



A new species of Caribbean toad (Bufonidae, *Peltophryne*) from southern Hispaniola

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Abstract

Peltophryne armata **sp. nov.** is described from the South paleoisland of Hispaniola, West Indies. This is the only native toad species known to inhabit the Barahona Peninsula, Dominican Republic, in the southernmost part of Hispaniola, and it is allopatric with the widely distributed Hispaniolan toad species, *P. guentheri* Cochran. However, in a molecular phylogeny, the closest relative of *P. armata* **sp. nov.** is the Puerto Rican species *P. lemur* Cope, with which it shares a protrusive snout, large orbits, a depressed head, indistinct or absent infraorbital crests, and a long and complex advertisement call, but differs from it greatly by the very long cephalic crests, and in the massive and spinose parotoid glands that converge medially on the dorsum. The new species is similar in ecology and larval morphology to the Cuban *P. florentinoi* Moreno & Rivalta, but differs from it in adult morphology. The tadpole of the new species is described. *Peltophryne fracta* is placed in the synonymy of *P. guentheri*.

Key words: Amphibia, Anura, Caribbean, Greater Antilles, South paleoisland, West Indies, oophagy, ecomorph

Resumen

Se describe una nueva especie de sapo, *Peltophryne armata* **sp. nov.**, de la paleoisla sur de la Hispaniola, Indias Occidentales. Esta es la única especie de sapo nativa que habita al sur en la península de Barahona, República Dominicana, la parte más meridional de la Hispaniola, y cuya ocurrencia es alopatrica a la de la especie de sapo nativa de más amplia distribución, *P. guentheri* Cochran. Sin embargo, en una filogenia molecular, el pariente más cercano de *P. armata* **sp. nov.** es la especie puertorriqueña *P. lemur* Cope, con la cual comparte un hocico protuberante, órbitas grandes, cabeza dorsoventralmente comprimida, crestas infraorbitales débiles o ausentes, y una llamada de anuncio larga y compleja, pero difiere mucho de esta por las crestas cefálicas muy largas, y en las enormes y espinosas glándulas parotoides que coinciden en el medio del dorso. La nueva especie es similar en ecología y en morfología larvaria a la especie cubana *P. florentinoi* Moreno & Rivalta, pero difiere de ella en morfología del adulto. Se describe el renacuajo de la nueva especie. *Peltophryne fracta* es puesto en sinonimia con *P. guentheri*.

Palabras claves: Amphibia, Anura, Caribe, Antillas Mayores, paleoisla Sur, Indias Occidentales, oofagia, ecomorfo

Introduction

The Caribbean genus *Peltophryne* Fitzinger contains 12 species distributed throughout most of the Greater Antilles, with eight species on Cuba, three on Hispaniola, and a single species on Puerto Rico and the Virgin Islands (Moreno & Rivalta 2007; Alonso *et al.* 2012; Powell & Henderson 2012). Details of the relationships of the species remain to be resolved (Pramuk *et al.* 2001; Alonso *et al.* 2012). The only Hispaniolan species previously included in a molecular analysis is *P. guentheri* (Hedges *et al.* 1992; Hass *et al.* 2001; Pramuk 2002; Pramuk 2006), since no fresh material has been available or analyzed from the other two species from Hispaniola, *P. fluviatica* Schwartz and *P. fracta* Schwartz. *Peltophryne fluviatica* is known only from the type series collected in 1971

(Schwartz 1972; Henderson & Powell 2009). *Peltophryne fracta* was originally described as a subspecies of *P. guentheri* (Schwartz 1972) based on a smaller body size and differences in color pattern. It was elevated to full species by Powell (1993) based on additional data from Pregill (1981), and has been recognized as such in checklists (e.g. Powell *et al.* 1996; Powell & Henderson 2012). *Peltophryne fracta* has remained poorly known, with only a few reported sightings (Powell 1992; Hedges & Díaz 2011; Landestoy & Ortíz 2015). In spite of some call differences based on anecdotal mentions and one single individual analyzed (Pregill 1981; Powell *et al.* 1996; Landestoy & Ortíz 2015), recent morphological data (males of *P. fracta* nearly match the upper size limit of *P. guentheri*; Landestoy & Ortíz 2015) and our molecular results reported here suggest that *P. fracta* is not as different from *P. guentheri* as previously thought to justify recognition as either a separate species or subspecies. Instead, we place *P. fracta* in the synonymy of the widespread *P. guentheri*. In this paper, we base the description of the new species from southern Hispaniola on both adult and larval external morphology, vocalization, and molecular analysis.

Materials and methods

The position of cephalic crests and head shape follows Narvaes & Rodrigues (2009), with adaptations from Pramuk (2006) only for the position of the postorbital and pretympanic crests. Given the highly developed crests in the new species and the partial covering of the posterior borders of tympana by the parotoid glands, we considered using the crests' outer edges as landmarks for head measurements ("HL2, HW2", see below). However, standard head measurements ("HL1, HW1") using the most common landmarks are also provided. Weight in grams (g). Measurements in millimeters (mm). Snout-vent length (SVL) was measured from cloacal opening to the tip of snout. Head length 1 (HL1) was measured from the anterior margin of snout to posterior border of tympanum (using the inside jaws of caliper for the new species). Head length 2 (HL2) was measured from the anterior margin of snout to posterior border of supratympanic crest. Head width 1 (HW1) was measured across the median portions of tympana. Head width 2 (HW2) was measured at the outer intersection of supratympanic and pretympanic crests (just below the former). Interorbital distance (IOD) was measured at the intersection of supraorbital with parietal crests (or at the corner of the angle formed by the supraorbital and postorbital crests in some specimens). Internarial distance (IND) was taken from median sections of nostrils. Eye to nostril distance (END) was measured from the anterior corner of eyelid to median section of nostril. Eye diameter (ED) was measured from posterior to anterior corners of eyelids using the inside jaws of caliper. Tympanum width (TW) was measured with the inside jaws of caliper (in the new species). Thigh length (THL) was measured from junction of the cloacal opening and the posteroventral median line of buttocks to the articulation with shank. Shank length (SHL) was measured from the knee joint to tibio-tarsal articulation. Foot length (FL) was measured from the proximal edge of outer metatarsal tubercle to tip of toe IV (flexing toe straight until tip slides from edge of caliper jaw). Sex was determined by: males with nuptial excrescences, calling, and emitted release calls when grabbed; females with eggs (examined), and of larger SVL. We make comparison with some species using data from the literature. New comparative data are presented in Appendix I.

Acronyms used in text: Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Museo Nacional de Historia Natural Prof. Eugenio de Jesús Marcano, Santo Domingo (MNHNSD); University of Kansas Herpetology Collection, Lawrence (KU); Miguel A. Landestoy T. (MALT); S. Blair Hedges collection (SBH). Weather data (air temperature and relative humidity) from the field were obtained with a Kestrel Pocket Weather Tracker 4000 registering only while the collecting and audio recording took place. Audio recordings were made using a Marantz PMD661 field recorder and a Sennheiser ME 67 shotgun microphone, and an Olympus DM-620 portable voice stereo recorder, in WAV format, and then converted to mono using Audacity software 2.0.5 (<http://audacityteam.org/>). For all call analysis Raven Pro software 1.5 Beta was employed; both programs were used in a Windows platform.

Call terminology in an ethological context follows Duellman & Trueb (1986). Call characterization (type pattern of amplitude modulation, call type) follows that of Martin (1972). Six acoustic characters were measured: call duration; call interval; number of pulses per call; pulse rate, consisting of number of pulses/call duration ratio; number of subpulses; and dominant frequency, in kilohertz (kHz); seconds (s). Bandwidth was determined as in Köhler *et al.* [2017 (90% found as the difference between 95% frequency and 5% frequency)]. Well-defined internal amplitude modulations within pulses were counted as individual subpulses (e.g. 2–4; Fig. 1C). Larval

morphology terminology follows Altig & McDiarmid (1999); second anterior tooth row (A-2), first and third posterior tooth rows (P-1 and P-3 respectively). Developmental staging is from Gosner (1960). Measurements in adult specimens were obtained using a digital caliper rounded to the nearest 0.1 mm, with a binocular magnifying visor for some characters. Measurements of larvae were under a Motic k-400 stereoscope coupled with an ocular micrometer.

The molecular data set comprised 26 *Peltophryne* samples. One outgroup taxon, *Rhaebo haematiticus*, was also included in molecular analyses, using sequence data collected from GenBank. Methods used for the collection of DNA sequences are detailed elsewhere (Hedges *et al.* 2008, Hedges & Conn 2012, Heinicke *et al.* 2007). Portions of three mitochondrial genes—12S ribosomal RNA (rRNA), 16S rRNA, and cytochrome b (cytb)—were sequenced for a total concatenated alignment of 1,768 aligned sites. Alignments (considering amino acid translations) were performed with MUSCLE in MEGA 6.06 (Tamura *et al.* 2013).

