



A new, long-standing misidentified species of *Psychrophrynella* Hedges, Duellman & Heinicke from Departamento Cusco, Peru (Anura: Strabomantidae)

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Abstract

We present the description of a new species of the recently described genus *Psychrophrynella*. Hitherto, frogs of this new species were traditionally misidentified as *Phrynopus peruvianus*. The new species is known only from elevations of 3270–3450 m in the vicinity of the type locality in the Cordillera de Paucartambo, Departamento Cusco, Peru. It is unique within *Psychrophrynella* in having a marked, oblique inner tarsal tubercle. The geographically closest species *Psychrophrynella bagrecito* Lynch, also possesses a tarsal tubercle.

Key words: Anura, Strabomantidae, *Noblella*, *Phrynopus*, *Psychrophrynella*, taxonomy, new species, Andes, Peru

Introduction

The study of the taxonomy of Andean frogs formerly included in the broad category of "eleutherodactylines" has accelerated in recent years with the description of dozens of species in the genera *Eleutherodactylus*, *Phrynopus* and *Phyllonastes*. In addition, the comprehensive phylogenetic studies of Heinicke *et al.* (2007) and Hedges *et al.* (2008) plus other, more partial studies (e. g., De la Riva *et al.*, 2008; Padial *et al.*, 2007; 2008) have led to a drastic taxonomic rearrangement of the whole group. As a result, the taxonomy of former Andean leptodactylid frogs is almost unrecognizable compared to what it was only five years ago. Former Andean Eleutherodactylinae are now in the family Strabomantidae; members of former Andean *Eleutherodactylus* are now mostly in the genus *Pristimantis*, whereas former species of *Phrynopus* are placed in six genera in two subfamilies—Strabomantinae (*Isodactylus* Hedges, Duellman & Heinicke, *Lynchius* Hedges, Duellman & Heinicke, *Niceforonia* Goin & Cochran, and *Phrynopus* Peters), and Holoadeninae (*Bryophryne* Hedges, Duellman & Heinicke, and *Psychrophrynella* Hedges, Duellman & Heinicke) (Hedges *et al.*, 2008).

This taxonomic research and the consequent rearrangements have altered previous classifications. For example, the Bolivian frog *Phrynopus laplacai* Cei (Leptodactylidae, Telmatobiinae) is now *Psychrophrynella wettsteini* (Parker) (Strabomantidae, Holoadeninae) (Lehr, 2006; De la Riva, 2007; Hedges *et al.*, 2008), but in the meantime, the species had a short placement in Brachycephalidae (Frost *et al.*, 2006), a family that has been redefined by Hedges *et al.* (2008). This state of flux, although perhaps surprising (or even annoying) for the lay person, technicians, and scientists working in other branches of biology, mostly represents good news for taxonomists, because it indicates that true scientific progress is being made; thus, it must be welcomed rather than seen as an impediment for getting stable, otherwise unrealistic species lists (see Padial & De la Riva, 2006).

Once systematics above species level has been properly addressed, alpha-taxonomy of these Andean anurans still needs to fill considerable gaps. Studies on the systematics of former members of the genus *Phrynopus* in Departamento Cusco, southern Peru, revealed that some taxonomic problems affect to a population of frogs identified by Lynch (1975) as *Phrynopus peruvianus*. The goal of this paper is to reassess the taxonomic status of this population.

Material and methods

Specimens were examined under stereomicroscopes. When necessary, we determined sex by the examination of gonads. Measurements were taken with a digital caliper to the nearest 0.01 mm, but we rounded all measurements to only one decimal to avoid pseudo precision (Hayek *et al.*, 2001). We omitted two characters traditionally used in anuran morphometric studies, eyelid width and interorbital distance, because of the poor accuracy obtained due to the fact that the involved structures are soft and prone to become deformed or present diffuse landmarks. The format of diagnosis and description follows De la Riva (2007).

