

TWO NEW SPECIES OF *PHYSALAEMUS* (ANURA: LEPTODACTYLIDAE) FROM WESTERN ECUADOR

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ABSTRACT: We describe two new species of the leptodactylid frog genus *Physalaemus* from the lowlands of western Ecuador. Both species belong to the *P. pustulosus* species group. They differ from other group members, except *P. coloradorum*, in their smaller size. They can be distinguished from *P. coloradorum* by their less tuberculate dorsal skin and a more depressed loreal region. The new species differ from each other markedly in advertisement call. Although the ranges overlap, body size, flank gland length, and parotoid gland length (relative to snout-vent length) are also significantly different. Overall the new species are similar in color patterns and body shape; they are difficult to diagnose from each other with morphological characters.

Key words: Anura; Ecuador; Leptodactylidae; New species; *Physalaemus montubio*; *Physalaemus pustulatus*; *Physalaemus pustulosus* group; *Physalaemus randi*

THE *Physalaemus pustulosus* group has been used as a model for the study of the evolution of animal communication systems and sexual selection (Greenfield and Rand, 2000; Rand and Ryan, 1981; Rand et al., 1992; Ryan, 1980, 1985; Ryan et al., 1990; Ryan and Rand, 1990, 1993, 1995). It contains four described species: (1) *P. coloradorum* Cannatella and Duellman, 1984; (2) *P. petersi* (Jiménez de la Espada, 1872); (3) *P. pustulatus* (Shreve, 1941); and (4) *P. pustulosus* (Cope, 1864). Cannatella et al. (1998) treated *P. freibergi* Donoso Barros, 1969 (type locality "Runerrabaque, Río Beni, Bolivia") as a species distinct from *P. petersi*. Molecular and morphological synapomorphies render support to the monophyly of the group (Cannatella and Duellman, 1984; Cannatella et al., 1998).

Despite the extensive knowledge accumulated on the behavior and ecology of the group (especially *P. pustulosus*), its taxonomy is still incompletely resolved, partly because the inventories of the amphibian fauna from western Ecuador, the most speciose region for the group, are yet to be completed. Calls recorded and specimens collected in February 2002 and March 2003 have clarified the distinctiveness of two species from that region, which we describe herein.

METHODS

Morphological terminology follows Lynch and Duellman (1997). Osteological characters used in the diagnosis were examined in clear- and stained specimens and are defined in Cannatella and Duellman (1984) and Cannatella et al. (1998). Sex was determined by the presence of nuptial pads or by gonadal inspection. Snout-vent length is abbreviated as SVL throughout. Examined specimens (listed in the type series and Appendix I) are housed in the California Academy of Sciences (CAS); Museo de Zoología de la Pontificia Universidad Católica del Ecuador (QCAZ); Museum of Comparative Zoology, Harvard University (MCZ); Museum of Vertebrate Zoology, University of California Berkeley (MVZ); and Natural History Museum of The University of Kansas (KU).

Recordings were made with a Sennheiser™ ME-67 directional microphone and a Sony™ WM-D6C analog tape recorder. Calls were analyzed using Canary™ 1.2.1 software (Charif et al., 1995) at a sampling frequency of 22.1 KHz and a frequency grid resolution (FTP) = 8192. We measured nine call parameters: call length (time from beginning to end of call), rise time (time from the beginning of the call to the point of maximum amplitude), interval between calls (time between the end of one call and the beginning of the next call), duration of the first component (time from beginning of the first pulse to the end of the

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TABLE 1.—Descriptive statistics for morphometric measurements of *Physalaemus montubio* from Puerto Rico (Provincia de Manabá) and *P. randi* (from Cerro Masvale and Puerto Inca, Provincia del Guayas). Mean \pm SD are given with range below. Bold figures are combined for males of both populations of *P. randi*. Abbreviations are SVL = snout-vent length; DW = dorsum width; TL = tibia length; FL = femur length; AL = arm length; HL = head length; HW = head width; EN = eye-nostril distance. All measurements are in mm.

