupi is superficially similar to P. katantika (DE LA RIVA & MARTÍNEZ-SOLANO, 2007), which occurs in the nearby valley of Pelechuco (air-line distance between the two type localities, 11.5 km). The new species is distinguished from P. katantika mainly by being smaller (maximum SVL in P. chaupi 22.2 mm, 27.7 mm in P. katantika) and having a visible tympanum. Other geographically close species are P. colla sp. n. and P. melanocheira sp. n., described herein, whose type localities are at air-line distances of 12.2 km and 18.5 km, respectively, to the southeast of the type locality of P. chaupi. Psychrophrynella chaupi differs from these two species by lacking dorsolateral folds, having a finely granular ventral skin (smooth in P. colla and P. melanocheira), and a uniformly greyish brown ventral coloration (beige with minute white flecks in *P. colla*; greenish grey, sometimes with a black belly, in *P. melanocheira*). The new species furthermore differs from P. colla by having slightly swollen tips of digits (slightly pointed in P. colla), and from P. melanocheira by having longer legs. Other, more geographically distant species of *Psychrophrynella* that occur in the Cordillera de Apolobamba, are P. boettgeri (in the Peruvian section of the range), P. guillei (DE LA RIVA, 2007), P. kallawaya (DE LA RIVA & MARTÍNEZ-SOLANO, 2007), and P. saltator (DE LA RIVA, REICHLE & BOSCH, 2007). Psychrophrynella boettgeri is smaller (maximum SVL 18.4 mm) than P. chaupi (22.2 mm) and has reddish brown blotches on the dorsum and orange blotches on the groins and venter; P. guillei has an olive green dorsum with dark blotches, and a yellowish white venter with black mottling; P. kallawaya is much larger (maximum SVL 30.9 mm); and P. saltator has narrow cream bands on the dorsal faces of its digits and a large vocal sac in males.

Description of the holotype: Body moderately robust; dorsal skin shagreen with scattered small pustules; ventral skin finely granular; no thoracic fold; head wider than long, its width 35.6% of SVL; head length 27.0% of SVL; snout moderately short, rounded in dorsal view, slightly slopping in profile; nostrils not protuberant, directed laterally, closer to snout than to eyes; canthus rostralis concave in dorsal view and slightly convex in profile; eye–nostril distance 68.2% of eye diameter; loreal region concave, interorbital region flat, lacking cranial crests; tubercles on upper eyelid absent; tympanic membrane and tympanic annulus present; tympanum diameter 55.5% of eve diameter; supratympanic fold weak, short, barely reaching the level of shoulder; a few small, round postrictal tubercles, below tympanum; tongue large, oval; choanae oval, small, widely spaced; dentigerous processes of vomers absent. Limbs moderately short; tips of digits slightly swollen, not expanded laterally; ulnar tubercle and fold absent; inner palmar tubercle single, oval, smaller than round outer palmar tubercle; fingers not fringed; subarticular tubercles large, round, moderately flattened; supernumerary tubercles flattened, irregular; first finger slightly shorter than second, relative lengths of fingers 1 < 2 < 4 < 3; tibia length 36.9% of SVL; tarsus lacking tubercle and fold; two metatarsal tubercles, the inner one slightly oval, approximately the same size as the round outer one; supernumerary tubercles round, small; subarticular tubercles round, small, moderately swollen; toes long, slender, not webbed, lateral fringes absent; relative lengths of toes 1 < 2 < 5 < 3 < 4; foot length 40.5% of SVL.

Measurements (in mm) of the holotype: SVL 22.2; HL 6.0; HW 7.9; IND 1.8; END 1.5; ED 2.2; TD 1.2; TL 8.2; FL 9.0.