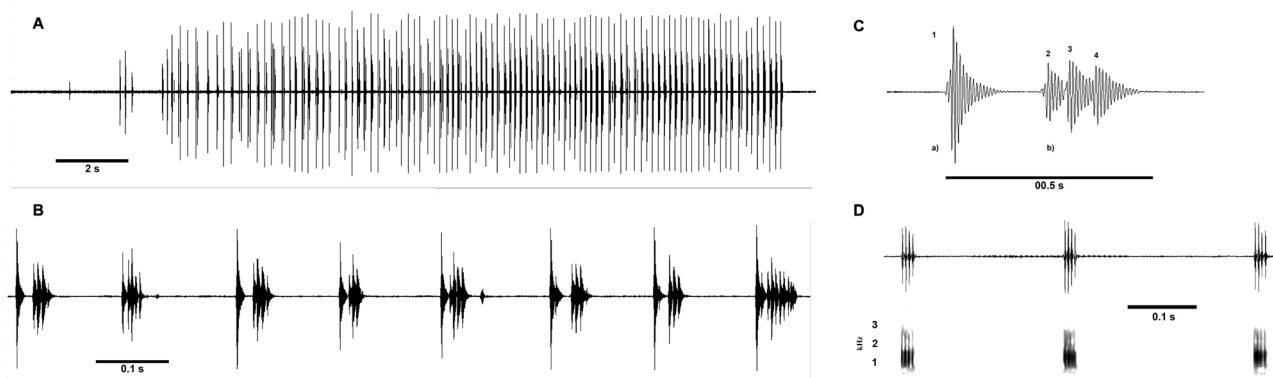


FIGURE 1. The advertisement call of *Peltophryne armata* sp. nov. (A–C). Complete call (A), and fragments of calls (B–C). Complex pulse consisting of a primary (a) and a secondary (b) subpulse (C); well-defined internal amplitude modulations within pulses (2–4) were counted as single subpulses. Waveform (above) and spectrogram (below) of a three pulse release call (D).

We first used PartitionFinder v1.1.1 (Lanfear *et al.* 2012) to determine the best partitioning strategy and molecular models under the Bayesian information criterion (BIC) and the “all” search scheme. Following the results of this analysis, we divided our dataset into two partitions: (1) all 12S and 16S sites, and the first and second codon positions of cytb, and (2) the third codon position of cytb. A maximum likelihood analysis was performed using RAxML 8.2.8 (Stamatakis 2014) through the CIPRES Science Gateway (Miller *et al.* 2010). All data were analyzed using the evolutionary model GTRGAMMA, the maximized available option in RAxML. Gaps were treated as missing data. All parameters for the ML analysis were estimated by the program during the run. Branch support in the trees was provided by rapid bootstrap analysis (1,000 replicates), using the GTRGAMMA method (as recommended for small datasets). A Bayesian phylogenetic analysis using MrBayes v3.2.5 (Ronquist *et al.* 2012) was also performed, again using the GTR + Γ model and the two-partition scheme. The Bayesian analysis was set to two parallel runs for five million generations, sampling every 100 generations. The first 10% of samples were discarded as burn-in. Convergence was assessed by the standard deviation of split frequencies (< 0.01 in all cases).

Results

The molecular phylogeny showed that *Peltophryne armata* sp. nov. is most closely related to *P. lemur*, from Puerto Rico (Fig. 2). This sister pairing is strongly supported (97% bootstrap support, 100% Bayesian posterior probability). Our phylogeny did not support the recognition of *P. fracta* as a species distinct from *P. guentheri* because there was no genetic differentiation among samples of true *P. guentheri* (samples 4–14) and some initially identified as “*P. fracta*” (samples 1–3) based on geographic location, and the remaining amount of genetic differentiation (< 0.5%) among samples of “*P. fracta*” was of the same degree as observed within valid species elsewhere in the tree (*P. taladai* Schwartz and *P. armata*). This agrees with the recent discovery that body size is not a valid diagnostic character of *P. fracta* (Landestoy & Ortiz 2015).

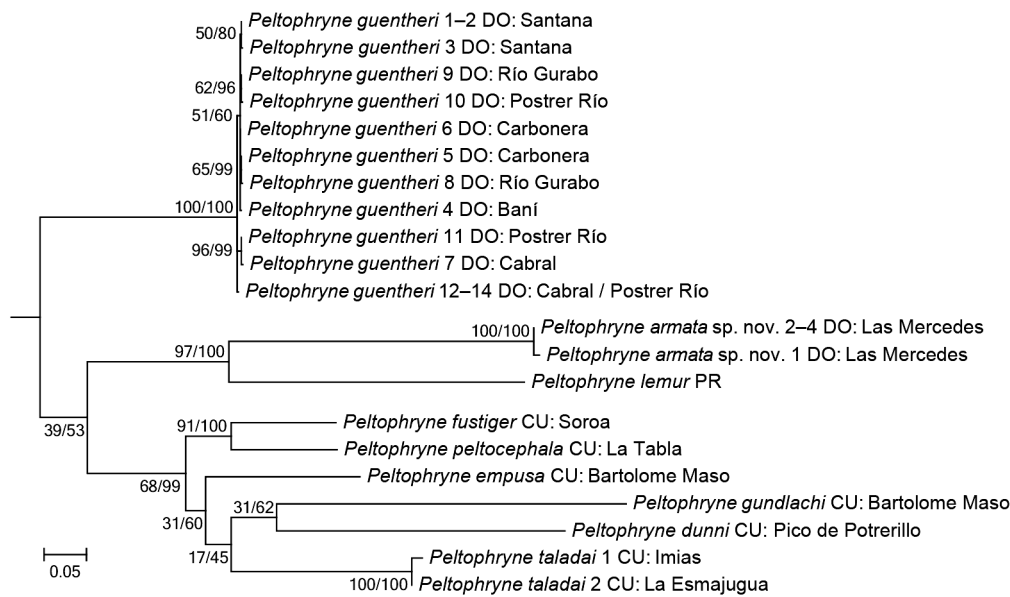


FIGURE 2. Phylogenetic tree of nine species of *Peltophryne* from a maximum-likelihood analysis of 12S, 16S, and cytochrome b sequence data. A scale bar (5% sequence divergence) is indicated. The numbers at nodes are bootstrap (left) and Bayesian (right) support values. The tree is rooted with *Rhaebo haematiticus*, not shown.

Peltophryne armata sp. nov.

Holotype: MCZ A-149839 (Fig. 3), an adult male with SVL of 76.8 mm (weight in life 35.2g), from 1.6 km SSW of Las Mercedes, Sierra de Bahoruco, 345 m elevation, Pedernales Province, Dominican Republic, collected by M. Landestoy, R. Ortíz and Y. Corona on the night of 23 August 2014.

Paratypes: (n=9; 7 males, 2 females) MCZ A-149840 (female), MCZ A-149841, MNHNSD 23.1375, collected by M. Landestoy and R. Ortíz on the 22 August 2014, 1 km SSW Las Mercedes, on the southern slopes of the Sierra de Bahoruco, Pedernales Province; MCZ A-149842, MNHNSD23.1376–78, same data as the holotype, collected by M. Landestoy, R. Ortíz and Y. Corona; MCZ A-149843, MNHNSD23.1379 (female), same locality as former, on 31 August 2014, by M. Landestoy and R. Ortíz.

Diagnosis. A medium-sized species of the genus *Peltophryne* (SVL in males to 78 mm, in females to 85.7 mm), possessing characteristics of the genus: T-shaped terminal phalanges and discrete glandular tubercles on tarsus (Fig. 4A–B, respectively; *sensu* Pramuk 2002), and placed within the genus in a molecular phylogeny (Fig. 2). It is distinguished from all other congeners by three unique characters: hypertrophic cephalic crests (supraorbital, postorbital, supratympanic, pretympanic and preorbital crests, the first two crests extended outwards largely covering eyelids and orbits in dorsal view; Fig. 5A–B), hypertrophic parotoid glands (longitudinally, transversely and obliquely massive) converging middorsally, and snout with a notched tip (distal ends of canthal crests create a gap in between). It is most closely related in a molecular phylogeny to the Puerto Rican species *P. lemur*, with which it shares a depressed head (in profile), very low or absent infraorbital crest (merged with the maxillary crest), a protrusive, slightly upturned snout, large orbits, and a long, complex (Type II) advertisement call. Beyond its unique characters, the new species also differs from that species by the geometry of crests on the dorsal surface of the head (intersection of postorbital and supraorbital crests forming obtuse angles—acute with canthal—versus these crests being nearly continuous and straight to slightly concave in *P. lemur*; Fig. 5C), by having the head rounded (versus subtriangular in *P. lemur*), by having the parotoid glands with spinose keratinized tubercles (versus subrounded keratinized tubercles in *P. lemur*), by having feet basally webbed (versus strongly webbed in *P. lemur*), and in having a large vocal sac (versus small to moderate in *P. lemur*).

