



The generic allocation of “*Hyla*” *antoniiochoai* De la Riva & Chaparro, 2005 (Anura), with description of its advertisement call and ecology

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Abstract

The description of the frog “*Hyla*” *antoniiochoai* is based on a subadult female and a juvenile collected in 2005 near Esperanza, Kosñipata Valley, *Región* (formerly *Departamento*) Cusco, southeastern Peru. The species was assigned to the genus *Hyla* (Hylidae) but could not be assigned to any species group within this genus. According to the original description, typical characters include the absence of webbing in hands, and vestigial webbing between Toes III and IV. In 2009, we collected additional specimens including adults of both sexes from the type locality. To our surprise these specimens show characters, such as a closed brood pouch, that are typical of *Gastrotheca* (Hemiphractidae). Furthermore, our analysis of the advertisement call supports its relation with *Gastrotheca*. Consequently, we assign “*Hyla*” *antoniiochoai* to *Gastrotheca*, compare it with its congeners, and improve the species diagnosis and description. *Gastrotheca antoniiochoai* lives in epiphytic bromeliads in the cloud forest and montane scrub between 2700 and 3300 m in Manu National Park. The new specimens were found inside bromeliads approximately 6–8 m from the ground. It shares with the central Peruvian *Gastrotheca zeugocystis*, and the Venezuelan *G. walkeri* and *G. williamsonii* a lateral, paired brood pouch (instead of the single, dorsomedian pouch found in most *Gastrotheca*).

Key words: Andes, *Gastrotheca antoniiochoai*, Hemiphractidae, marsupial frog, new combination, vocalization

Resumen

La descripción de la rana “*Hyla*” *antoniiochoai* está basada en una hembra subadulto y un juvenil colectados en 2005 cerca de Esperanza, valle de Kosñipata, *Región* (previamente *Departamento*) Cusco, sureste de Perú. La especie fue asignada al género *Hyla* (Hylidae), pero no pudo ser incluida en ninguno de los grupos de especies del género. Según la descripción original, caracteres típicos de la especie incluyen la ausencia de palmadura en las manos, y palmadura vestigial entre los dedos III y IV de los pies. En el 2009, colectamos en la localidad tipo nuevos especímenes, incluyendo adultos de ambos sexos. Para nuestra sorpresa, estos especímenes muestran caracteres, como la presencia de una bolsa incubatriz dorsal, que son típicos del género *Gastrotheca* (Hemiphractidae). Además, nuestro análisis del canto nupcial apoya la relación de la especie con *Gastrotheca*. Por lo tanto, asignamos “*Hyla*” *antoniiochoai* a *Gastrotheca*, la comparamos con especies del mismo género, y mejoramos la diagnosis y descripción de la especie. *Gastrotheca antoniiochoai* vive en bromelias epífitas en el bosque nublado y matorral montano entre 2700 y 3300 m en el Parque Nacional del Manu. Los nuevos especímenes fueron encontrados en bromelias a aproximadamente 6–8 m de altura sobre el suelo. Esta especie comparte con *Gastrotheca zeugocystis* de los Andes del centro de Perú y *G. walkeri* y *G. williamsonii* de Venezuela la presencia de un par de bolsas incubatrices laterales (y no una bolsa dorsal mediana, como en la mayoría de las especies de *Gastrotheca*).

Introduction

The species “*Hyla*” *antoniiochoai* was originally described as a tree frog (genus *Hyla*) that “cannot be assigned to any of the eight Andean groups of *Hyla* recognized” (De la Riva & Chaparro 2005). The area around the type locality of “*Hyla*” *antoniiochoai*, the Kosñipata valley on the eastern slopes of the Andes in *Región* (formerly *Departamento*) Cusco, has been relatively well studied since the construction of the Paucartambo–Shintuya road in the early 1970’s, which has resulted in the discovery of new species and an important increase in the known amphibian alpha-diversity of the adjacent Manu National Park. Recent fieldwork 600 m from the type locality of “*Hyla*” *antoniiochoai* resulted in the discovery of additional specimens of this taxon and revealed characters not mentioned in the original description. Based on the study of the newly discovered specimens, we present new morphological data, describe the advertisement call and provide notes on the ecology and reproduction of the species. We use these data to assess the taxonomic status of “*Hyla*” *antoniiochoai*.