Colour pattern: In preservative, the dorsum, head, and upper parts of the extremities are dark greyish brown with irregular darker areas. There are some reddish brown, small, irregular markings in the tympanic region; the tympanum is reddish brown. There is a fine, pale grey middorsal stripe from snout to cloaca, surrounding the cloaca and continuing along the posterior faces of the thighs. The venter and ventral faces of the limbs, as well as the palmar and plantar faces are dirty greyish brown; a pale grey line runs from the middle of the chest to the elbow along the lower face of the arm; the throat and chest are pale brown. The venter is dark grey. In life, the dorsal faces were reddish brown, the flanks greyish brown, the vertebral line pale cream, the belly and ventral faces of limbs dark grey, and the palmar surfaces black; the iris was greyish green, with metallic reflections.

Variation: Males are more variable than females in colour pattern. They have a dark grey or brown throat with an undeveloped subgular sac and lack vocal slits and nuptial pads. Male specimen CBF 5697 has a pale vertebral line, and pale areas between the eves, in the suprascapular regions, and the sacral region, and exhibits a thin, pale midventral line that forms a cross with similar lines that are on the throat and the ventral faces of forelimbs; male specimen CBF 5698 has an irregular pattern of grey and brown blotches and two suprainguinal dark spots; male specimen CBF 5703 has two broad, pale, laterodorsal bands; male specimen CBF 5691 is similar to male specimen CBF 5697, but lacks a vertebral line, and its pale sacral area is triangular and reaches the end of the stylum. Females are more alike in general. Female specimen CBF 5695 is similar to the holotype, but has its dorsolateral ridges formed by small tubercles; female specimens CBF 5696 and 5708 have X-shaped suprascapular ridges made up by small tubercles



Figure 1. Dorsal and ventral views of the adult female holotype of P. chaupi sp. n. (CBF 5694; SVL = 22.2 mm).

| Species Sex Samples | P. chaupi Males n=2 | <i>P. chaupi</i> Females n=6 | <i>P. colla</i> Male CBF5759 | <i>P. colla</i> Female CBF5757 | P. melanocheira Males n=2 | P. melanocheira Females n=4 |
|---------------------------|---------------------------|------------------------------------|------------------------------------|--------------------------------------|---------------------------------|-----------------------------------|
| SVL | 19.0 (18.4–19.6) | 21.2 (19.6–22.2) | 20.1 | 17.7 | 17.2 (16.5–17.9) | 23.6 (23.4–23.9) |
| HL | 5.3 (5.0-5.7) | 5.9 (5.7-6.0) | 5.1 | 5.2 | 4.8 (4.8-4.8) | 6.1 (6.0-6.4) |
| HW | 7.4 (7.0-7.8) | 7.8 (6.7-8.1) | 6.9 | 6.8 | 6.1 (5.9–6.3) | 8.0 (7.3-8.6) |
| IND | 1.8 (1.7-2.0) | 1.8 (1.7-2.0) | 2.0 | 1.9 | 1.6 (1.6-1.7) | 1.9 (1.8-2.1) |
| END | 1.4 (1.3–1.6) | 1.5 (1.4–1.6) | 1.2 | 1.4 | 1.3 (1.1–1.6) | 1.6 (1.6–1.8) |
| ED | 1.9 (1.8-2.0) | 2.1 (2.0-2.2) | 1.8 | 1.8 | 1.6 (1.3-1.9) | 2.2 (1.9-2.5) |
| TL | 6.8 (6.7-6.9) | 7.7 (7.2-8.2) | 6.9 | 7.1 | 6.0 (6.0-6.0) | 7.5 (7.4–7.8) |
| FL | 7.5 (7.4–7.7) | 9.0 (8.3-9.6) | 6.9 | 7.1 | 6.6 (6.5-6.7) | 8.4 (8.0-8.8) |

Table 1. Measurements in mm (mean followed by range in parentheses) of adult males and adult females of the three new species of *Psychrophrynella* from Bolivia described herein. For abbreviations, see text.

and are tan above, with darker areas on the canthus rostralis and in the supratympanic and subocular regions; female specimen CBF 5704 has its dorsolateral ridges formed by small, low tubercles, and exhibits two diffuse, dark, middorsal lines. The juvenile specimen CBF 5692 has pale grey, irregular blotches on its throat and venter. For morphometric variation, see Table 1.