Results

The status of "*Phrynopus*" *peruvianus* from Cusco

Species of former *Phrynopus* from southern Peru are now placed in two genera, *Psychrophrynella* and *Bryophryne*, both described by Hedges *et al.* (2008). All Bolivian species are assigned to *Psychrophrynella*. *Bryophryne* was described to accommodate *Phrynopus cophites* Lynch, which seems to represent a divergent lineage [the species recently described as *Phrynopus bustamantei* (Chaparro *et al.* 2007), from Departamento Cusco, has also been placed in *Bryophryne* (Hedges *et al.* 2008), and a third species, *B. nubilosus*, has been recently described by Lehr & Catenazzi (2008)]. *Bryophryne cophites* is sympatric at its type locality (Abra Acjanacu, Departamento Cusco) with members of a species previously identified by Lynch (1975) as *Phrynopus peruvianus* (Noble). However, De la Riva *et al.* (2008) reexamined Noble's type specimens of *Sminthillus peruvianus* and concluded that they were members of the genus *Phyllonastes* Heyer. They further resurrected *Noblella* Barbour from the synonymy of *Phrynopus* and *Eleutherodactylus*, and synonymized *Phyllonastes* with *Noblella*. Thus, all species originally placed under *Phyllonastes* plus *Sminthillus peruvianus* were transferred to *Noblella*. At the same time, De la Riva *et al.* (2008) stated that the frogs from Abra Acjanacu belonged to an undescribed species of *Psychrophrynella*.

Besides morphological coincidences, such as the presence of an inner tarsal tubercle and certain osteological characters, the identification of the Abra Acjanacu sample as *Phrynopus peruvianus* by Lynch (1975) is explainable by two facts: (1) at that time, *Noblella*-like frogs were unknown in western South America and, when examining the types of *S. peruvianus* Lynch did not suspect that these frogs deserved to be considered a different genus in which many species would be discovered in forthcoming years; (2) he erroneously considered the type series of *Sminthillus peruvianus* to be composed by juveniles and, with this assumption in mind, he found them similar to the smallest specimens from Abra Acjanacu. Actually, adult specimens from Abra Acjanacu are much larger than those of the type series of *S. peruvianus* (24.1 mm SVL versus 16 mm). On the other hand, despite the presence of an inner tarsal tubercle, the frogs from Abra Acjanacu do not have any digits with pointed tips, and the digits lack circumferential grooves. In addition, their general external morphology is quite different, with characters clearly corresponding to *Psychrophrynella*, namely head narrow, not as wide as body, cranial crests absent, dentigerous processes of vomers absent (present in some species), tips of digits narrow (rounded or bulbous in some species), circumferential grooves absent, and Finger I shorter than

Finger II (equal or longer in some species). Tissues of specimens (for example, KU 173495) from Abra Acjanacu assigned by Lynch (1975) to *Phrynopus peruvianus* were used by Heinicke *et al.* (2007) and Hedges *et al.* (2008) in their molecular phylogenies; this population clustered within the *Psychrophrynella* clade and was clearly separated from *Noblella*.

We examined Lynch's material and additional specimens from Abra Acjanacu and compared them with known species of *Psychrophrynella*, which led us to conclude that they represent a new species that is described herein. It is worth noting that Lynch's diagnosis and purported redescription of *Phrynopus peruvianus* are based on both the type series of *Sminthillus peruvianus* and specimens from Abra Acjanacu. Thus, it is essential to completely redescribe the specimens representing the unnamed species in order to prevent further confusion.

***Psychrophrynella usurpator*, new species**

(Figs. 1–3)

Holotype. KU 138939, adult female, one of a series collected by W. E. Duellman, T. H. Fritts, I. Ceballos, and O. Ochoa on 16 January 1971 at N slope of Abra Acjanacu, 29 km NNE Paucartambo (13°12'S, 71°37'W), Departamento Cusco, Peru, 3400 m.