Peltophryne armata is less closely related to Hispaniolan species and it is not known to be sympatric with any of its congeners from that island. Nonetheless, besides its unique characters it can also be distinguished from its geographic neighbor on Hispaniola, *P. guentheri*, by the obtuse angles at intersection of supra- and postorbital

crests (versus right angles in *P. guentheri*; Fig. 5E–F), rounded head shape in dorsal view (versus subtriangular in *P. guentheri*), a Type II call (versus short Type I call with evenly spaced, rapid rising simple pulses in *P. guentheri*), the presence of a thick and pad-like tarsal fold (versus a narrow and sharp flap-like ridge in *P. guentheri*), in the basal, short foot webbing (versus large foot webs in *P. guentheri*), and a whitish or cream-colored throat in adults of both sexes (versus dark olive pigmentation in males of *P. guentheri*).

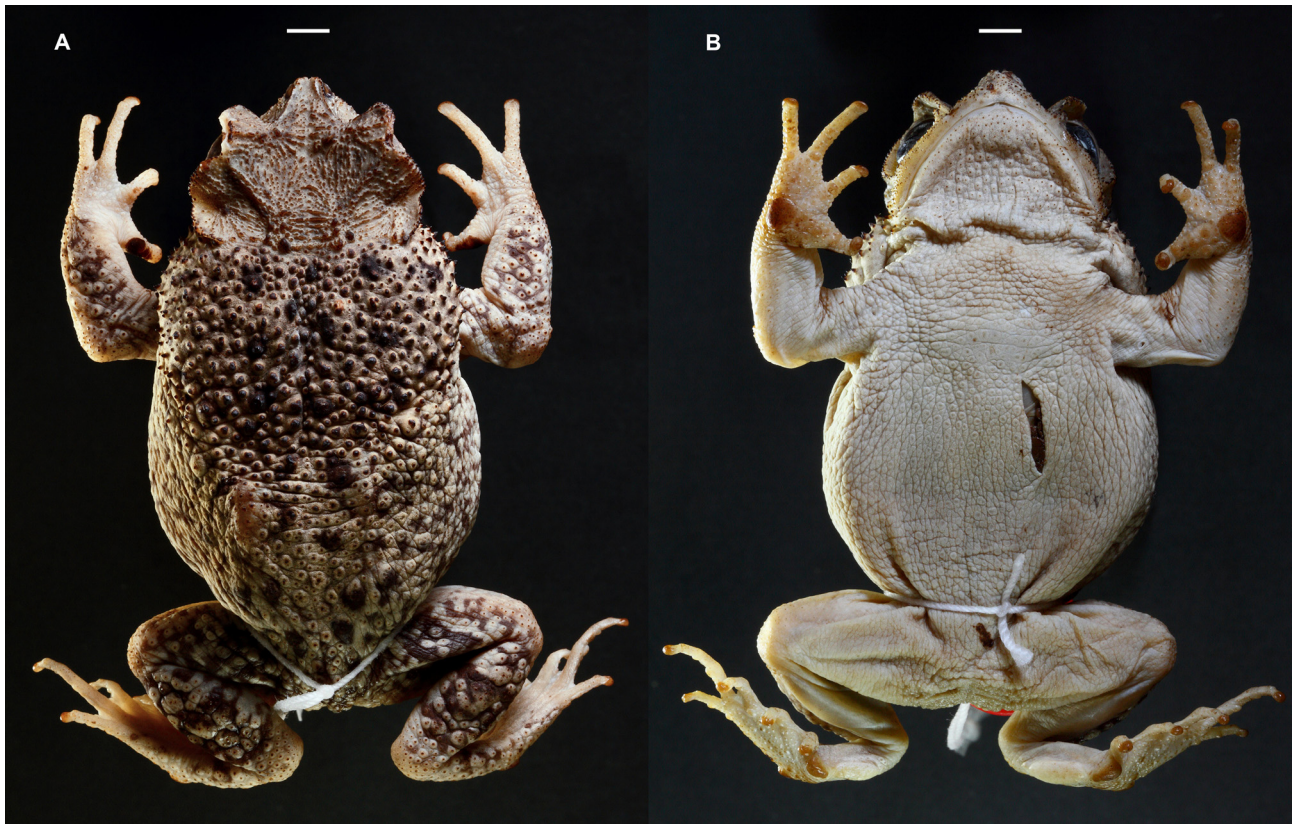


FIGURE 3. Holotype of *Peltophryne armata* sp. nov., in dorsal (A) and ventral (B) views. Scale bars equal 5 mm. Photographs by MALT.

Description of the holotype. MCZ A-149839 (Fig. 3), measurements in Table 1. Habitus stout and head broader than long (HL1 87.4% of HW1), nearly rounded in dorsal view, relatively depressed (dorsoventrally) in profile. Supraorbital and postorbital crests very long, directed anterolaterally, gradually elevated from interorbital and parietal areas (creating a concavity in those areas), extended far outwards (in dorsal view) covering most of the eyelids, the intersection of both crests creating a rather obtuse angle, and a high, broad arch well above the eye (in profile), its edges with granular keratinization, the surface of each of those crests bearing several (4–6) transverse keratinized ridges arranged parallel to each other. Supratympanic crest long, extended laterally and elevated from its junction with postorbital crest, covering tympana and curved inward at posterior end (dorsal view) with its outer edges bent upward, the crest oriented diagonally in profile with its lower end joining pretympenic crest. Pretympenic crest prominent, directed anterolaterally. Infraorbital crest undistinguished or absent, overlapped by a prominent maxillary crest. Preorbital crest long, with a median notch, continuous to supraorbital crest but transversed by 4–6 prominent keratinized ridges, and ventrally in contact with and protruding transversely to maxillary crest, its lower end sinuate, bent anteriorly before joining the maxillary crest. Canthal crest prominent, sharp and slightly concave, the distal ends of canthals leaving a gap or notch in between. The convergence of the canthal, supraorbital and preorbital crests forming acute angles, the intersection of the latter two crests projecting anteriorly, sharply convexed in a horn-like form (in dorsal view). Subnasal crest low. Parietal crest relatively low and an indentation between its posterior end and the supratympanic crest. All cephalic crests beaded with moderate level of granular keratinization. Upper eyelid with a prominent row of glandular keratin-tipped tubercles on outer margin. Orbits large, directed anterolaterally. Snout rather short, protruding, semi-truncate in dorsal view (with a notch at tip), sub-acuminate in profile. Nostrils near the tip of snout, directed dorsolaterally. Interorbital and

parietal areas heavily ornamented with numerous keratinized ridges and rugosities. Posterior of head with high bony conical tubercles. Loreal area slightly concave, with spinose keratinized tubercles scattered around snout and below tympanum down to the angle of jaw. Tympanum distinct, nearly rounded, its posterior partially overhung by parotoid gland. Parotoid glands very large and spinose (multiple keratin tips), elongate longitudinally and very broad transversely, almost touching each other middorsally (with a narrow groove in between them which widens anteriorly towards the head), and obliquely large, extending down below the level of the angle of jaw where distinct, but indistinct posteromedially, breaking into large keratinized tubercles and warts dispersed middorsally, decreasing in size, prominence and level of keratinization dorsolaterally and towards the cloaca. Flanks with low and small tubercles. Forelimbs with moderate keratin-tipped rounded tubercles, decreasing in size and prominence towards elbows and hands. Hindlimbs rather short. Dorsal surface of shanks with enlarged rounded glandular tubercles each with multiple keratin tips, smaller tubercles on thighs. Tarsus with moderate rounded tubercles on outer margin, its inner margin with an elongate and thick tarsal fold, pad-like (Fig. 4B). Skin of venter granular, the granules low, keratin-tipped anteromedially. Throat with higher keratin-tipped granules. Margins of jaw with a row of low keratin tips.

TABLE 1. Measurements (in mm) of *Peltophryne armata* sp. nov., and *P. guentheri*.