Distribution and ecology: This species is known only from the type locality and its surroundings, from 3,580 to 3,940 m (Fig. 5). The holotype and other individuals were collected under stones in grassy humid puna ("pajonal"), near a peat bog ("bofedal"). Two individuals were found in elfin forest under forest litter and lichens. Examined females had large oviducts, indicating reproductive activity at or around the collecting dates. The Tojoloque valley is a wet and narrow valley ranging from 3,000 to 4,200 m a.s.l. Above the cloud forest treeline at around 3,550 m, wet puna grasslands grazed by cattle are interspersed with potato fields.

Etymology: The specific epithet *chaupi* refers to the highest peak of the Cordillera de Apolobamba, the snow-covered ("nevado") Chaupi Orco (6,044 m; literally, "central mountain" in Quechua), on the Bolivian-Peruvian border.

Psychrophrynella colla DE LA RIVA, APARICIO, SOTO & RÍOS, sp. n. (Figs 2, 4A)

ZooBank LSID: urn:lsid:zoobank.org:act: 9DD554AD-AD48-46B1-AE87-D5C6B69D9235

Holotype: CBF 5759, an adult male from Palcabamba Valley, 14°49'40.0" S, 68°56'36.0" W, 2,466 m, Province Franz Tamayo, Department La Paz, Bolivia, collected on 17 November 2001 by G. SOTO and J. APARICIO.

Paratypes: Three specimens, CBF 5756 (juvenile), 5757 (adult female), and 5758 (male), same data as the holotype, collected on 24 November 2001.

Diagnosis: 1) small size (maximum SVL 20.1 mm), body moderately robust, legs moderately short (male, TL + FL = 69.0% SVL, N=1) to moderately long (female, TL + FL = 80.0% SVL, N = 1); 2) tympanic membrane and tympanic annulus present and clearly visible; 3) first finger slightly shorter than second; 4) tips of digits slightly pointed, not expanded laterally; 5) no webbing of toes or lateral fringes; 6) two metatarsal tubercles, tarsal fold absent; 7) dorsal skin and flanks shagreen with scattered small warts; two faint, short dorsolateral folds; ventral skin smooth; 8) snout rounded in dorsal view and in profile; 9) dorsum mostly dark brown, with a pattern of darker markings; 10) venter beige with minute white flecks.

The new species is assigned to the genus Psychrophrynella as defined by HEDGES et al. (2008) and DUELLMAN & LEHR (2009). Frogs of the allied genus Bryophryne are morphologically similar to Psychrophrynella, but Bryophryne does not occur in Bolivia, being restricted to the Department of Cusco in southern Peru. Psychrophrynella colla differs from P. melanocheira sp. n., whose type locality is only at an air-line distance of 4.3 km to the southeast, and from P. chaupi sp. n., which occurs in Tojologue at an air-line distance of 12.3 km to the northwest, by having slightly pointed tips of digits (barely swollen, not pointed in *P. melanocheira*, and slightly swollen in *P. chaupi*), and a uniformly beige venter with minute white flecks (greenish grey or grey, sometimes with a black belly, in P. melanocheira, and grevish brown in P. chaupi). Psychrophrynella colla furthermore differs from P. melanocheira by having a brown dorsum with darker markings (uniformly dark brown), and from P. chaupi by having two faint dorsolateral folds (absent) and a smooth ventral skin (finely granular), From P. katantika, which occurs in Pelechuco, 15.5 km to the west of the type locality, P. colla differs mainly by its smaller size (maximum SVL in P. colla 20.1 mm, 27.7 in P. katantika), having a visible tympanum (not visible), slightly pointed tips of digits (slightly swollen), and a beige ventral coloration with minute white flecks (uniformly dark brown or grey). Other, more geographically distant species of Psychrophrynella that occur in the Cordillera de Apolobamba are P. boettgeri (in the Peruvian section of the range), *P. guillei*, *P. kallawaya*, and *P. saltator. Psychrophrynella boettgeri* has reddish brown blotches on its dorsum and orange blotches on groins and venter; *P. guillei* has an olive green dorsum with dark blotches, and a yellowish white venter with black mottling; *P. kallawaya* is much larger (maximum SVL 30.9 mm); and *P. saltator* has narrow cream bands on the dorsal faces of its digits and a large vocal sac in males.