Paratypes. KU 138937–8, 138940–9, and 138951–62, same data as holotype; MHNC (Museo de Historia Natural de Cusco) 4642–3, collected by J. C. Chaparro on 19 February 2003 at Pantillacocha, Kosñipata Valley, Provincia Paucartambo (13°12'S, 71°33'W), Departamento Cusco, Peru, 3539 m.

Diagnosis. (1) Medium size (maximum SVL 24.1 mm in females), body moderately robust; legs moderately long (TL + FL 78–87% SVL in females); (2) tympanic membrane absent; tympanic annulus visible through the skin; (3) first finger slightly shorter than second (Fig. 2); (4) tips of digits barely swollen, not expanded laterally; (5) webbing of toes and lateral fringes absent; (6) two metatarsal tubercles; an oblique, prominent, elongate inner tarsal tubercle, clearly separated from inner metatarsal tubercle; tarsal fold absent (Fig. 2); (7) dorsal skin and ventral skin smooth; (8) snout rounded in dorsal view and in profile; (9) dorsum gray to brown; (10) venter brown flecked with cream.

At the type locality, *P. usurpator* is syntopic with *Bryophryne cophites*, which is distinguished from *P. usurpator* by being more robust, lacking a visible tympanic annulus, having Finger I shorter than Finger II, and having dorsal and ventral skin areolate (see Fig. 96 in Hedges *et al.*, 2008, and Fig. 1 in Lehr & Catenazzi, 2008). Within *Psychrophrynella*, *P. usurpator* is unique in having a prominent, elongate, oblique tarsal tubercle. For *Pristimantis*, Lynch & Duellman (1997) described a tarsal fold as "a more or less clearly defined ridge extending a variable distance proximal to the inner metatarsal tubercle", and distinguished it from a tarsal tubercle when it is within one length of the inner metatarsal tubercle and if it appears to be connected to it. In *P. usurpator*, the tarsal tubercle is usually clearly separated from the inner metatarsal tubercle and it is not a simple dermal structure but a true tubercle; however, it may be prolonged as a fine rim toward the inner side of the tarsus, forming a structure similar to a tarsal fold (but perhaps not homologous to it). Another species, *P. bagrecito* (Lynch), from Río Marcapata below Marcapata, ca. 2740 m, Departamento Cusco (approximately 90 km airline SE of Abra Acjanacu), also has a tarsal tubercle, but it is smaller and sickle-shaped; in addition, *P. bagrecito* is smaller (maximum SVL of males 16.3 mm, females 18.6; Lynch, 1986) than *P. usurpator* (20.3 and 24.1 mm, respectively). The second geographically closest species, *P. boettgeri* Lehr occurs in Departamento Puno, approximately 220 km (airline) SE of Abra Acjanacu. *Psychrophrynella usurpator* differs from *P. boettgeri* in having smooth ventral skin (areolate in *P. boettgeri*), a tarsal tubercle (absent), larger size (maximum SVL 24.1 in *P. usurpator*; 18.4 in *P. boettgeri*), and lacking dorsolateral folds (present). Seventeen species of *Psychrophrynella* are known from Bolivia (De la Riva 2007; Hedges *et al.* 2008); besides some morphological and color pattern differences, none has a tarsal tubercle, as in *P. usurpator*.