Character	<i>P. armata</i> sp. nov.				<i>P. guentheri</i>				
	Holotype	Males (n= 8)		Females (n= 2)		Males (n= 50)		Females (n= 7)	
		\bar{x}	Range	\bar{x}	Range	\bar{x}	Range	\bar{x}	Range
SVL	76.8	75.0	72.8–78.2	85.2	84.6–85.7	62.0	45.4–78.2	84.8	69.7–99
HL1	22.8	21.9	21.3–22.8	24.8	24.8–24.8	18.0	13.4–22.3	23.8	21.2–26.8
HL2	24.3	23.1	22.1–24.3	26.6	26.6–26.6	18.9	14.0–22.8	24.7	21.5–28.7
HW1	26.1	25.8	24.3–26.9	30.0	29.9–30.1	20.1	14.7–24.7	26.8	24.1–31.4
HW2	28.4	27.8	27–28.9	31.4	30.1–32.6	19.1	13.8–22.9	26.0	22.8–30.7
IOD	20.3	19.3	16.5–22.2	22.2	20.4–24	10.0	7.2–12.7	13.7	12.5–15.9
IND	4.1	4.0	3.8–4.2	4.6	4.5–4.6	3.1	2.4–3.6	4.1	3.4–4.6
END	6.9	6.7	6.4–7	7.3	7.0–7.6	5.4	3.9–6.8	7.1	6.5–7.9
ED	7.9	7.7	7.2–8.2	8.6	8.5–8.7	6.4	4.5–7.8	8.0	7.1–8.4
TW	3.8	3.7	3.4–4.1	4.0	3.7–4.3	3.2	2.4–4.2	3.6	3.3–3.8
THL	26.3	25.9	24.6–26.9	29.0	27.4–30.5	22.2	15.6–28.1	29.5	24.8–34.1
SHL	24.7	24.6	23.8–25.9	28.0	27.5–28.4	21.4	15.3–26.6	27.5	23.4–31.3
FL	25.7	24.8	23.5–26.2	27.5	26.8–28.2	22.8	15.5–28.2	28.5	23.1–32.1

All palmar tubercles keratinized. Thenar tubercle small, rounded, nearly one-third the size of the oval palmar tubercle. Median subarticular tubercles in fingers divided or bifid, proximals single and rounded to subconical. Supernumerary tubercles rounded and low. Fingers with well-developed lateral fringe, unwebbed, their relative lengths III>IV>I=II.

All plantar tubercles keratinized. Inner metatarsal tubercle large, ovoid. Outer metatarsal tubercle oval, two-thirds the size of the inner metatarsal tubercle. Subarticular tubercles of toes single, rounded and low. Supernumerary tubercles low. Tarsal fold elliptical and thick, pad-like (Fig. 4B). Toes with well-developed lateral fringe, basally webbed (distinct between toes II-III and III-IV), their relative lengths IV>III>V>II>I.

Color in life. (Fig. 6B) Dorsal ground color (including dorsal surfaces of limbs and eyelids) bright yellow with several black spots on dorsum, arranged paravertebrally with fewer, smaller spots scattered in parotoid glands. The head is darker yellow, with shades of dark brown in the interorbital and parietal areas, and some dark spots in its posterior among the bony conical tubercles. There is a subtle greenish cast behind head, at the middorsal intersection of parotoid glands, and on thighs. Diffuse and disrupted charcoal-gray vermiculations in dorsolateral and posterior areas of body, and on forelimbs, with the vermiculations darker, continuous and broader on hindlimbs, with three transverse bands across thighs and shanks. The large and glandular tubercles and warts on hindlimbs are predominantly yellow, encircled by very dark pigmentation, similar to those tubercles on forelimbs.

Flanks have fainter dorsal ground color and pigmentation of the vermiculated pattern, fading into cream-white lateroventrally. Hands and feet are cream-pinkish, with supernumerary tubercles buffy in hand, cream in feet. The venter is unpatterned, cream-white anteriorly, flesh-colored posteriorly (including limbs), with somewhat translucent skin revealing a blue-purplish hue most noticeable lateroventrally, and under shanks and tarsi. All granules and tubercles on venter are cream-white. The chin, the mid-throat and its edges are cream-white finely stippled with light gray, and the vocal sac is cream-white. The iris is greenish-gold, with many black venations in its lower section, less so in its upper section. Pupils are bordered with black extended across the corners of eye.

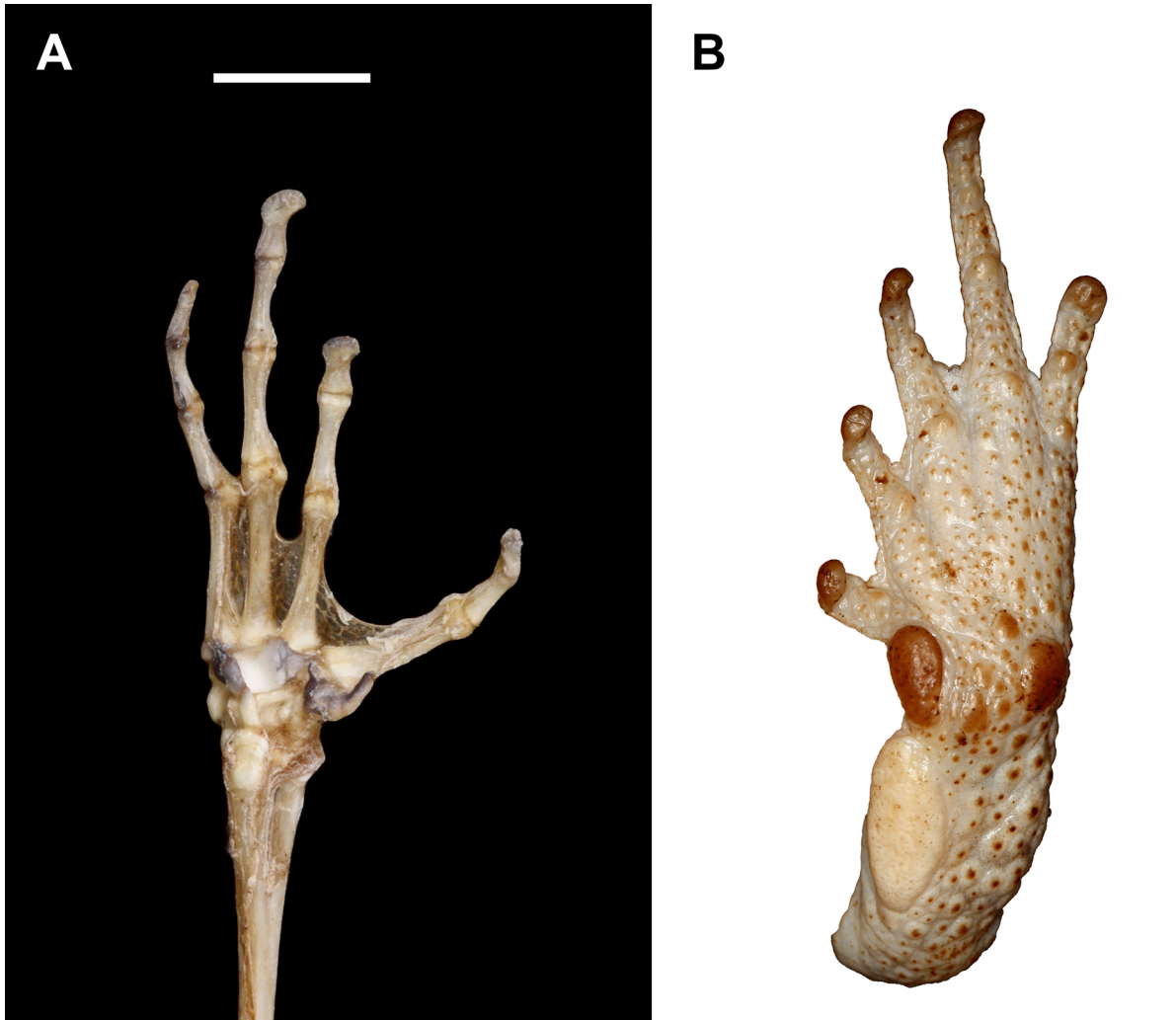


FIGURE 4. Ventral view of the right manus of *Peltophryne armata* **sp. nov.** (A; MNHNSD 23.3218) with the T-shaped terminal phalanges. Ventral view of the left foot of *P. armata* **sp. nov.** (B; holotype) showing tarsal fold and basal webbing. Scale bars 5 mm. Photographs by MALT.

Color in preservative. Dorsum and limbs light tan, with diffuse charcoal-gray vermiculations, and dark blotches as described above (in life); head of a darker brownish color; venter grayish.

Variation. Cephalic crests slightly variable in extension, especially the supraorbitals, and to a lesser extent, the postorbitals and preorbitals. A female (MCZ A-149840) has significantly shorter crests than those in the rest of the series. Apparent sexual dimorphism: males are smaller (SVL up to 78 mm, versus 85.7 mm in females) and with more developed cephalic crests. Dichromatism: males with bright yellow dorsal ground coloration, females with a more tan yellow to light ochre color. In most males, the intersection of supraorbitals and preorbitals is convex, directed anteriorly in the form of horns in dorsal view; parietal crests generally prominent, inconspicuous in one side in some specimens (MCZ A-149839 and MCZ A-149843), and inconspicuous in both sides in others (MNHNSD-23.1376–77). An elevated, prominent knob is at the posterior edge of the supratympanic crest in MNHNSD-23.1378 and MCZ A-149839. The interorbital area has either continuous or discontinuous ridges and

bony tubercles. In some specimens the snout is nearly rounded in profile. The tympanum is oval to nearly rounded in all specimens except in female MCZ A-149840 in which it is nearly rectangular. Description of coloration and pattern in life of the holotype consistent with rest of males in series. A male (MCZ A-149843) with broader black vermiculations and blotches. Some specimens have single orange spots on the head (MCZ A-149840, MNHNSD-23.1375). Males turned dark brown (dorsal surfaces) when in concealed places, and changed to a bright yellow when exposed. Venter and throat are pattern-less cream-white in all specimens.