Description of the holotype: Body moderately robust; dorsal skin shagreen with scattered small pustules; a pair of short dorsolateral folds from behind the eye to the scapular region; ventral skin smooth; no thoracic fold; head wider than long, its width 34.3% of SVL; head length 25.4% of SVL; snout moderately short, rounded in dorsal view and in profile; nostrils not protuberant, directed laterally, closer to snout than to eyes; canthus rostralis concave in dorsal view and slightly convex in profile; eye–nostril distance 66.7% of eye diameter; loreal region concave, interorbital region flat, lacking cranial crests; tubercles on upper eyelid absent; tympanic membrane visible and tympanic annulus present; tympanum diameter 55.6% of eye diameter;

supratympanic fold absent; no prominent postrictal tubercles; tongue large, oval; choanae oval, small, widely spaced; dentigerous processes of vomers absent; no vocal slits. A subgular vocal sac. Limbs moderately short; tips of digits slightly pointed, neither swollen nor expanded laterally. Ulnar tubercle and fold absent; inner palmar tubercle single, oval, smaller than the round outer one; fingers not fringed; subarticular tubercles large, round; supernumerary tubercles small, irregular; first finger slightly shorter than the second, relative lengths of fingers 1 < 2 < 4 < 3; tibia length 34.3% of SVL; tarsus lacking tubercle and fold; two metatarsal tubercles, the inner one slightly oval and approximately three times the size of the round outer one; supernumerary tubercles round, small; subarticular tubercles round, moderately swollen; toes moderately long, slender, not webbed, lateral fringes absent; relative lengths of toes 1 < 2 < 3 = 5 < 4; foot length 34.3% of SVL.

Measurements (in mm) of the holotype: SVL 20.1; HL 5.1; HW 6.9; IND 2.0; END 1.2; ED 1.8; TD 1.0; TL 6.9; FL 6.9.

Colour pattern: In preservative, the dorsum, head, and upper parts of the extremities are brown with a pat-



Figure 2. Dorsal and ventral views of the adult male holotype of *P. colla* sp. n. (CBF 5759, SVL = 20.1 mm).

tern of nine irregular darker flecks. The face, top of head, and a stripe below the dorsolateral fold are dark brown; the flanks are beige with minute white flecks. The throat is brown in the two anterior thirds, then beige, the venter is beige, and all the lower faces of the body are covered by small white flecks; there is an extremely fine, irregular, medial, white line on the throat. The palmar and plantar surfaces are brown with white tubercles and the tips of digits pale cream. In life, the dorsal faces were dark brown and the belly and ventral faces of the limbs were dark brown with white dots; the iris was metallic golden.

Variation: The four specimens are similar in colour pattern. For morphometric data of the holotype and one paratype, see Table 1.

Distribution and ecology: This species is known only from the type locality (Fig. 5). The female CBF 5757 (SVL 17.7 mm) contains many small, white ovarian eggs. The holotype and other individuals were collected in the forest litter of the eastern versant of the valley. The Palcabamba Valley is narrow and humid, ranging from 2,400 to 4,200 m a.s.l., with the treeline at around 3,000 m.

Etymology: The specific epithet *colla* refers to the word "colla", that is used in Bolivia to refer to the people from the Andean region.