Description of the holotype. Body moderately robust; dorsal skin smooth with some scattered minute tubercles; ventral skin smooth; no dorsolateral or pectoral folds; head wider than long, its width 30% of SVL; head length 29% of SVL; head length 94% of head width; snout rounded in dorsal view and in profile; nostrils not protuberant, directed laterally, closer to snout than to eyes; canthus rostralis moderately sharp, slightly concave in dorsal view, convex in profile; eye-nostril distance 81% of eye length; loreal region barely concave, interorbital region flat, lacking cranial crests; no tubercles on upper eyelid; tympanic membrane absent; tympanic annulus visible through skin; supratympanic fold weak; three conical postrictal tubercles on left side, two on right side; tongue large, oval, not notched; choanae round, small, widely spaced; vomerine odontophores absent. Limbs moderately long; tips of digits barely swollen, not expanded laterally; ulnar tubercles and fold absent; thenar tubercle single, oval, flattened, smaller than round palmar tubercle; fingers moderately long, not fringed; subarticular tubercles round, those at the bases of proximal phalanges swollen; first finger slightly shorter than second, relative length of fingers $1 < 2 < 4 < 3$; tibia length 41% of SVL; an inner, oblique tarsal tubercle; no tarsal fold; two metatarsal tubercles, the oval inner one approximately same size as conical outer one; supernumerary tubercles small, poorly defined; subarticular tubercles of toes round, moderately large; toes not webbed, lateral folds absent; relative length of toes $1 < 2 < 5 < 3 < 4$; foot length 46% of SVL.



FIGURE 1. Living specimen of *Psychrophrynella usurpator* sp. nov. (MHNC 4642, paratype) from Pantillacocha, N slope of Abra Acjanacu, Departamento Cusco, Peru. Photograph by JCC.

Measurements (in mm) of the holotype. Snout-vent length, 24.1; head length (from rictus to tip of snout), 7.0; head width (at level of rictus), 7.4; internarial distance, 2.8; eye-nostril distance (straight line distance between anterior corner of orbital opening and posterior margin of external nares), 2.6; eye diameter, 3.1; tibia length, 10.0; foot length (from proximal margin of inner metatarsal tubercle to tip of fourth toe), 11.0.

Color and variation. In preservative, the holotype has dorsum, head, extremities, and groin uniformly chocolate brown; throat and venter brown, paler than dorsum, with beige flecks; ventral surfaces of thighs uniformly brown; dark brown stripe from tip of snout to above insertion of hind limb, outlined by fine cream line; pale cream transversal line above the vent. Overall, color in life is similar, but no particular data are available on the color of the living holotype.

Living specimens have “venter bluish-gray with brown reticulations; throats in males dull grayish-brown; iris dark brown with gold flecks; dorsal coloration highly variable but predominately dark brown with orange and dull red markings; some have tan and/or gray markings” (W. E. Duellman’s field notes on the series KU 138937–64). Lynch (1975) stated that, in life, the dorsal ground color varies from dull brown, tan, tannish-

orange, to reddish; if dorsal markings are present, they are dull red, tan, or gray; also, there may be an orange or yellow middorsal stripe (Fig. 3; see also Fig. 100 in Hedges *et al.*, 2008); the venter is bluish-gray with brown reticulations, and males have dull grayish-brown throats; the iris is dark brown with gold flecks. Males have vocal sacs and vocal slits, but no nuptial pads. For morphometric variation, see Table 1.

TABLE 1. Morphometrics of *Psychrophrynella usurpator* **sp. nov.** Means followed by ranges in parentheses. For abbreviations, see text.

	Females (n = 7)	Males (n = 8)
SVL	23.4 (22.7–24.1)	20.0 (19.5–20.3)
HL	8.0 (7.0–8.7)	7.5 (7.3–7.8)
HW	7.7 (7.4–7.9)	7.2 (7.1–7.2)
IND	2.7 (2.7–2.8)	2.0 (1.9–2.1)
END	2.5 (2.4–2.6)	2.1 (1.9–2.1)
ED	3.1 (3.1–3.2)	3.0 (2.9–3.0)
TL	9.8 (9.5–10.1)	8.6 (8.5–8.8)
FL	10.3 (9.8–11.1)	9.3 (9.2–9.3)
HL/SVL	0.3 (0.3–0.4)	0.4 (0.4–0.4)
HW/SVL	0.3 (0.3–0.3)	0.4 (0.4–0.4)
END/ED	0.8 (0.8–0.8)	0.7 (0.6–0.7)
TL/SVL	0.4 (0.4–0.4)	0.4 (0.4–0.4)
FL/SVL	0.4 (0.4–0.5)	0.5 (0.5–0.5)



FIGURE 2. Palmar and plantar surfaces of holotype (KU 138939) of *Psychrophrynella usurpator* **sp. nov.** The arrow points the prominent, oblique tarsal tubercle. Photograph by JMP.