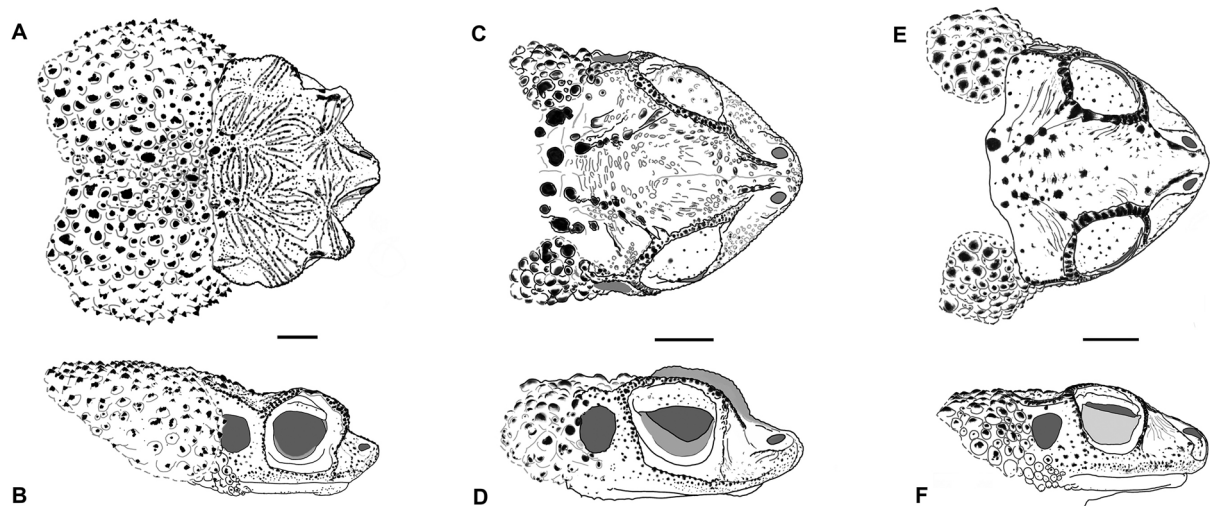


FIGURE 5. Crest geometry, sculpturing, cutaneous texture and shape of the head of *Peltophryne armata* sp. nov. (A–B [dorsal and profile views, respectively]; MCZ A-149839), *P. lemur* (C–D; KU 288691), and *P. guentheri* (E–F; MNHNSD 23.1396). Parotoid glands are delimited by gray dashed lines. Scale bars 5 mm. Illustrations by MALT.

Juveniles. Metamorphs of *Peltophryne armata* measure ~9.5 mm in SVL (Fig. 7A), and are distinct from those of *Peltophryne guentheri* in having a dark chocolate brown dorsal ground color with light salmon-colored blotches in the supra- and post-tympanic areas and in the sacral area (larger blotches) that extend laterally. An interorbital bar of same color extends at times as an inverted T towards the snout. Limbs are predominantly bone-colored with dark brown elbows, knees and dorsal surface of hands with a continuous dark stripe that crosses the thigh, shank, tarsus, and foot. Venter dark to rich brown, freckled with grayish-bone color. Toadlets (Fig. 7C) begin acquiring a green coloration replacing the dark brown dorsal ground color from a size of >20 mm SVL. Venter turns predominantly bone color with light brown to pinkish vermiculations. Hands and feet ivory-yellow, the palmar and plantar bases being brownish, with tubercles bright yellow. The parotoid glands, pointy snout (in profile), and cephalic crests become evident at such size range.

Vocalization. The advertisement call of *Peltophryne armata* is a series of clucking pulses (range 24–103 pulses, Tab. 2, Fig. 1A–C). The call sequences (n=12) are composed of trains of pulses, most of which contain subpulses within (Fig. 1C), characterized by a pattern of amplitude modulation of the Type II. Call duration range is 5.8–19.6s (\bar{x} = 16), and can bear 24–103 (\bar{x} = 78.3) pulses per call. Pulses (n=959) can bear 1–10 subpulses (\bar{x} = 4.1). The DF of calls was 1.2 kHz, although single component pulses in the beginning of call have DF of 0.86 kHz, and 5 components of 1.37 kHz (n=1). Intervals between calls range from 41 to 180s (\bar{x} = 93). Bandwidth 1.03–1.55 kHz (\bar{x} = 0.52). 90% bandwidth was measured at \pm .52 kHz in the power spectrum of a call -10 dB from the peak. Data are from a recording made of male MCZ A-149843 just before being collected at 2030 h, sitting next to (78 cm) and facing a water hole (already with tadpoles); air temperature was 24.2°C, and relative humidity 80.7%.

The release call (Fig. 1D) is a soft, three to four note bark-like staccato (n= 2): “peck peck peck”, of a duration of 0.5–0.6s; intervals between the pulsatile notes (n= 5) 0.20–0.28s (\bar{x} = 0.23); subpulses in a note 2–4; dominant frequency 1.31 kHz. When handled or pressed in refugia, individuals are capable of emitting a high-pitched “scream” as their distress call.

TABLE 2. Call analysis comparison of *Peltophryne armata* sp. nov., and *P. guentheri*. See above for abbreviations.

Acoustic Characters	<i>P. armata</i> sp. nov. n=12	<i>P. guentheri</i> n=12
Call Type	II	I
Call Duration (s)	16 ± 4.1 (5.9–19.6)	0.43 ± 0.02 (0.37–0.45)
Call Interval (s)	93 ± 38.2 (40.8–180.4)	0.91 ± 0.07 (0.79–1.10)
Number of Pulses	78.3 ± 23.7 (24–103)	36.3 ± 3.7 (27–39)
Pulse Rate	4.82 ± 0.47 (3.87–5.41)	83.7 ± 5.24 (72–88.4)
Subpulses	1–10	N/A
Dominant Frequency (kHz)	1.2	1.31 (1.12–1.31)

Distribution (Fig. 6A). Known only from the vicinity of the type locality, south of Las Mercedes in the southern slopes of the Sierra de Bahoruco north of the Barahona peninsula, Pedernales Province, bordering both the Sierra de Bahoruco and Jaragua national parks in the karst foothills (330–400 m) of the Sierra de Bahoruco.

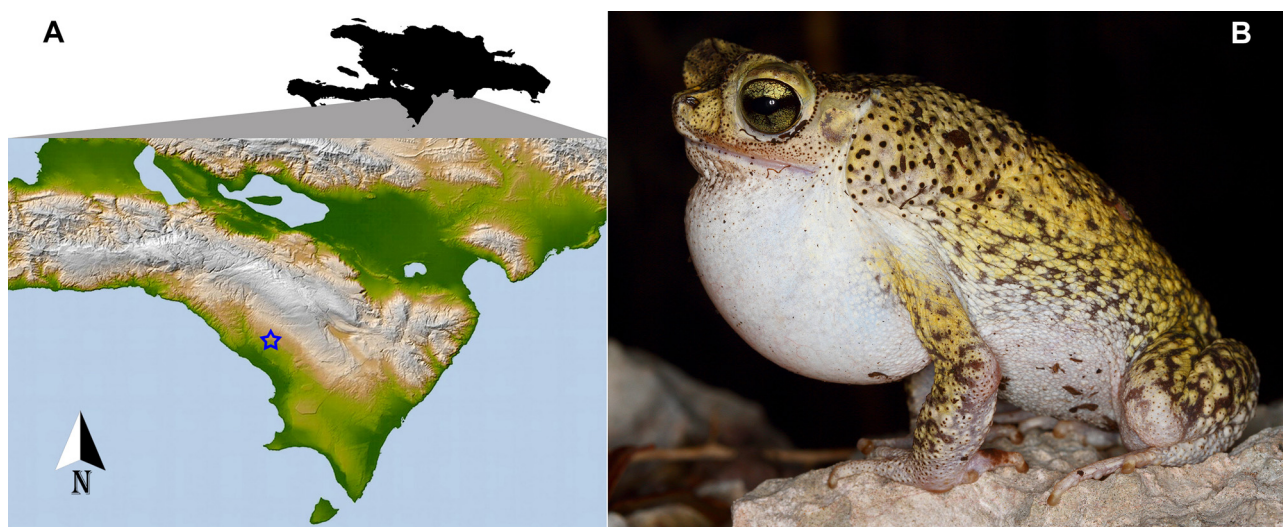


FIGURE 6. Map of Hispaniola (silhouetted), with the south-central section amplified, showing the type locality (star) of *Peltophryne armata* sp. nov., in between the Barahona Peninsula and the southern slopes of the Sierra de Bahoruco (A). Male calling at the type locality, not collected (B), photograph by MALT.