Remarks: The fact that *P. colla* has slightly pointed tips of digits is peculiar in members of the genus *Psychrophrynella* described thus far and deserves further investigation. The Peruvian species *P. bagrecito* (LYNCH, 1986) and *P. chirihampatu* CATENAZZI & TTITO, 2016 also have pointed digits. Furthermore, at least *P. bagrecito* and *P. usurpator* DE LA RIVA, CHAPARRO & PADIAL, 2008 exhibit some peculiar osteological traits, and both share with *P. chirihampatu* the presence of a large tarsal tubercle (LYNCH 1975, 1986, DE LA RIVA et al. 2008, CATENAZZI & TTITO 2016). New evidence suggests that these three Peruvian species represent a separate lineage (DE LA RIVA et al. unpubl. data) and this might be the case with *P. colla* as well.

Psychrophrynella melanocheira DE LA RIVA, Ríos & Aparicio, sp. n. (Figs 3, 4B)

ZooBank LSID: urn:lsid:zoobank.org:act: 6EF9FDoA-oBA3-437B-B75A-45933056DA83

Holotype: CBF 5789, an adult female from Valle de Cargatero, Province Franz Tamayo, Department La Paz, Bolivia, 14°54'5.9" S, 68°58'34.5" W, 3,664 m., collected on 28 November 2001 by J. APARICIO and J. N. Ríos.

Paratypes: Twenty two specimens; CBF 5783, 5785–87, 5792, adult females; CBF 5781–82, 5784, 5788, 5790, immature females; and CBF 5791, juvenile, all of them collected with

the holotype; CBF 5770, 5772, 5776, 5778, 5780, adult males; CBF 5771, 5774–75, 5779, adult females; and CBF 5773, 5777, juveniles, from Apacheta, Palcabamba Valley, Province Franz Tamayo, Department La Paz, Bolivia, 14°51'57.11" S, 68°58'0.1" W, 3,823 m, collected on 27 November 2001 by J. APARICIO and J. N. RÍOS.

Diagnosis: 1) small to medium size (maximum SVL 23.9 mm), body moderately robust, legs short or moderately short (TL + FL = 69.4% SVL; range = 66.2-75.7%; N = 6); 2) tympanic membrane and tympanic annulus clearly visible; 3) first finger slightly shorter than second; 4) tips of digits barely swollen, not expanded laterally; 5) no webbing of toes and lateral fringes absent; 6) two metatarsal tubercles, tarsal fold absent; 7) dorsal skin and flanks shagreen with scattered small warts; faint, short dorsolateral folds; ventral skin smooth; 8) snout rounded in dorsal view and in profile; 9) dorsum varying from uniformly dark brown to pale beige; 10) venter greenish grey or grey with or without black belly, throat beige.

The new species is assigned to the genus Psychrophrynella as defined by HEDGES et al. (2008) and DUELLMAN & LEHR (2009). Frogs of the allied genus Bryophryne are morphologically similar to Psychrophrynella, but Bryophryne does not occur in Bolivia, being restricted to the Department of Cusco in southern Peru. Psychrophrynella *melanocheira* is easily distinguished from most congeneric species by having dark grey or black palmar and plantar surfaces. It is superficially similar to P. ankohuma (PADI-AL & DE LA RIVA, 2007), which occurs eastwards in the distant Illampu-Ankohuma Massif (approximate air-line distance between the two type localities, 122 km). The new species is distinguished from P. ankohuma by being smaller in size (maximum SVL in P. melanocheira 23.9 mm, 28.0 mm in *P. ankohuma*), tympanum visible (not visible), dorsal skin shagreen (smooth), and venter greenish grey or grey, sometimes with a black belly (black with large pale grey blotches). Psychrophrynella melanocheira occurs 6 km from the type locality of P. colla sp. n., albeit at different altitudes and in a different habitat, and differs from the latter by having barely swollen tips of digits (slightly pointed in *P. colla*), a uniformly dark brown dorsum (brown with darker markings), and a greenish grey venter (beige with minute white flecks). From P. katantika, which occurs in Pelechuco (about 16 km to the west), P. melanocheira differs mainly by its smaller size (maximum SVL in P. melanocheira 23.9 mm, 27.7 in P. katantika), and by having a visible tympanum (not visible) and smooth ventral skin (granular). From P. chaupi sp. n., which occurs 18.5 km to the northwest, P. melanocheira furthermore differs by having dorsolateral folds and a smooth ventral skin (finely granular in P. chaupi). Other, more geographically distant species of Psychrophrynella that occur in the Cordillera de Apolobamba, are *P. boettgeri* (in the Peruvian section of the range), P. guillei, P. kallawaya, and P. saltator. Psychrophrynella boettgeri is smaller (maximum SVL 18.4 mm) than P. melanocheira (23.9 mm) and has reddish brown blotches on its dorsum and orange blotches on groins