	SVL	DW	TL	FL	AL	HL	HW	EN
<i>P. montubio</i> (males, $n = 27$)	20.76 \pm 0.99 18.67–22.56	7.60 \pm 0.44 6.72–8.77	9.74 \pm 0.53 8.40–10.71	9.41 \pm 0.64 8.01–10.46	4.95 \pm 0.33 4.39–5.63	6.58 \pm 0.35 5.81–7.43	6.93 \pm 0.34 6.31–7.82	2.13 \pm 0.21 1.72–2.60
<i>P. randi</i> ($n = 33$)	17.11 \pm 0.68	6.53 \pm 0.30	8.09 \pm 0.33	7.8 \pm 0.32	4.19 \pm 0.29	5.68 \pm 0.27	5.84 \pm 0.33	1.75 \pm 0.14
Cerro Masvale (males, $n = 29$)	17.05 \pm 0.69 15.80–18.65	8.28 \pm 0.36 7.53–9.27	8.07 \pm 0.35 7.38–8.73	7.81 \pm 0.34 7.09–8.34	4.15 \pm 0.28 3.50–4.62	5.66 \pm 0.27 5.09–6.40	5.86 \pm 0.34 5.21–6.79	1.72 \pm 0.13 1.39–2.00
Cerro Masvale (females, $n = 4$)	18.81 \pm 0.66 18.26–19.71	6.83 \pm 0.32 6.52–7.16	8.19 \pm 0.17 8.00–8.34	8.44 \pm 0.12 8.30–8.53	4.52 \pm 0.25 4.27–4.78	5.87 \pm 0.37 5.45–6.09	5.90 \pm 0.2 5.77–6.13	1.91 \pm 0.16 1.72–2.01
Puerto Inca (males, $n = 4$)	17.58 \pm 0.29 17.26–17.95	6.52 \pm 0.24 6.26–6.80	8.22 \pm 0.16 8.05–8.37	7.78 \pm 0.13 7.59–7.87	4.46 \pm 0.27 4.18–4.76	5.87 \pm 0.22 5.69–6.20	5.72 \pm 0.23 5.50–5.96	1.93 \pm 0.07 1.83–2.00

last pulse of the first component of the call, expressed as percentage of call length), call repetition rate (number of calls/min), fundamental frequency of the first component (frequency of the first harmonic over the duration of the first component of the call), fundamental frequency of the second component, (frequency of the first harmonic over the duration of the second component of the call), number of harmonics, and number of pulses of the first component. Original recordings are deposited in the audio archive of the QCAZ.

Shape and size of parotoid glands and flank glands were determined by making a middorsal incision to pull up the skin for inspection of its internal surface. Gland length was measured from the anterior to the posterior edge of the gland. Dorsum width was measured at the level of the insertion of the arms, perpendicularly to the dorso-ventral and antero-posterior axes, at the longest distance between the left and right margins of the dorsum. Femur length was measured from the vent to the distal edge of the flexed knee. Arm length was measured from the posterior edge of the thenar tubercle to the posterior end of the flexed elbow. Other measurements follow Duellman (1970). Measurements were made with Fowler digital calipers (nearest 0.01 mm) from specimens fixed in 10% formalin and preserved in 70% ethanol. To eliminate transcription errors, the calipers were connected to a computer and readings were automatically entered into a spreadsheet by pressing an attached foot pedal. Because of small sample sizes for females, most morphometric comparisons were only made among adult males. Only well-preserved specimens were measured (Simmons, 2002; Table 1). Principal Components Analysis (PCA) was applied to SVL, head length, head width, eye-nostril distance, femur length, tibia length, arm length, and dorsum width. Because of differences in body size among species, we removed the effect of size by regressing all morphological variables against SVL, retaining the residuals for the PCA (Vitt et al., 2000). Minitab 10 Xtra (Minitab, 1995) was used to perform the PCA.

Climate parameters for localities were estimated from digital climate maps compiled by C. Graham, using ArcMap 8.2 with the SpatialAnalyst extension (ESRI, 2001).

RESULTS

Physalaemus randi sp. nov.