Material and methods

We follow Frost (2009) for taxonomy and Duellman *et al.* (2001, 2004) for morphological measurements and the format of the revised diagnosis. Specimens were preserved in 10% formalin and stored in 70% ethanol. Measurements were taken with calipers under a microscope and rounded to the nearest 0.1 mm, including snout–vent length (SVL), tibia length (TL), foot length (FL, distance from proximal margin of inner metatarsal tubercle to tip of Toe IV), head length (HL, from angle of jaw to tip of snout), head width (HW, at level of angle of jaw), eye diameter (ED), tympanum diameter (TY), interorbital distance (IOD), upper eyelid width (EW), internarial distance (IND), eye–nostril distance (E–N, straight line distance between anterior corner of orbit and posterior margin of external nares). Comparative lengths of Toes III and V were determined by adpressing both toes against Toe IV; lengths of Fingers I and II were determined by adpressing the fingers against each other. We determined webbing formula by following the method proposed by Savage & Heyer (1967) and modified by Myers & Duellman (1982). Photographs taken by A. Catenazzi were used for descriptions of color in life and are available for all new specimens at the Calphoto online database (<http://calphotos.berkeley.edu>). Specimens were obtained from the Wayqecha Research Center, along the Paucartambo–Shintuya road (GPS coordinates 13°11’07.8’’S, 71°35’18.5’’W) at 2950 m elevation on 10 February 2009 by A. Catenazzi, A. Machaca, and C. Quispe and were deposited at the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima (MUSM). These new specimens include three juveniles (MUSM 27945–47) and three adults (two males: MUSM 27944 and MUSM 27948, one brooding female: MUSM 27949).

We recorded advertisement calls in uncompressed wav format with a Zoom H2 digital recorder equipped with an Azden SMX-10 microphone. Male MUSM 27948 was recorded on 13 and 16 February 2009. We used Cool Edit version 96 (Syntrillium Software Corporation) and Raven Lite, version 1.0 (Cornell Laboratory of Ornithology) to digitize calls and analyze sonograms. We digitized and edited vocalizations at a sampling frequency of 44 KHz, FFT with 512 points, and 16-bit resolution. Average is followed by \pm standard deviation. Following Sinsch & Joermann (1989) we studied the structure of recorded vocalizations to differentiate advertisement from aggressive calls. However, we found that male MUSM 27948 produced vocalizations that would be identified as aggressive calls based on Sinsch & Joermann (1989) in absence of males, and interchangeably produced the two putatively advertisement and aggressive calls when vocalizing in presence of female MUSM 27949. Therefore, we refer to all calls as advertisement calls for the purpose of this paper.

Locality names follow the spelling of the US Board on Geographic Names (<http://gnswww.nga.mil>) and, for localities not listed in this database, according to the Carta Nacional “Calca” (Hoja 27-s), Instituto Geográfico Nacional, Lima (except for Acjanaco = Acanaco, Acanacu and Kosñipata = Cosñipata). We

deposited specimens in the herpetological collections of the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (MUSM) in Lima, Peru. For specimens examined, see Appendix.

***Gastrotheca antonii choai* new combination (De la Riva & Chaparro, 2005)**

(Fig. 1)

“*Hyla*” *antoniiochoai* De la Riva & Chaparro, 2005

Holotype. MHNC 0068, a subadult female from near Quebrada Toqoryuoc, Wayqecha Research Center, Kosñipata Valley, Provincia de Paucartambo, Región Cusco, Peru, 13°11'21.0''S, 71°35'05.5''W, 2845 m, obtained on 4 March 2003 by Juan Carlos Chaparro.

Additional specimens. MUSM 27944–49, from the Wayqecha Research Center, near the Paucartambo–Shintuya road at 2950 m, 13°11'07.8''S, 71°35'18.5''W, obtained on 10 February 2009 by A. Catenazzi, A. Machaca and C. Quispe.

Genus reallocation. We assign “*Hyla*” *antoniiochoai* to the genus *Gastrotheca* because it shares with species of that genus the presence of a closed brood pouch, overall morphological similarity, and similar structure of the advertisement call.