and venter; *P. guillei* has an olive green dorsum with dark blotches, and a yellowish white venter with black mottling; *P. kallawaya* is much larger (maximum SVL 30.9 mm); and *P. saltator* has narrow cream bands on the dorsal faces of its digits and a large vocal sac in males.

Description of the holotype: Body moderately robust; dorsal skin shagreen with scattered small pustules; ventral skin finely granular; no thoracic fold; head wider than long, its width 36.0% of SVL; head length 26.8% of SVL; snout moderately short, rounded in dorsal view, slightly slopping in profile; nostrils not protuberant, directed laterally, closer to snout than to eyes; canthus rostralis straight in dorsal view and slightly convex in profile; eye-nostril distance 72.0% of eye diameter; loreal region moderately concave, interorbital region flat, lacking cranial crests; tubercles on upper eyelid absent; tympanic membrane visible and tympanic annulus present; tympanum diameter 56.0% of eye diameter; supratympanic fold weak, reaching the level of shoulder; a few small, round postrictal tubercles, inferoposterior to tympanum; tongue large, oval; choanae oval, small, widely spaced; dentigerous processes of vomers absent. Limbs moderately short; tips of digits barely swollen, not expanded laterally; ulnar tubercle and fold absent; inner palmar tubercle single, oval, smaller than the round outer one; fingers not fringed; subarticular tubercles moderately large and round; no supernumerary tubercles; first finger slightly shorter than the second one, relative lengths of fingers 1 < 2 < 4 < 3; tibia length 32.6% of SVL; tarsus lacking tubercle and fold; two metatarsal tubercles, the inner one slightly oval and approximately the same size as the round outer one; supernumerary tubercles absent; subarticular tubercles round, moderately swollen; toes moderately long, not webbed, lateral fringes absent; relative lengths of toes 1 < 2 < 3 = 5 < 4; foot length 36.8% of SVL.

Measurements (in mm) of the holotype: SVL 23.9; HL 6.4; HW 8.6; IND 1.8; END 1.8; ED 2.5; TD 1.4; TL 7.8; FL 8.8.

Colour pattern: In preservative, the dorsum, head, and upper parts of the extremities are uniformly dark grey, almost black. The upper lip and the tympanum have a dark brown tone. The flanks have some grey dots that coalesce towards the venter, which is grey in its anterior half, and black in the posterior half; the groins are black. The chest is black with a fine, irregular band crossing from arm to arm. The throat is beige. The lower faces of the limbs, as well as the palmar and plantar surfaces are uniformly black. In life, the dorsal and lateral surfaces were dark brown, with flanks showing grey dots; the throat was beige and the venter and ventral faces of limbs, including plantar and palmar surfaces, were dark brown. The iris was pale yellow with fine dark brown flecks.



Figure 3. Dorsal and ventral views of the adult female holotype of P. melanocheira sp. n. (CBF 5789; SVL = 23.9 mm).