Holotype.—QCAZ 19563 (field no. SCPUCE 4885; Fig. 1), adult male from Ecuador, Provincia del Guayas, Cerro Masvale (2.394° S, 79.642° W), 92 m, collected by D. C. Cannatella, L. A. Coloma, A. Holloway, and S. R. Ron on 20 February 2002.

Paratopotypes.—QCAZ 19558, 19560, 19563–66, 19569–71, 19573–79, 19580, 19582, 19585–88, 19590–91, 19597, 19752–55, adult males; 19570, 19583 (clear-and-stained), 19584, 19589, adult females. Collected by D. C. Cannatella, L. A. Coloma, A. Holloway, and S. R. Ron on 20 February 2002.

Paratypes.—Ecuador: Provincia del Guayas: 11 km N Cerro Masvale, on the road to Virgen de Fátima (2.300° S, 79.639° W), 40 m, QCAZ 23461, 23523, adult males collected by M. R. Bustamante, I. G. Tapia, and S. R. Ron on 23 March 2003; Puerto Inca (2.536° S, 79.550° W), QCAZ 23489–92, adult males, collected by M. R. Bustamante and S. R. Ron on 20 March 2003; “10 mi E Guayaquil on road to Quito,” MVZ 77184, adult male, collected by T. J. Papenfuss in 4 March 1964; El Piedrero, 15 km E from El Triunfo on the road to Pallatanga, QCAZ 11638, adult male, 11639, adult female, collected by N. Acosta-Buenaño on 21 November 1997.

Diagnosis.—A member of the genus *Physalaemus* and the *P. pustulosus* group, sensu Cannatella and Duellman (1984) and Cannatella et al. (1998); see Remarks. *Physalaemus randi* is characterized by: (1) SVL 17.10 mm in males (range 15.45–18.65; $n = 35$), 18.52 mm in females (range 17.34–19.71; $n = 5$); (2) skin on dorsum bearing numerous tubercles; (3) snout rounded in dorsal and lateral views; (4) vomerine teeth and odontophores absent; (5) maxillary teeth present; (6) parotoid glands present, mean length = 2.03 mm ($n = 11$, SD = 0.51; 5.8–17.0% of SVL); (7) flank glands present, mean length = 4.21 mm ($n = 11$, SD = 1.13; 11.7–32.1% of SVL); (8) tarsal tubercle absent; (9) nuptial pads present; (10) finger I shorter than II; (11) tympanic annulus evident, concealed dorsally, tympanic membrane not tuberculate; (12) dentigerous process of the vomer thin and spikelike.

Physalaemus randi differs from the much larger *P. pustulosus*, and *P. petersi* by the

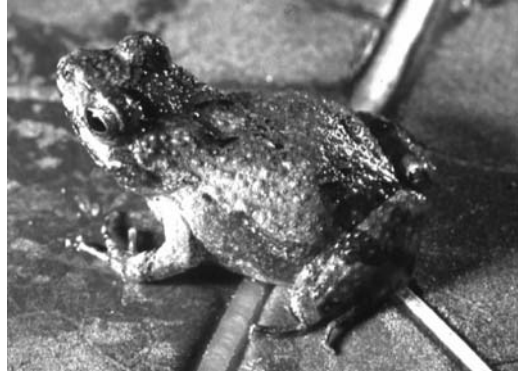


FIG. 1.—Dorsolateral view of the holotype of *Physalaemus randi*, QCAZ 19563 (adult male from Cerro Masvale, Ecuador).