Diagnosis. A small species of *Gastrotheca* characterized by (1) snout-vent length of 26.5 mm in males ($n = 2$) and 32.5 mm in a single female, tibia length 51.6% of SVL and 108.5% of foot length; (2) interorbital distance about 1.36x larger than width of upper eyelid; (3) skin on dorsum smooth to finely rugose, not ossified with skull, lacking transverse ridges; (4) supraciliary processes absent; (5) heel lacking calcar and tubercles; (6) tympanic annulus smooth; (7) Finger I < II, with discs from 1.1 (Finger I) to 1.6 (Fingers III and IV) wider than digits; (8) fingers unwebbed; (9) webbing extending maximally to point midway between preantepenultimate and antepenultimate subarticular tubercles on Toe IV, to point midway between antepenultimate and penultimate subarticular tubercles on Toe V; (10) in life, dorsum brown to golden tan with dark and green flecks; (11) head markings consisting dorsally of narrow dark flecks along eyelids and laterally of tan stripe extending from nares to posterior end of cilia; (12) pale dorsolateral stripe absent; (13) flanks beige with dark brown flecks; (14) venter gray-brown or beige with minute dark brown spots and diffuse pigmentation; (15) brood pouch paired, lateral.

The reallocation of “*Hyla*” *antoniiochoai* to *Gastrotheca* brings the number of *Gastrotheca* species known from southern Peru, Bolivia and northern Argentina to fourteen (Duellman & Köhler 2005). The most striking features of *G. antoniiochoai* are its lateral, paired brood pouch, its small size (<30 mm in males, 32.5 mm in females) and a bromeliad life style. Paired brood pouches are known in only three species of *Gastrotheca* besides *G. antoniiochoai*: *G. walkeri*, *G. williamsoni*, and *G. zeugocystis* (Duellman *et al.* 2004, this paper). *Gastrotheca williamsoni* (SVL to 54 mm in females, based on the holotype and only known specimen) and *G. walkeri* (SVL 43.7–47.3 mm in males, 60.3–70.1 mm in females), both from northern Venezuela, are much larger than *G. antoniiochoai* and have a triangular calcar on the heel (absent in *G. antoniiochoai*). *Gastrotheca antoniiochoai* is most similar to the central Peruvian *G. zeugocystis*. Both species lack interorbital or T-shaped marks on the dorsum, have unwebbed fingers and basal webbing between Toes III and V. However, *G. antoniiochoai* is smaller in size than *G. zeugocystis* (32.5 vs. 37.5 mm in brooding females and 26.8–27.0 vs. 28.2 mm in adult males, $n = 1$ female and 2 males for *G. antoniiochoai*, $n = 1$ female and 1 male for *G. zeugocystis*), has Finger I shorter than Finger II (equal in size in *G. zeugocystis*) and a relatively longer shank in proportion to SVL (51.6% vs. 46.9%) and to foot length (108.5% vs. 98.3%). None of the other species of *Gastrotheca* known to occur in the Andes of southern Peru and Bolivia has a lateral, paired brood pouch (see Duellman & Köhler 2005 for a list and comparison of diagnostic traits among these species).

Variation. The two males are smaller than the single female. Both males show well-developed, tan nuptial pads. The three juveniles are like the juvenile paratype by having dark bars on the limbs (Figure 1E). Moreover, in juveniles the tan stripe originating from the nares extends dorsolaterally to the midbody (only to

the eyes in adults), and increases in width posterior to the tympanum, with an interruption at the point of arm insertion. In all juveniles the iris is reddish-bronze (bronze in adults) with black reticulations, the canthus rostralis is reddish-bronze, and the throat, chest, and belly are white. In adults all ventral surfaces are homogeneously gray-brown or beige with numerous minute black melanophores. The dorsum in one male (MUSM 27945) is pale beige, whereas the other male (MUSM 27948) has a golden-beige dorsum, and the female (MUSM 27949) has a darker, almost brown, dorsum. All adults have minute dark brown and green flecks from the interorbital region posteriorly to the sacral region.