Variation: Adult males have a large subgular vocal sac and lack nuptial pads and vocal slits. There is remarkable variation in colour patterns, but the palmar and plantar surfaces are always dark grey or black in colour. Male specimen CBF 5780 is greyish brown above with tan dorsolateral regions and flanks with irregular brown markings, and the venter is cream with irregular, diffuse, dark grey areas; male specimen CBF 5778 has a uniformly grevish green dorsum and uniformly cream throat and venter; male specimen CBF 5770 is dark grey above with two broad greenish grey dorsolateral bands, and its venter is dark grey with abundant pale grey flecks; male specimen CBF 5776 has a fine pale grey middorsal line surrounded by irregular dark markings and a fine cream-coloured line from chin to vent, crossed by a similar line running along the ventral faces of the arms. Female specimen CBF 5775 is dark brown above and below, with a paler throat, also has a ventral cross marking, and a middorsal line from snout to vent



Figure 4. Right hand, left foot, and head in lateral view of adult female paratypes of three new species of *Psychrophrynella* from Apolobamba, Bolivia. A) *Psychrophrynella colla* sp. n. CBF 5757 (SVL = 17.7 mm); B) *Psychrophrynella melanocheira* sp. n. CBF 5775 (SVL = 23.8 mm); and C) *Psychrophrynella chaupi* sp. n. CBF 5705 (SVL = 22.1 mm).

and along the posterior faces of the thighs; female specimen CBF 5779 is uniformly grey above, and has a creamcoloured throat, a greenish-grey venter with a metallic shine, black axillae, and black irregular markings on the lower faces of its thighs; in female specimen CBF 5771, the central part of the dorsum is grey, and there are two broad, greenish beige dorsolateral bands, the flanks are grey, paler than the dorsum, and all lower parts are uniformly greenish cream. For morphometric variation, see Table 1.

Distribution and ecology: This species is known from two close localities at an elevation around 3,500 m (Fig. 5). The type locality at the Cargatero valley lies besides the Chipini river, following the trail between the small locality of Chiata and the summit ("apacheta") of the Palcabamba valley, where individuals were found amidst vegetation and under rocks near a "bofedal" (peat bog). The second locality lies 6 km northeast of the type locality, near the summit, where individuals were found also near a bofedal. Vegetation at both localities is wet puna. The Cargatero valley is narrow and humid, ranging from 3,000 to 4,200 m. The large females examined present well-developed oviducts, suggesting reproductive activity at the time of collecting.

Etymology: The specific epithet *melanocheira* comes from the Greek words "melano", a prefix meaning black, and "cheiros", meaning hand; it makes reference to the black hands (and feet) of this species.

Discussion

With the addition of the three new species described herein, the number of *Psychrophrynella* species described from Bolivia rises to 21, seven of which occur in the Cordillera de Apolobamba; these seven species occur in an area of approximately 50 \times 12 km within the limits of the protected Area Natural de Manejo Integrado Nacional Apolobamba (Apolobamba National Natural Integrated Management Area). Only a small proportion of the many valleys suitable for habitation by Psychrophrynella species have been properly explored (see Fig. 5). To the west, this area is contiguous to another protected area, the National Park and ANMIN Madidi, whose highlands contain additional undescribed species (APARICIO unpubl. data). The overall number of *Psychrophrynella* species in the whole Apolobamba region is undoubtedly higher than the figures currently known. For example, in a small but steep area around Charazani, two species, P. guillei and P. saltator occur in different habitats, but occupy essentially the same point on the map; P. saltator lives in the bottom of the valley, whereas P. guillei lives on the ridge, at an altitude 1,000 m above the valley bottom, while the horizontal distance between the two localities is only 1.2 km (DE LA RIVA 2007). Nearby, at a distance of only 16.5 km and at an intermediate altitude, lies the type locality of a third species, P. kallawaya (DE LA RIVA 2007). Similar patterns of allopatric distribution can be expected for other species of *Psychrophrynella* in other areas of Apolobamba, resulting in high levels of beta-diversity.