absence of a tarsal tubercle and the presence of teeth in the maxilla. *Physalaemus coloradurum* has a different advertisement call (Ryan and Rand, 2001), more tuberculated skin than *P. randi*, and a loreal region nearly vertical (slopes gradually towards the labial region in *P. randi*). *Physalaemus pustulatus* is larger than *P. randi* (non-overlapping adult size, male SVL range 25.17–29.88 mm [$n = 31$], and 15.45–18.65 mm, respectively) and has an advertisement call approximately twice the duration with a lower fundamental frequency (Table 2 and Figs. 2 and 3). *Physalaemus randi* is most similar to *P. montubio* sp. nov. Both species differ markedly in advertisement call (Fig. 2, Table 2). The call of *P. randi* has longer duration (approximately three times that of *P. montubio*; Table 2), longer rise time (approximately five times that of *P. montubio*), lower call repetition rate (approximately half that of *P. montubio*) and a longer sequence of amplitude-modulated pulses at the beginning of the call (11–15 in *P. randi*, 2–5 in *P. montubio*). *Physalaemus montubio* is larger than *P. randi* (male mean SVL = 20.59 mm [$n = 38$, SD = 1.26] and 17.10 [$n = 35$, SD = 0.74], respectively; $t = 14.21$, $df = 71$, $P < 0.0001$). *Physalaemus montubio* has proportionally shorter flank and parotoid glands than *P. randi* (Mann–Whitney U for flank gland length/SVL = 54, $P = 0.014$; U for parotoid gland length/SVL = 51, $P = 0.010$; 11 *P. randi* vs. 21 *P. montubio*, all males; Fig. 4) and proportionally narrower dorsum (Mann–Whitney U for dorsum width/SVL = 209,

TABLE 2.—Call parameters of *Physalaemus randi*, *P. montubio*, and *P. pustulatus* from western Ecuador (ranges are in parenthesis). The calls of *P. montubio* and *P. randi* consist of one note with an amplitude-modulated portion (“first component”) followed by a nearly pure tone with a frequency sweep (“second component”). Specimen’s catalog no. at the Museo de Zoología de la Pontificia Universidad Católica del Ecuador (QCAZ) are shown. Unless otherwise indicated, samples sizes (number of calls) are: QCAZ 19752 = 17, QCAZ 23462 = 16, QCAZ 19517 = 13, QCAZ 19524 = 13, QCAZ 19518 = 10. Abbreviations are MFF = mean fundamental frequency, FC = first component, SC = second component. See text for details.

Specimen	Mean duration of each call (ms)	Call repetition rate (notes/min)	Mean interval between calls (ms)	Rise time (ms)	Mean No. of harmonics	MFF of the FC (KHz)	MFF of the SC (KHz)	Mean No. of pulses in FC
<i>P. randi</i>								
(QCAZ 19752)	241 (231–247)	114.3	284 (232–355)	68 (56–93)	4.0	1.314 (1.141–1.351; n = 9)	0.997 (0.985–1.006)	14.53 (14–15)
<i>P. randi</i>								
(QCAZ 23462)	246 (225–267)	120.5	252 (202–340)	75 (57–89)	5.1 (5–6)	1.358 (1.305–1.434)	0.925 (0.915–0.936)	13.00 (11–15)
<i>P. montubio</i>								
(QCAZ 19517)	82 (79–86)	218.2	193 (176–216)	14 (8–24)	5.5 (5–6)	1.369 (1.308–1.448; n = 5)	1.081 (1.071–1.087)	2.92 (2–5)
<i>P. montubio</i>								
(QCAZ 19524)	68 (63–76)	227.3	196 (138–314)	14 (10–29)	4.0	1.336 (1.114–1.550)	0.977 (0.931–1.001)	2.40 (2–3)
<i>P. pustulatus</i>								
(QCAZ 19518)	475 (397–535)	17.4	2985 (1629–6553)	130 (114–139)	5.6 (5–6)	—	0.723 (0.650–0.744)	—