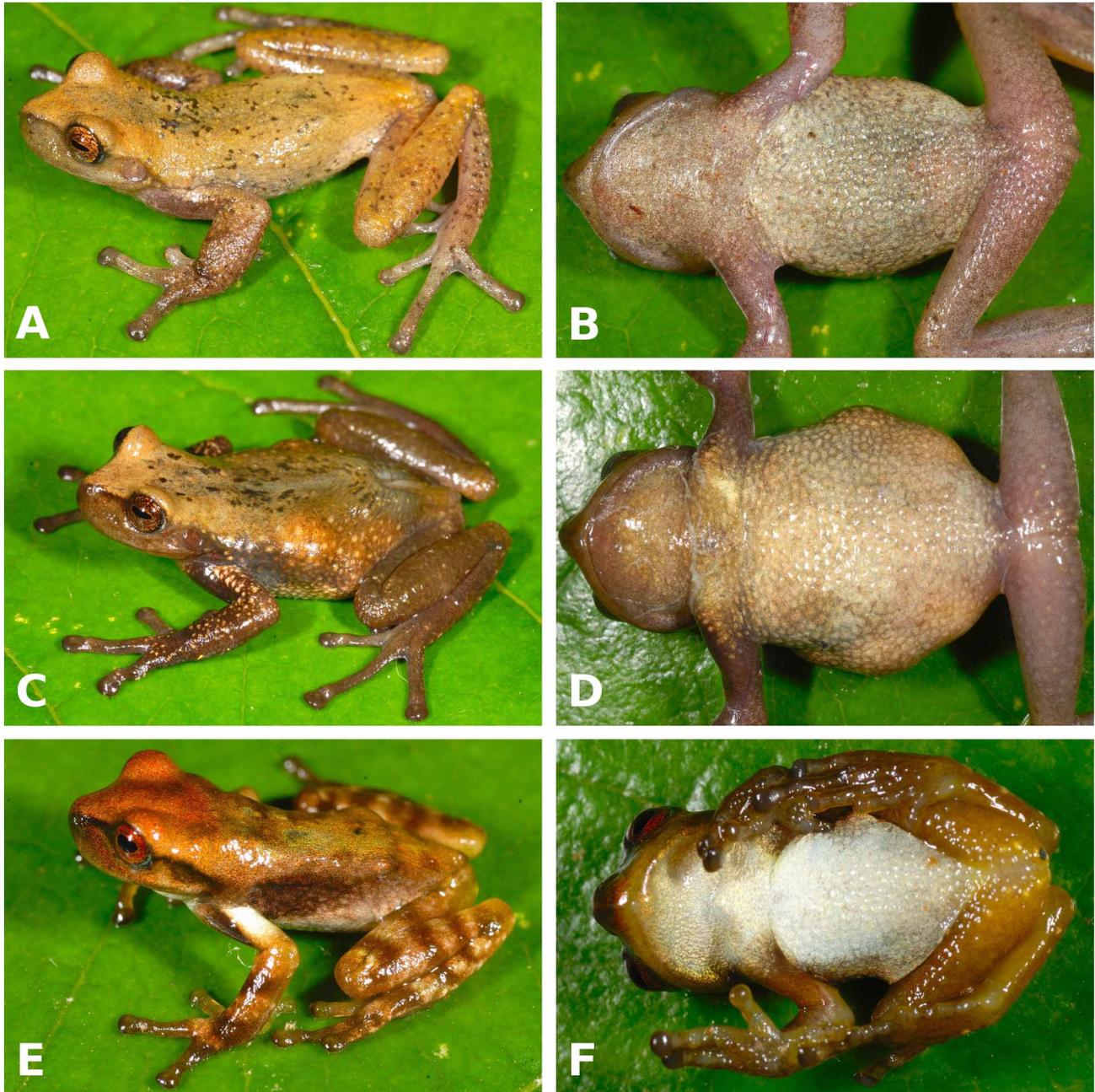


FIGURE 1. Upper row: Live adult male *Gastrotheca antonii choai* (MUSM 27944, SVL 27.0 mm) in lateral (A), and (B) ventral views; middle row: live adult female *Gastrotheca antonii choai* (MUSM 27949, SVL 32.5 mm) in lateral (C), and ventral (D) views; lower row: juvenile *Gastrotheca antonii choai* (MUSM 27947, SVL 13.4 mm) in lateral (E), and ventral (F) views. Photos by A. Catenazzi.