For the three new species described herein, we propose the IUCN Red List category of Vulnerable, based on their extent of occurrence of less than 20,000 km², an area of occupancy of less than 2,000 km², all individuals in fewer than ten locations, and a projected decline in the extent and quality of its habitat due to climate change.

Besides *Psychrophrynella* frogs, the ANMIN Apolobamba holds some anuran species that might be severely threatened. The endemic bufonid *Nannophryne apolobambica* (DE LA RIVA, RÍOS & APARICIO, 2005), is known from its type locality (Laitique, along the Pelechuco river downstream of Pelechuco; DE LA RIVA, RÍOS & APARICIO 1995) and the Palcabamba Valley, where it was last found in 2006 (APARICIO unpubl. data). This species, albeit currently considered as "Data Deficient" by the IUCN (DE LA RIVA 2006) and subsequent assessments (AGUAYO 2009, DE LA RIVA & REICHLE 2014), might be highly threatened by the fungal disease chytridiomycosis, which has decimated other anuran species in Bolivia, including other cloud-forest bufonids (DE LA RIVA & BURROWES 2011, DE LA RIVA & REICHLE 2014, BURROWES & DE LA RIVA unpubl. data).

The treefrog *Colomascirtus charazani* (VELLARD, 1970) is, as far as it is known, another Apolobamban endemic, and considered Critically Endangered (STUART et al. 2008, AGUAYO 2009). This species is similar to the cloud forest dweller *Colomascirtus armatus* (BOULENGER, 1902) and

perhaps conspecific with it (M. RIVERA-CORREA pers. comm.), but the few known populations of *C. charazani* (see APARICIO 2009) seem to represent a unique lineage of *Colomascirtus* frogs adapted to drier, temperate environments.

Finally, Apolobamba is home to five species of Telmatobius WIEGMANN, 1834, a genus of mostly aquatic frogs severely threatened by chytridiomycosis (DE LA RIVA & LAVILLA 2008). The highland species T. marmoratus (DUMÉRIL & BIBRON, 1841) is widespread in the puna and altiplano of southern Peru and northern Bolivia, albeit at decreasing population abundances; it is categorized as Vulnerable by the IUCN Red List (STUART et al. 2008, IUCN 2015), and national assessments have considered it first Vulnerable (AGUAYO 2009), and then Endangered (DE LA RIVA & REICHLE 2014). The other four species of Telmatobius present in Apolobamba - T. bolivianus PARKER, 1940, T. sanborni SCHMIDT, 1954, T. timens DE LA RIVA, APARI-CIO & RÍOS, 2005, and T. verrucosus WERNER, 1899 -, which inhabit more humid environments, were all considered Critically Endangered by DE LA RIVA & REICHLE (2014). Two of them, T. bolivianus and T. verrucosus, are Bolivian endemics and the ANMIN Apolobamba is one of the few protected areas from where they have been reported.

Besides the endemic fauna mentioned above, Apolobamba harbours many other species of amphibians, especially at lower altitudes. However, upper cloud forests and wet puna habitats have the highest beta-diversity due



Figure 5. Map of the Bolivian part of the Cordillera de Apolobamba as seen from the northeast with Google Earth[®], showing the localities of the seven endemic species of *Psychrophrynella* known so far from the area. In the background are the altiplano and Lake Titicaca. The yellow line separates Peru from Bolivia. The air-line distance between the localities of *P. saltator* and *P. chaupi* is 50.8 km.

to the high degree of endemism. The rich amphibian fauna of Apolobamba is, on its own, already an important reason to conserve this area. The fact that so many species of a single group of vertebrates are endemic to a single protected space is unusual and should promote that the highest effective protection measures be granted to the ANMIN Apolobamba. Furthermore, Apolobamba has been considered an area of major endemism based on studies on mammals, birds, amphibians, and vascular plants and, at the same time, one of the most understudied areas on the eastern slopes of the tropical Andes (YOUNG 2007). Thus, protection is needed for this region to warrant the very existence of the many species already known, as well as those still awaiting discovery.

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