Distribution and ecology. The species is known only from elevations of 3270–3539 m in the vicinity of the type locality (Fig. 4). Abra Acjanacu is a high pass in the Cordillera de Paucartambo, which is the easternmost Andean range facing the Amazonian lowlands in Departamento Cusco. Duellman (1978) described the locality and provided a detailed map of the area.

Individuals are commonly found under rocks in humid puna. *Psychrophrynella usurpator* was found syntopically with *Bryophryne cophites* (Lynch), *Gastrotheca excubitor* Duellman & Fritts, *G. marsupiata* (Duméril & Bibron), and *Telmatobius timens* De la Riva, Aparicio & Ríos (W. E. Duellman, pers. comm.).

Etymology. The specific name is a substantive in apposition and it is the Latin word for usurper. The name refers to the fact that this species has been using a name that actually belongs to frogs of another genus.

Remarks. Calls of *Psychrophrynella usurpator* have not been analyzed. Individuals were heard calling in mid-afternoon, and the call is a series of short, quickly repeated, moderately high notes (W. E. Duellman's field notes). No data are available on life history.



FIGURE 3. Specimen of *Psychrophrynella usurpator* sp. nov. (KU 173323) with yellow middorsal stripe. Photograph by WED.

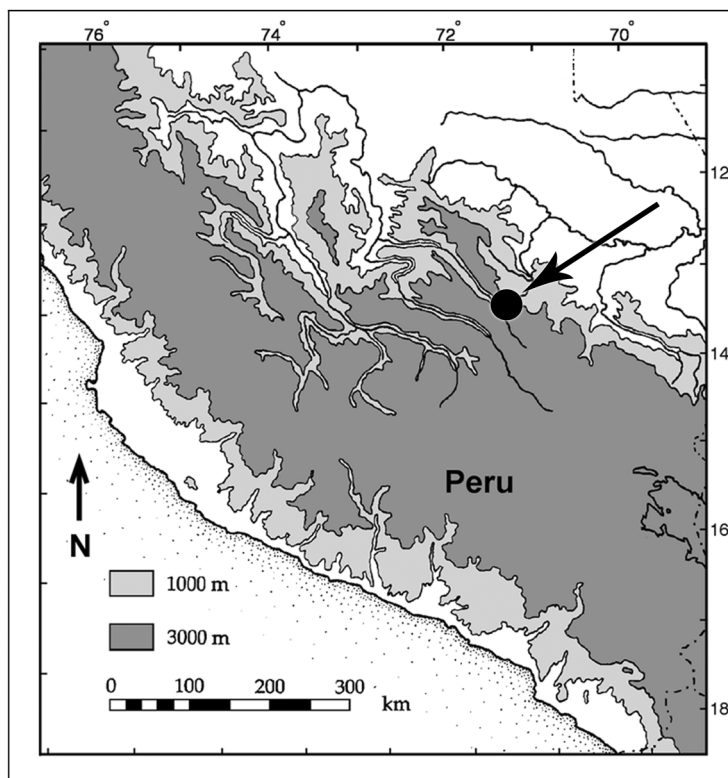


FIGURE 4. Map of western South America showing the type locality of *Psychrophrynella usurpator* sp. nov. in southern Peru.



FIGURE 5. Dorsal and ventral view of two paratypes of *Psychrophrynella bagrecito* (KU 196513, 196516). Photograph by JMP.