TABLE 1. Measurements of male, female and juvenile *Gastrotheca antoniiochoai*. Data for MHNC 0068 (holotype) and MNCN 42013 (paratype) are from De la Riva & Chaparro (2005).

| Character | MHNC 0068 | MNCN 42013 | MUSM 27944 | MUSM 27948 | MUSM 27949 | MUSM 27945 | MUSM 27946 | MUSM 27947 |
|-----------------------|--------------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|
| Sex | subadult female | juvenile | male | male | female | juvenile | juvenile | juvenile |
| Snout-vent length | 27.8 | 18.8 | 27.0 | 26.8 | 32.5 | 14.2 | 14.1 | 13.4 |
| Tibia length | 15.1 | 9.7 | 14 | 13.2 | 16.5 | 7.0 | 7.0 | 6.8 |
| Foot length | 13.3 | 8.2 | 13.0 | 12.4 | 17.1 | 6.3 | 6.0 | 5.9 |
| Head length | 7.5 | 5.6 | 9.0 | 8.9 | 10.3 | 5.1 | 4.8 | 4.5 |
| Head width | 8.9* | 6.6* | 9.1 | 8.8 | 11.8 | 4.6 | 4.6 | 4.6 |
| Eyelid width | — | — | 2.4 | 2.0 | 2.7 | 1.3 | 1.3 | 1.3 |
| Interorbital distance | 2.3 | 1.8 | 3.2 | 2.9 | 3.5 | 1.9 | 1.9 | 1.9 |
| Eye diameter | 2.6** | 2.0** | 3.0 | 2.9 | 3.4 | 1.8 | 1.7 | 1.5 |
| Internarial distance | 1.8 | 1.3 | 1.5 | 1.4 | 1.8 | 1.1 | 1.0 | 1.0 |
| Eye-nostril | 2.8 | 2.2 | 2.5 | 2.3 | 2.7 | 1.5 | 1.5 | 1.4 |
| Orbit-jaw | — | — | 1.5 | 1.4 | 1.7 | 0.5 | 0.5 | 0.5 |
| Nostril-jaw | — | — | 2.1 | 1.8 | 2.4 | 0.9 | 1.0 | 1.0 |
| Tymp. diameter | 1.5 | 0.9 | 1.6 | 1.3 | 1.6 | 0.8 | 1.0 | 0.8 |
| Thumb length | — | — | 4.2 | 3.9 | 5.8 | 2.1 | 2.1 | 2.2 |
| Third finger length | — | — | 8.3 | 8.0 | 10.1 | 4.5 | 4.6 | 4.4 |
| Finger III disc width | — | — | 1.3 | 1.1 | 1.6 | 0.9 | 0.9 | 0.9 |

* reported as “head: 8.9 (6.6)” in De la Riva & Chaparro 2005

**reported as “eye length” in De la Riva & Chaparro 2005

Vocalization and notes on reproduction. We analyzed the call of male MUSM 27948 ($n = 15$ calls, $T = 20.0^\circ\text{C}$). The advertisement call consisted of a long note 544.8 ± 27.5 ms (range 412–601 ms) in duration with 33.6 ± 1.9 pulses (range 26–38 pulses) and one, two, or three single-pulsed, short secondary notes 21.3 ± 1.8 ms (range 17–22 ms) in duration (Fig. 2). The average call frequency was 32.2 ± 6.4 calls/minute (range 18–40 calls/minute) and call length was 603.3 ± 70.3 ms (range 377–674 ms). The long note overall had little frequency modulation, and the fundamental frequency ranged between 2544–2968 Hz (median 2915 Hz). The dominant frequency in short notes was 1749–3445 Hz with maximum call energy between 3180 and 3445 Hz (median 3286 Hz). The average interval between long and short notes was 218.0 ± 22.8 ms (range 192–277 ms).

A male (MUSM 27948) and a female (MUSM 27949) were found inside the same bromeliad, and this male repeatedly attempted to mate with the female when placed in the same plastic bag after capture. The female contained six eggs ~6.5 mm in diameter in her lateral brood pouches (Figure 1C, D). This female was maintained in captivity for several weeks in a bromeliad filled with water, but the eggs slipped out of the pouches and did not complete development. Based on the small number and relatively large diameter of eggs, we suspect this to be a direct-developing *Gastrotheca*. Direct-developing species usually have fewer than 40 eggs 5–10 mm in diameter, whereas species that deposit tadpoles in water after they hatch usually have more than 70 eggs less than 4 mm in diameter (Duellman & Köhler 2005; Duellman *et al.* 2001). This is the second Peruvian *Gastrotheca* known to possess paired lateral brood pouches; the other is *G. zeugocystis* (Duellman *et al.* 2004).