Natural history. The habitat of *Peltophryne armata* sp. nov. is semideciduous forest in the limestone-based southern slopes of the Sierra de Bahoruco. Males call (Fig. 6B) next to rain water-filled holes in the limestone of mean dimensions (n=4, with eggs) of 17.2x32.5 cm in diameter and 21.9 cm in depth, where paired strings of eggs are laid and the larvae develop. One clutch contained 420 eggs. Neither amplexus nor oviposition were observed. Several males vocalized in proximity to cavities in the limestone floor where they retreated when disturbed. Two of these males experienced quick metachrosis, having a bright yellow dorsal ground color when exposed but turning brown once inside such cavities. Males MCZ A-149839 and MCZ A-149843 called in concealment from holes. Males MNHNSD-23.1376 and MCZ A-149843 performed phragmosis while hiding in such cavities, and when pushed, used their heads as shields and inflated their bodies. One individual (MNHNSD-23.1376) emitted a distress call when removal was attempted; those males and others also observed entered their respective cavities by walking backwards. All males (except MCZ A-149841 and MNHNSD-23.1375) had supraorbital crests that were injured (bleeding), missing some of the keratin and dermal tissue. This was apparently caused by the sharp surfaces of the karst substrate. The highly developed crests likely serve as a protection from the harsh environment as well as from potential predators. Individuals inflate their bodies when handled and are capable of a sudden release of air as a distress call. Skin secretions, besides those expelled from the distinctive glandular areas, are spread over dorsal surface (including eyelids) and are of a yellowish-ochre color.

On the second night of the first documented breeding event, 23 August 2014, there were approximately 18 calling males, five of which were collected. Other anurans observed and frequently heard at the type locality were

the direct-developing frogs (terraranans) *Eleutherodactylus alcoae* and *E. pictissimus*. No other larvae-rearing anuran was observed using the breeding microhabitat at the same time as *Peltophryne armata*, although during an earlier visit (February 2013) to the area, tadpoles of the Hispaniolan Laughing Treefrog (*Osteopilus dominicensis*) were observed in a large hole nearby to the north of the type locality within a disturbed area, and that species has been heard calling at Las Mercedes village.

Toadlets larger than 20 mm (Fig. 7C) become greenish in dorsal ground color, retaining the large light blotches. This pattern matches the surrounding substrate, composed mostly of a limestone-based floor with scattered debris and the abundant herbaceous plant *Callisia repens* (Commelinaceae; Fig. 7B). Similarly, a species of pyrgomorphid grasshopper found near the type locality resembles the plant leaves in shape and color, probably for protection from predators (Perez-Gelabert 2000; Perez-Gelabert pers. comm.).



FIGURE 7. Metamorph (A) of *Peltophryne armata* sp. nov., scale bar equals 5 mm. A toadlet (C; ~23 mm SVL) and the predominant substrate found in its habitat during the rainy season (B). Photographs by MALT.

Tadpole. Lots MNHNSD 23.1425-A–T, 23.1426-A–D, 23.1427-A–D; Fig. 8A–E. Works on tadpoles of Hispaniola's native bufonids were lacking just until recently, when Incháustegui *et al.* (2014) offered the first descriptions of the tadpoles of *Peltophryne guentheri*. Rivero *et al.* (1980) provided a textual description of the tadpole of the Puerto Rican Crested Toad (*P. lemur*); Díaz & Cádiz (2008) presented tadpole descriptions for Cuban toad species with illustrations of body and mouth morphology, accompanied by a brief account on their biology. Earlier descriptions of Cuban toad tadpoles were for *P. longinasus* Stejneger (Ruíz García 1980), and *P. taladai* (Díaz *et al.* 2000).

Twenty eight tadpoles of *Peltophryne armata* in Gosner stages 31–42 were examined. Nineteen measurements (in mm), taken as in Altig & McDiarmid (2006), were made on specimen MNHNSD 23.1427-B, stage 36: 27.5 total length, 9.5 body length, 18.2 tail length, 2.9 tail muscle height at base, 2.6 tail muscle width at base, 2.1 maximum dorsal fin height and 1.7 maximum ventral fin height located 11.2 from body terminus, 6.7 body width located 6 from snout, 5.5 body height located 6.9 from snout, 1.1 eye diameter, 0.4 pupil diameter, 3.2 interorbital distance, 0.4 narial diameter, 1.5 internarial distance, 1.7 snout to naris, 3.2 snout to eye, 6.8 snout to spiracle, 1.4 naris to eye, and 3.2 transverse diameter of oral disc.

Body ovoid (dorsal view), slightly depressed (profile), and somewhat flat ventrally unless eggs have been ingested (globular, see below); eyes dorsal, directed dorsolaterally; snout long, protruding in a shark-like manner (profile); spiracle sinistral; vent tube medial; nostril nearer the eye than snout, of semi-circle ("D") shape, bearing a surrounding rim with a middorsal protuberance; guts thick and not covering most of the belly, easily visible through the largely translucent venter; belly globular after ingestion of eggs; tail musculature dorsally and ventrally convexed; conspicuous pustulose tubercles on dorsum from stage 41.

Oral disc anteroventral, emarginated, with submarginal papillae; a wide dorsal gap, and a very narrow ventral gap; labial tooth row formula 2(2)/3[1] (in most specimens the labial ridge of P-1 is interrupted medially, which may bear hillocks in between containing several teeth); second upper row of teeth (A-2) with a moderately wide

median gap; third lower row of teeth (P-3) very short, almost of same length of that of the ventral gap; jaw sheaths keratinized, its edges unserrated; upper jaw with a slight median indentation.

In life, the tadpole of *P. armata* (Fig. 8D) is light brown dorsally and nearly translucent lateroventrally, having a scattering of brown color laterally; dorsum mainly brown with some melanophores and golden iridophores becoming evident at advanced stages (>34), extending from nostrils to dorsal base of tail; venter translucent, with scarce scattered pigmentation; hindlimbs and dorsum with white to salmon color blotches (stages >38); iris very dark brown with some lighter brown venations.

The tadpole can be diagnosed by the following combination of characters: total length (TL) large (30.5 mm); light brown coloration; body slightly depressed; oral disc anteroventral; submarginal papillae present; a gap in P-1 present in most specimens (23 of different stages out of 28); unserrated jaw sheaths; long and pointed shark-like snout (in profile); fins and venter largely translucent; at advanced stages, presence of prominent dorsal tubercles, and dorsum and hindlimbs with large whitish patches. The gap in P-1 and the elongate snout appear to be unique among known tadpoles of *Peltophryne*.

On Hispaniola, the tadpole of *P. armata* differs from that of *P. guentheri* in its larger size (30.5 mm TL), while tadpoles of *P. guentheri* can reach up to 20.6 mm and have a reticulated dorsal pattern (Incháustegui *et al.* 2014). It also differs in having an oral disc in anteroventral position (ventral in *P. guentheri*; MALT pers. obs.) and a very short P-3, as well as a short ventral gap (wide P-3 and gap in *P. guentheri*; Incháustegui *et al.* 2014). The tadpole of the introduced *Rhinella marina* Linnaeus has a mostly black body and tail (Duellman 1978; Incháustegui *et al.* 2014). In the tadpole of the Puerto Rican *P. lemur* the gut is not visible through the belly (Rivero *et al.* 1980), being translucent in *P. armata*. In many aspects, the larval morphology of *P. armata* is more similar to that of *P. florentinoi* (no specimens examined in this study, but see Table 3), which is also the most distinctive of all other tadpoles of Cuban *Peltophryne* (Díaz & Cádiz 2008). Reproduction of *P. florentinoi* takes place in small holes in the karst filled with rainwater (Díaz & Cádiz 2008), which is the same and only situation in which *P. armata*'s tadpoles have been observed. The tadpole of *P. armata* is a facultative oophagous. Larvae (from Gosner stage 26) were observed feeding on conspecific eggs, larger larvae engulfing eggs whole while the smaller rasped upon them; larvae also fed on algae (*in situ*), and scavenged on conspecifics (*ex situ*).

TABLE 3. Tadpole comparison based on major morphological characters in *Peltophryne* (*sensu* Díaz & Cádiz 2008). *Very light patches present at advanced stages (in dorsum and hindlimbs). **Recorded from stage 41.

Characters	<i>P. armata</i> sp. nov.	<i>P.</i> <i>florentinoi</i>	In other Cuban spp.
1 Oral disc in anteroventral position (ventral in other [7] Cuban species)	X	X	
2 Submarginal papillae present	X	X	
3 Ventral gap very narrow (and of about same length as the P-3)	X	X	
4 Jaw sheaths unserrated (with a slight median notch in upper jaw sheath)	X	X	
5 Belly transparent	X	X	
6 Gut not compact nor covering much of the belly	X	X	
7 Olive-brown coloration, not very dark and almost homogeneous, with groups of iridophores	X*	X	
8 Prominent dorsal tubercles present at advanced stages	X**	X	
9 Body somewhat depressed (dorsoventrally)	X	X	X
10 Size large (TL >23 mm)	X	X	X
11 Tail musculature with dorsal and ventral margins convexed	X	X	X
12 Fins transparent or with moderate density of melanophores	X	X	X
13 Thin gap in A-2 (between two series of teeth rows that practically come into contact)		X	X

Eggs. Eggs with pigmented (melanic) animal pole; measured 1.8 mm of diameter (*P. guentheri* eggs measure ~1 mm). Egg strings paired, collected in the field on 23 August 2014, from several clutches in slightly different stages. A portion of these eggs were left for hatching, of which tadpoles developed to complete metamorphosis.