Comments on *Psychrophrynella bagrecito* (Lynch)

Lynch (1986) described the small species *Psychrophrynella bagrecito* (as *Phrynopus*) from the Marcapata Valley, 2740 m, Departamento Cusco, Peru, and he stressed that the skulls of *P. bagrecito* and *P. usurpator* (as *P. peruvianus*) were almost identical. Also, he observed that both species share a tarsal tubercle, which he described as sickle-shaped in *P. bagrecito* and prominent, elongate, sigmoid-shaped, not continuous with inner metatarsal tubercle in *P. usurpator*. For these reasons, he considered *P. bagrecito* as the second species in his *Phrynopus peruvianus* group. Furthermore, the morphology of *P. bagrecito* led Lynch (1986) to comment on the overall similarity and possible close relationships of the *Phrynopus peruvianus* group with the genus *Noblella* (as *Phyllonastes*). Recently, Lehr *et al.* (2004) described *Noblella duellmani* (as *Phyllonastes duellmani*) and considered it as the species of *Noblella* morphologically closest to *Phrynopus*, because of the absence of several characters previously considered diagnostic of *Noblella*, including circumferential grooves; the only diagnostic feature of *Noblella* remaining in *N. duellmani* is the presence of tips slightly acuminate in Toes III–V. More recently, Lehr (2006) noted that *P. bagrecito* shares some morphological features with *Noblella*. Our examination of the holotype (KU 196512) and some paratypes of *P. bagrecito* (KU 196513–18, 196520–21, 196523–25; Fig. 5) from the type locality and other recent specimens collected nearby (Quebrada de Iskaybamba, Marcapata, Cusco, 13°30'15.22"S, 70°54'58.84"W, 2244 m; MHNC 5255–56) confirms Lehr's (2006) impression. These specimens have weakly pointed tips of the digits and even possess rudiments of circumferential grooves. We think that if *Noblella duellmani* is correctly placed in this genus, *P. bagrecito* might make a stronger case to be included in *Noblella* as well. However, we refrain from formally transfer *P. bagrecito* to *Noblella* because characters such as circumferential grooves have high intrageneric variation in Strabomantidae. On the other hand, specimens of what seem to be undescribed species of *Noblella* from Bolivia show all the typical characters of the genus plus a prominent tarsal tubercle, like the one in *P. bagrecito* or even *P. usurpator* (I. De la Riva, unpublished.) Phylogenetic analyses based on DNA sequences by Hedges *et al.* (2008) placed *Noblella lochites* in a different clade than *P. usurpator*. Thus, it seems that the character of a prominent tarsal tubercle might have evolved more than once in Holoadeninae. For the moment, the phylogenetic relationships between Lynch's putative "peruvianus" group and *Noblella* are still obscure, and the osteological peculiarities of *P. usurpator* commented by Lynch (1975) suggest that all these species need a more detailed study.

Four specimens in the type series of *P. bagrecito* are from Hacienda Huyro, a locality at an elevation of 1830 m between Huayopata and Quillabamba (Departamento Cusco), almost 200 km (airline) NW from the type locality. We examined two of these specimens (KU 196527–28) and observed some differences in relation to those from the type locality, being the most remarkable a much weaker tarsal tubercle. The taxonomic status of this population deserves further research.

Acknowledgments

Specimens were kindly loaned by D. Frost and D. Kizirian (AMNH), and W. E. Duellman and J. Simmons (KU); W. E. Duellman also provided comments and photographs and, together with S. B. Hedges, important unpublished data. JCC is grateful to the Asociación para la Conservación de la Cuenca Amazónica (ACCA) – Amazon Conservation Association (ACA), for its collaboration through the Director of Conservation, Dr. Steven Panfil. We are grateful to O. Aguilar (MHNC) for providing administrative support and part of the material for this study, and to A. Mendoza for the support to carry out the fieldwork. The Instituto Nacional de Recursos Naturales (INRENA) facilitated collecting permits (N° 014-2003-INRENA-IFFS-DCB). This paper was funded by project CGL2005-03156 of the Spanish Ministry of Education and Science (I. De la Riva, Principal Investigator).