Distribution and ecology. The species seems to have a patchy distribution in montane scrub and cloud forests between 2800 and 3300 m. The two types were collected at 2845 and 2817 m, but our specimens were captured in bromeliads 6–8 m above the ground in the cloud forest at 2950 m. In addition, we heard the

species in cloud forest at 3300 m along the Ericsson trail connecting Acjanaco with Pillahuata, within Manu National Park, on 11 February 2009, and in montane scrub adjacent to our collecting site on 9 February 2009. Therefore, this *Gastrotheca* occurs in sympatry with *G. excubitor* throughout its elevational range (albeit *G. excubitor* becomes rare below 3200 m), and with *G. ochoai* at the lower end of its elevational range (Catenazzi & Rodríguez 2001). Of these two species, the first is primarily found in grassland habitats dominated by *Stipa ichu* (*puna*) and montane scrub, whereas *G. ochoai* inhabits montane scrub and cloud forest. Interestingly, *G. ochoai* is also known to use bromeliads as microhabitats (Duellman & Fritts 1972), although we never found this species in bromeliads at heights comparable to those used by *G. antoniichoai*. Other sympatric frogs include *Bryophryne hanssaueri*, *B. nubilosus*, *Centrolene* sp., *Hyloscirtus armatus*, *Noblella pygmaea*, *Oreobates lehri*, *Pristimantis pharangobates*, *Psychrophrynella usurpator* and *Telmatobius* sp. (Catenazzi *et al.* 2009, Lehr & Catenazzi 2008, 2009a,b).

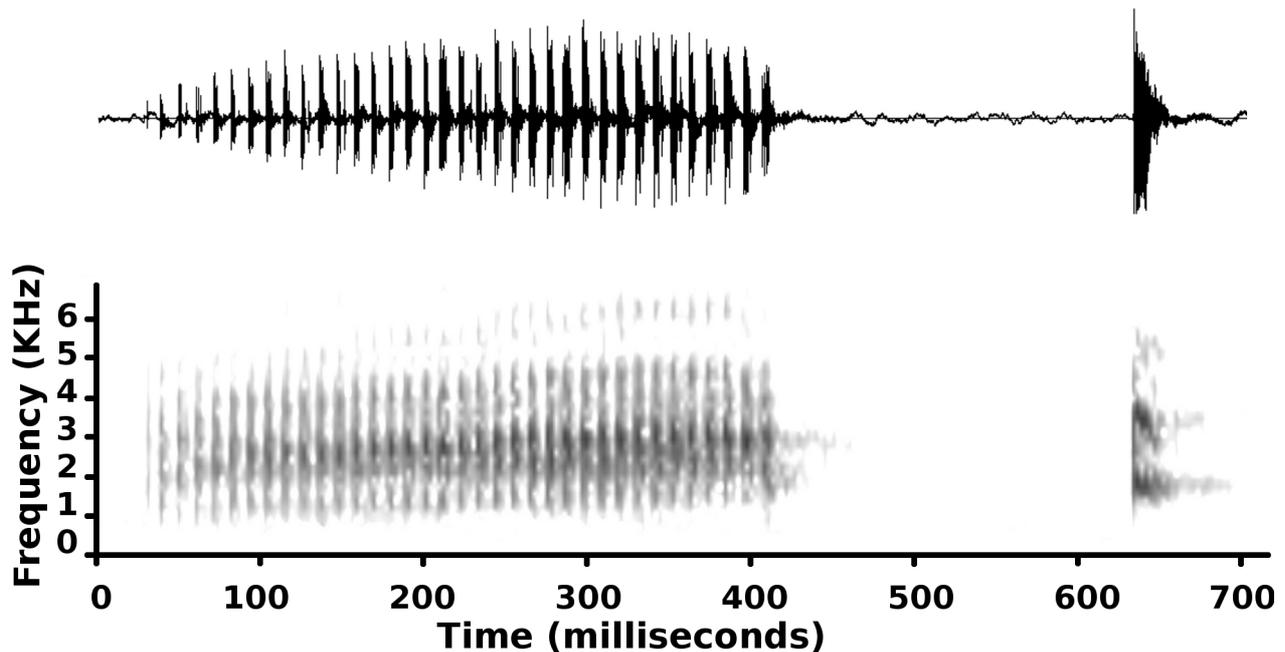


FIGURE 2. Spectrogram and oscillogram of the advertisement call of *Gastrotheca antoniichoai* (MUSM 27948, SVL 26.0 mm) from the Wayqecha Research Station, Paucartambo, *Región* Cusco. Recorded on 16 February 2009 at 9h30, air temperature 20.0°C.