Suggested common name. Hispaniolan Armoured Toad

Etymology. The specific name is a Latin singular feminine nominative adjective meaning “armored,” in allusion to the highly developed and extended cephalic crests that cover most of the head, and to the massive parotoid glands bearing spinose keratinized tubercles.

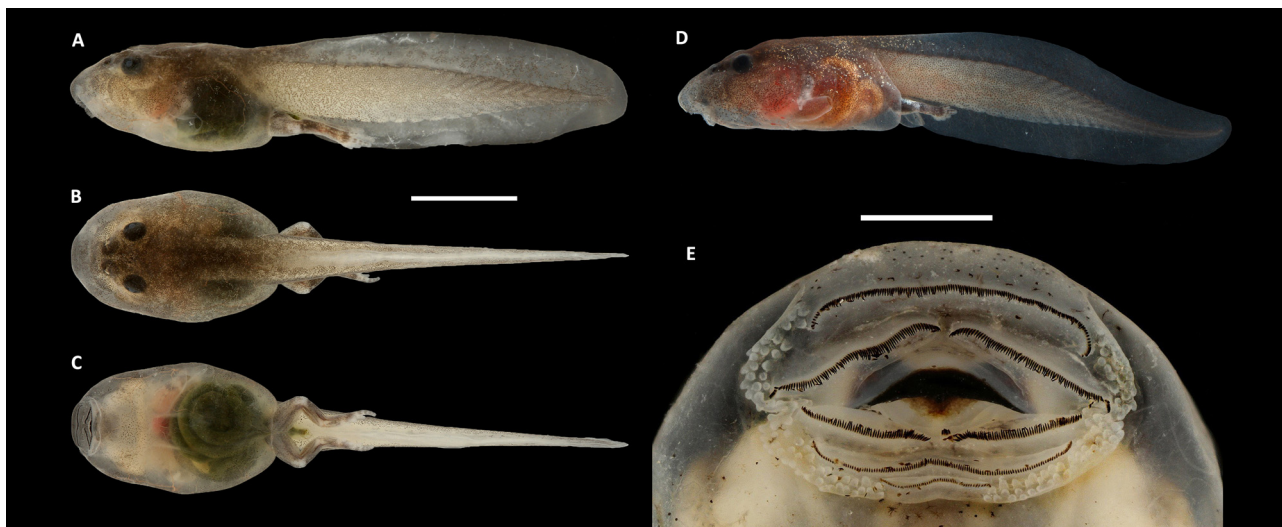


FIGURE 8. Tadpole of *Peltophryne armata* sp. nov.: profile view (A), dorsal view (B), and ventral view (C), scale bar equals 5 mm (stage 38, MNHNSD 23.1427-A). Captive live individual at stage 36, unvouchered, left for metamorphosis (D). Mouth parts (E), scale bar 1 mm (stage 37, MNHNSD 23.1425-B). Photographs by MALT.

Discussion

There is a recognized association between ecology and morphology (ecomorphs) in other Greater Antillean groups such as lizards of the genera *Anolis* (Williams 1972) and *Sphaerodactylus* (Thomas et al. 1992) and frogs of the genus *Eleutherodactylus* (Hedges 1989). Similar evolutionary convergence appears to have occurred in these Caribbean toads. For example, *Peltophryne armata* and *P. florentinoi* are not closest relatives (Fig. 2), but share a striking similarity in calling and oviposition site where the eggs are laid and the larvae develop, in rain-filled depressions in the karst. Both species have small ranges confined to semideciduous forest on limestone substrate. The most obvious, shared morphological features of adults are the wide interorbital distance and a poorly developed foot webbing (Moreno & Rivalta 2007). The larvae of the two species share more similarities with each other than with any of the known larvae of other *Peltophryne* species. These similarities are morphological characters (Tab. 3), as well as ecological and behavioral, with tadpoles of *P. armata* feeding on conspecific eggs and those of *P. florentinoi* feeding on other animal matter (chironomid and mosquito larvae; Díaz & Cádiz 2008).

In recognition of the convergence between *Peltophryne armata* and *P. florentinoi*, we place those species in a Karst-hole Ecomorph. Species in this ecomorph share wide interorbital distances and basal foot webbing, as well as a suite of larval traits (Tab. 3). We place the other large Cuban species (*P. fustiger* Schwartz, *P. peltocephala* Tschudi and *P. taladai*) in a Giant Ecomorph, primarily for their large size and terrestrial habits. A Riparian Ecomorph includes *P. fluviatica* and *P. longinasus*, two small species that occur in riparian habitats on Hispaniola and Cuba, respectively (Schwartz 1972). These two species share acuminate snouts, lack cephalic crests, and have a mostly green dorsal coloration (Schwartz 1972; Pregill 1981). Phylogenetic relationships (Fig. 2) support the karst-hole species as being convergent and the giant species as being a monophyletic group, although the unrelated *Rhinella marina* could be placed in the Giant Ecomorph as well. The riparian species are likely convergent, but no sequence data are yet available for *P. fluviatica*. The remaining species are mostly intermediate in size (*P. empusa* Cope, *P. gundlachi* Ruibal, *P. cataulaciceps* Schwartz [which is the smallest species], and *P. guentheri*; Henderson & Powell 2009), share well-developed cephalic crests, are of burrowing habits, and are explosive breeders (Díaz & Cádiz 2008; Henderson & Powell 2009), in which case they could be placed in a Burrowing Ecomorph.

Some amphibians are obligate burrowers for which they are morphologically specialized, while others are opportunistic burrowers that make use of natural holes, crevices, or tunnels made by other animals (Wells 2007).

Burrowing has not been confirmed in *P. lemur*. For refugia, the species has been reported to use holes in rocks or other animals' burrows (Pacheco & Barber 2013). It is also known to use large ponds for breeding (not small holes in the karst). Its historical occurrence is not limited to the karst, being also found in grassy fields (Rivero *et al.* 1980; Moreno 1985; Henderson & Powell 2009), hence it is not placed in either the Burrowing or Karst-hole Ecomorph. However, more data on the relationships and ecological habits of Caribbean toads are needed before the ecomorph concept can be applied rigorously in this group. The hypertrophied parotoid glands converging middorsally in *P. armata* (Fig. 3, Fig. 5A–B) seem to be an unusual trait at least among Neotropical bufonids. In *Peltophryne*, the most common relative size and shape of the parotoid glands are those found in *P. guentheri* (i.e. short, Fig. 5E–F), an exception being *P. longinasus*, which has elongate glands expanded dorsally (Ruibal 1959), and in both patterns the glands are widely separated medially. A poorly developed foot webbing is seen in both *P. florentinoi* (Moreno & Rivalta 2007) and *P. armata*, which is likely a result of atrophy due to the limited water volumes available at the specialized oviposition sites where the two species are known to breed.

Pramuk (2002) listed the "suborbital crest" to be present (herein called infraorbital crest) in all *Peltophryne*, however, at least externally, that crest is merged with maxillary crest in the related taxa *P. armata* and *P. lemur*. If present at all, an infraorbital crest appears only barely noticeable posteroventrally to the orbital cavity and ventrally to the pretympenic crest (or as a brief extension of the latter). A more prominent, flared maxillary crest is visible continuous to the snout.

The Type II pattern of amplitude modulation that characterize the advertisement call of *P. armata* has also been described for the large-bodied Cuban species (Alonso & Rodríguez 2003; Hernández *et al.* 2010) and is also seen in *P. armata*'s closest relative *P. lemur*, differing from the known (examined) advertisement calls of Hispaniolan species (*P. guentheri*), which fit the Type I pattern, although similar in the dominant frequency (above 1 kHz; Alonso & Rodríguez 2003; Alonso 2011; MALT pers. obs.). Despite sharing the same type pattern with the large-bodied Cuban toads, the dominant frequencies above 1 kHz of the advertisement calls of *P. armata* and *P. lemur* differ from the lower pitched calls (below 1 kHz) of the former group (Alonso & Rodríguez 2003; Hernández *et al.* 2010), a feature that is known to be correlated to male body size in bufonids (Martin 1972; Alonso & Rodríguez 2003; Alonso & Rodríguez 2005).