References

- Chaparro, J.C., De la Riva, I., Padial, J.M., Ochoa, J.A. & Lehr, E. (2007) A new species of *Phrynopus* from Departamento Cusco, southern Peru (Anura: Brachycephalidae). *Zootaxa*, 1618, 61–68.
- De la Riva, I. (2007) Bolivian frogs of the genus *Phrynopus* with the description of twelve new species (Anura: Brachycephalidae). *Herpetological Monographs*, 21, 242–278.
- De la Riva, I., Chaparro, J.C. & Padial, J.M. (2008) The taxonomic status of *Phyllonastes* Heyer and *Phrynopus peruvianus* (Noble) (Lissamphibia, Anura): resurrection of *Noblella* Barbour. *Zootaxa*, 1685, 667–68.
- Duellman, W.E. (1978) New species of leptodactylid frogs of the genus *Eleutherodactylus* from the Cosñipata Valley, Perú. *Proceedings of the Biological Society of Washington* 91, 418–430.
- Frost, D., Grant, T., Faivovich, J., Bain, R.H., Haas, A., Haddad, C.F.B., De Sá, R., Channing, A., Wilkinson, M., Donnellan, S.C., Raxworthy, C.J., Campbell, J.A., Blotto, B.L., Moler, P., Drewes, R.C., Nussbaum, R.A., Lynch, J.D., Green, D.M. & Wheeler, W.C. (2006) The Amphibia tree of life. *Bulletin of the American Museum of Natural History*, 297, 1–370.
- Hayek, L.A., Heyer, W.R. & Gascon, C. (2001) Frog morphometrics: a cautionary tale. *Alytes*, 18, 153–177.
- Hedges, S.B., Duellman, W.E. & Heinicke, M.P. (2008) New World direct-developing frogs (Anura: Terrarana): Molecular phylogeny, classification, biogeography, and conservation. *Zootaxa*, 1737, 1–182.
- Heinicke, M.P., Duellman, W.E. & Hedges, S.B. (2007) Major Caribbean and Central American frog faunas originated by ancient oceanic dispersal. *Proceedings of the National Academy of Sciences USA*, 24, 10092–10097.
- Lehr, E. (2006) Taxonomic status of some species of Peruvian *Phrynopus* (Anura: Leptodactylidae), with the description of a new species from the Andes of southern Peru. *Herpetologica*, 62, 331–347.
- Lehr, E. & Catenazzi, A. (2008) A new species of *Bryophryne* (Anura: Strabomantidae) from southern Peru. *Zootaxa*, 1784, 1–10.
- Lehr, E., Aguilar, C. & Lundberg, M. (2004) A new species of *Phyllonastes* from Peru (Amphibia, Anura, Leptodactylidae). *Journal of Herpetology*, 38, 214–218.
- Lynch, J.D. (1975) A review of the Andean leptodactylid frog genus *Phrynopus*. *Occasional Papers of the Museum of Natural History, University of Kansas*, 35, 1–51.
- Lynch, J.D. (1986) New species of minute leptodactylid frogs from the Andes of Ecuador and Peru. *Journal of Herpetology*, 20, 423–431.
- Lynch J. D. & Duellman, W.E. (1997) Frogs of the genus *Eleutherodactylus* (Leptodactylidae) in western Ecuador: systematics, ecology, and biogeography. *University of Kansas Natural History Museum Special Publications*, 23, 1–236.
- Padial, J. M., & De la Riva, I. (2006) Taxonomic inflation and the stability of species lists: the perils of ostrich's behavior. *Systematic Biology*, 55, 859–867.

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Padial, J. M., Chaparro, J. C. & De la Riva, I. (2008) Systematics of *Oreobates* and the *Eleutherodactylus discoidalis* species group (Anura) based on two mtDNA genes and external morphology. *Zoological Journal of the Linnean Society*, 152, 737–773.