Discussion. Immature specimens have limited value for descriptions of species, because the absence of diagnostic characters can lead to supraspecific misallocations. De la Riva & Chaparro (2005) cautioned against introducing “taxonomic confusion” when describing “*Hyla*” *antoniichoai*; unfortunately, given the number of specimens available to them, they erroneously placed the species in *Hyla*. De la Riva & Chaparro (2005) found “immature white ovarian eggs, developed fat bodies, and undeveloped oviducts” in the holotype and considered the female to be an adult and “probably ready to lay eggs in the following days or weeks”. Because female *Gastrotheca* are unmistakable when they reach reproductive age (see Figure 1 for a picture of dorsal invagination in *G. antoniichoai*), we disagree with their assessment of the reproductive status and age of the holotype; we consider the holotype to be a subadult female. In support of this conclusion, we found the same color pattern reported in life for the holotype (white throat and chest and reddish-bronze eyes, De la Riva & Chaparro 2005) in all three juvenile specimens studied, but in none of the three adults. The new generic allocation also makes the species less unique with respect to congeners [e.g., vestigial webbing between toes, a character that according to De la Riva & Chaparro (2005) made the species distinct from other Peruvian and Bolivian *Hyla*].

Concerning the reproduction of *Gastrotheca antoniochoai*, the availability of water in bromeliads might not be necessary to complete its reproductive cycle, because females likely carry eggs until froglets hatch and emerge from the dorsal pouch. Direct development also would be in line with previous findings that in cloud forest *Gastrotheca* species, embryos complete development and hatch into froglets inside the dorsal brood pouch (Duellman & Maness 1980; Wassersug & Duellman 1984).

We hypothesize that *Gastrotheca antoniochoai* is related to *G. zeugocystis*, because both species share lateral brood pouches and are similar in general appearance and coloration. Both species inhabit cloud forest at similar elevations (around 2900 m) and use bromeliads as diurnal refuges. Additional research is needed to establish the relationship between these two species. The type localities are separated by 624 km in straight line and by the proposed biogeographic barrier of the deep valley of the Río Apurimac (Lehr & Catenazzi 2008). This barrier seems to have isolated several anuran clades (e.g., strabomatid frogs), but its effect on the distribution of marsupial frog is presently unknown.

Although not a new description, this proposed new combination, as well as recent work pointing to past misidentification of species and genera in the Kosñipata valley (e.g., De la Riva *et al.* 2008 for the strabomantid frog *Psychrophrynella usurpator*) shows that much work remains to be done to gain a better understanding of anuran diversity in southeastern Peru.

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Appendix: Specimens examined

- Gastrotheca antoniichoai*: PERU: Cusco: Paucartambo: near Quebrada Toqoryuoc, Wayqecha Research Center, Cosñipata Valley, Provincia de Paucartambo, Región de Cusco, Peru, 13°11'21.0''S, 71°35'05.5''W, 2845 m, MHNC 0068 (photo of live holotype); near Quebrada Huancohumanio, Esperanza, Cosñipata Valley, 13°10'59.5''S, 71°36'29.2''W, 2817 m, MNCN 42013; Paucartambo–Shintuya road, Wayqecha Research Center, 13°11'07.8''S, 71°35'18.5''W, 2950 m, MUSM 27944–49.
- Gastrotheca excubitor*: PERU: Cusco: Paucartambo: Abra Acjanaco, MUSM 27934–35, 27872–74.
- Gastrotheca marsupiata*: PERU: Cusco: Paucartambo: Tres Cruces, 18 km north of Paucartambo, 3670 m, MVZ 57804.
- Gastrotheca ochoai*: PERU: Cusco: Paucartambo: Paucartambo–Shintuya road, MUSM 27888; La Convención: Alfamayo, MUSM 27889.
- Gastrotheca testudinea*: PERU: Cusco: Paucartambo: Paucartambo–Shintuya road, MUSM 27942–43.
- Gastrotheca williamsoni*: VENEZUELA: Carabobo: San Esteban, UMMZ 55559 (photographs of preserved holotype).
- Gastrotheca zeugocystis*: PERU: Huánuco: Cordillera de Carpish, 2920 m, MUSM 18675 (holotype), MTD 45984 (Cleared & Stained).