Conservation concerns. Several habitats in the southern slopes of the Sierra de Bahoruco face serious threats. Among the threats in the vicinity of the type locality are the forest clearing (slash and burn) for intensive agriculture and livestock farming, habitat alteration by selective wood harvesting, and more directly, the use of water-filled holes (the species' only known breeding microhabitat) by free roaming cattle for drinking and by farm workers as their main water source (there are no rivers or reservoirs in the general area). Also, road reconstruction and currently inactive bauxite mining operations in the proximity of the type locality are considered potential threats. We recommend that this species be considered critically endangered (CR) because of its small distribution and these threats to its survival. The first specimens in the series were found at the edge of a large land plot where the agricultural technique of slash and burn were just applied. The introduced Cane Toad (*Rhinella marina*) has been observed 1.5 km NE from the vicinity of the type locality of *Peltophryne armata*. Its distribution in the area seems to be limited to human disturbance, since it has been found in the outskirts of the village of Las Mercedes where the habitat is highly disturbed with extensive farms and a currently inactive bauxite mine. Cane toads have also been observed along the Alcoa road, next to newly deforested areas. This species represents a potential competitor in an apparently limited breeding microhabitat available for the new species.

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APPENDIX I. Specimens examined.

Peltophryne armata (skeleton): Dominican Republic: Pedernales: 1.6 km S of Las Mercedes, MNHNSD 23.3218. *Peltophryne cataulaciceps*: Cuba: Isla de la Juventud: near Santa Fe, Isle of Pines, MCZ A-30860. *Peltophryne empusa*: Cuba: Pinar del Río: near Herradura, MCZ A-2833, 98685–89; Camaguey: Finca Sta Teresa 9 km W Camaguey, MCZ A-30547; between Camaguey + Sierra de Cubitas, MCZ A-30548; Granma: 32 km SW of Victoria de las Tunas, MCZ A-31602–12. Isla de la Juventud, Isle of Pines, MCZ A-3730–35; MacKinley, Isle of Pines W.I., MCZ A-4169; Isle of Pines: Nuevo Gerona, MCZ A-6068. *Peltophryne fluviatica*: Dominican Republic: Santiago Rodríguez: 1.8 mi W Los Quemados, MCZ A-84611–20; KU263856–81, 263883–87, 264189–93; 2 km E Santiago Rodríguez, KU 263888. *Peltophryne fustiger*: Cuba: Pinar del Río: San Diego de los Baños, MCZ A-2838; Habana: S. Antonio de los Baños, MCZ A-3723; Pinar del Río: Banas San Vicente, MCZ A-19905. *Peltophryne guentheri*: Dominican Republic: Monte Cristi: Copey, MNHNSD 23.3–9, 23.1408–18; Carbonera, MNHNSD 23.1405–07; Santiago Rodríguez: Río Gurabo, MNHNSD 23.1381, KU 264154–56, 264158–59; Elías Piña: Bánica, MCZ A-30739 (skeleton); Independencia: Postrer Río, MNHNSD 23.1382–94, 23.1399–1404; Tierra Nueva, MNHNSD 23.1396–98; Boca de Cachón, MNHNSD 23.1419–22; Barahona: La Lista, MNHNSD 23.1395; Peravia: 11 km S Los Ranchitos, MNHNSD 23.2 (A-B); Baní, MNHNSD 23.1423. As "*Peltophryne fracta*": La Altagracia: Las Limas, Matachalupe, MNHNSD 23.1; Santana, MNHNSD 23.919–20; Rancho de Mana, MNHNSD 23.1424; 8.5 km E La Enea, MCZ A-84601; 6.6 km W Higüey, MCZ A-84603–06. *Peltophryne gundlachi*: Cuba: Camaguey: Between Camaguey + Banao, MCZ A-30552–81; Habana: Havana, MCZ A-19394; Habana: Marianao, MCZ A-31061; Pinar del Río: near Herradura: MCZ A-30582–84; Granma: Finca La Bahía near Birama, 32 km SW Victoria de las Tunas, MCZ A-31613–14, 31616–17. Isla de la Juventud: near Santa Fe, Isle of Pines, MCZ A-30859, 30861–63. *Peltophryne lemur*: Puerto Rico: Bayamón, MCZ A-30614–15; Guánica: Tamarindo Section, KU 288689–91, (larvae) KU 288685–88, KU 288692–98; British Virgin Islands: Virgin Gorda Island: Spanish Town, KU 264172–73; Virgin Gorda BWI, MCZ A-4099. *Peltophryne longinasus*: Cuba: Sancti Spiritus: 3–4 km from Topes de Collantes, Sierra de Trinidad, MCZ A-31620–23; Cienfuegos: Cumanayagua, Mina Carlota, MCZ A-11084, 11086, 11090, 11101–02. *Peltophryne pectocephala*: Cuba: Holguín: Banes, MCZ A-13238; Granma: Finca La Bahía near Birama, 32 km SW Victoria de las Tunas, MCZ A-31631; Guantánamo: US Naval Base, MCZ A-37354, SBH 162000; Santiago de Cuba: 1.5 km WSW of La Tabla, SBH 191380. *Peltophryne taladai*: Cuba: Santiago de Cuba: La Esmajagua (SW slope of Pico Turquino), SBH 190537; Guantánamo: 2 km N of La Municipión, SBH 191067. *Rhinella marina* (skeletons): México: Guerrero: 2 km E Tixtla, KU 117380; Nicaragua: Rivas: Isla Ometepe, Moyogalpa, KU 84937.

APPENDIX II. Sequences used in molecular analyses.

GenBank accession numbers are listed for each of the three genes (12S, 16S, cyt b). Analyses were rooted with *Rhaebo haematiticus* MVZ:164805 (HM563815, HM563857, HM563930).

Peltophryne armata sp. nov.: Dominican Republic. Pedernales: 1.6 km S Las Mercedes: SBH 274939/MALT 85 (genetic sample 1; GenBank accessions KX788965, KX788939, KX788991), SBH 274940/MALT 90 (genetic sample 2; KX788964, KX788938, KX788990), SBH 274941/MALT 91 (genetic sample 3; KX788962, KX788936, KX788988), SBH 274942/MALT 92 (genetic sample 4; KX788963, KX788937, KX788989).

Peltophryne longinasus dunni: Cuba. Sancti Spiritus: Pico de Potrerillo, N slope (ca. 3 km SSE Topes de Collantes): SBH 266461/JPB 15620 (KX788970, KX788944, KX788996).

Peltophryne empusa: Cuba. Granma: ca. 3 km SW Bartolome Maso (0.9 km SW Rio Yara Bridge): SBH 193517 (KX788967, KX788941, KX788993).

Peltophryne fustiger: Cuba. Pinar del Río: Soroa: SBH 172586 (KX788969, KX788943, KX788995).

Peltophryne guentheri: Dominican Republic. Barahona: 12.2 km W Cabral: SBH 101227 (genetic sample 7; KX788974, KX788948, KX789000), SBH 101174 (genetic sample 12; KX788961, KX788935, KX788987). Dajabón–Monte Cristi: Carbonera: SBH 274943/MALT 106 (genetic sample 5; KX788957, KX788931, KX788983), SBH 274944/MALT 108 (genetic sample 6; KX788960, KX788934, KX788986). Independencia: Postrer Río: SBH 274936/MALT 62 (genetic sample 10; KX788959, KX788933, KX788985), SBH 274937/MALT 63 (genetic sample 11; KX788956, KX788930, KX788982), SBH 274934/MALT 60 (genetic sample 13; KX788954, KX788928, KX788980), SBH 274935/MALT 61 (genetic sample 14; KX788955, KX788929, KX788981). La Altagracia (previously considered "*P. fracta*" by distribution): Rancho de Mana, 5.8 km NNW Santana: SBH 274946/MALT PF1 (genetic sample 2; KX788950, KX788924, KX788976), SBH 274947/MALT PF2 (genetic sample 3; KX788951, KX788925, KX788977); Rancho, 5.4

km NNW Santana: SBH 274938/MALT 84 (genetic sample 1; KX788949, KX788923, KX788975). Peravia: Baní: SBH 274945/MALT 126 (genetic sample 4; KX788958, KX788932, KX788984). Valverde: Río Gurabo (Furnia): SBH 274932/MALT 48 (genetic sample 8; KX788952, KX788926, KX788978); Río Gurabo (Gurabo Adentro): SBH 274933/MALT 49 (genetic sample 9; KX788953, KX788927, KX788979).

Peltophryne gundlachi: Cuba. Granma: ca. 3 km SW Bartolome Maso (0.9 km SW Rio Yara Bridge): SBH 193518 (KX788971, KX788945, KX788997).

Peltophryne lemur: United States. Puerto Rico: specific locality unknown: SBH 190657 (KX788966, KX788940, KX788992).

Peltophryne peltoccephala: Cuba. Santiago de Cuba: 1.5 km WSW Santiago de Cuba: SBH 191380 (KX788972, KX788946, KX788998).

Peltophryne taladai: Cuba. Guantanamo: 7.7 km N Imias: SBH 191345 (genetic sample 1; KX788973, KX788947, KX788999). Santiago de Cuba: La Esmajugua (SW slope of Pico Turquino): SBH 190537 (genetic sample 2; KX788968, KX788942, KX788994).