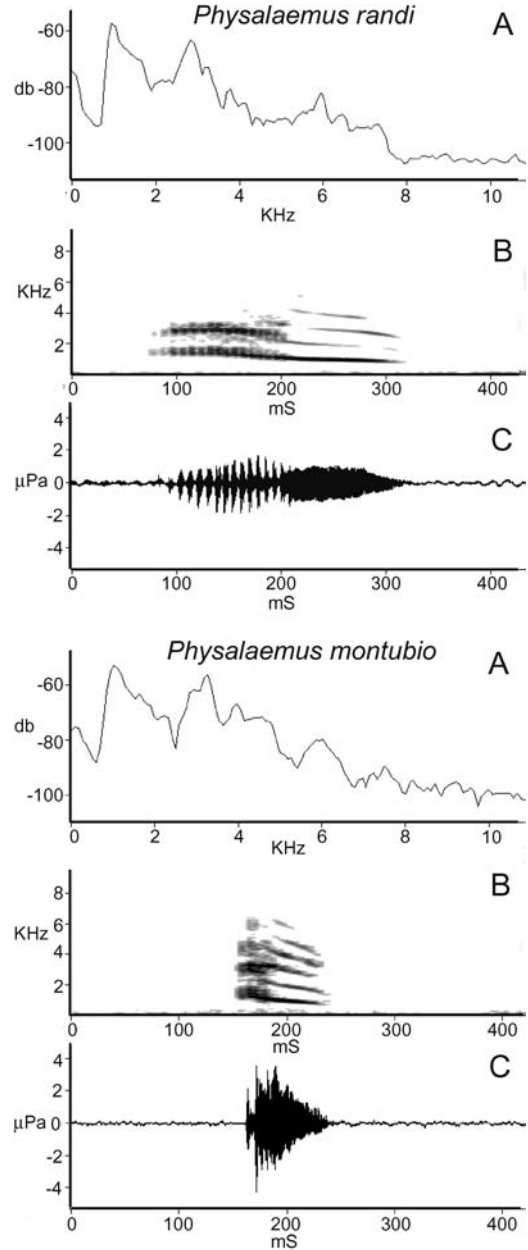


FIG. 2.—(A) Power spectrum, (B) sonogram, and (C) oscillogram of the advertisement call of *Physalaemus randi* (QCAZ 19752), and *P. montubio* (QCAZ 19517). The power spectra were measured along the entire duration of the calls.

$P < 0.001$; 35 *P. randi* vs. 26 *P. montubio*, all males).

Description of holotype.—Adult male, 17.55 mm SVL, foot length 8.46 mm, tibia length

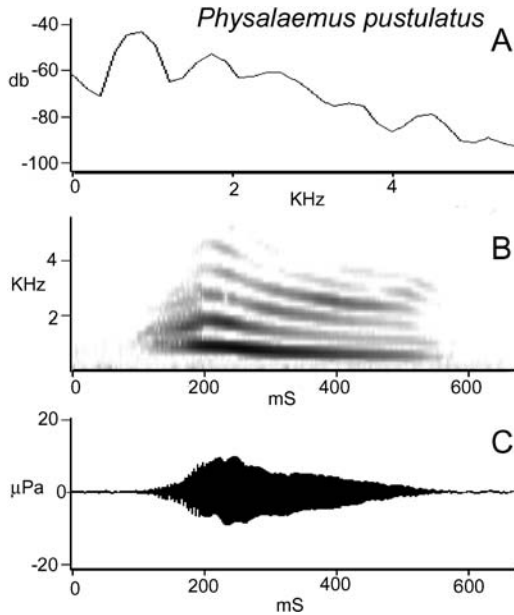


FIG. 3.—(A) Power spectrum, (B) sonogram, and (C) oscillogram of the advertisement call of *Physalaemus pustulatus* (QCAZ 19518). The power spectrum was measured along the entire duration of the call.

7.49 mm, femur length 7.96 mm, arm length 4.08 mm, head length 5.81 mm, head width 5.40 mm, eye–nostril distance 1.83 mm, dorsum width 6.24, body wider than head; diameter of eye twice diameter of tympanic annulus; tympanic membrane and tympanic annulus barely evident; tympanic annulus

ovoid, longer dorsoventrally; supratympanic fold absent; head slightly convex between orbits and flat in intercanthal region; snout rounded in profile and in dorsal view; nostrils slightly elevated, internarial region concave; canthus rostralis rounded; loreal region convex with concave depression extending from posterior border of nostril to ventral border of orbit.

Fingers without expanded discs; nuptial pad present, brown, divided in two portions, one covering thenar tubercle posteroventrally, other covering base of Finger I posterodorsally. Base of palmar tubercle slightly bifid, base of thenar tubercle ovoid; palmar tubercle less prominent than thenar tubercle; subarticular tubercles conical with round base; low supernumerary tubercle on Finger III between first and second subarticular tubercles; low supernumerary palmar tubercles present (Fig. 5). Webbing between fingers absent; relative lengths of adpressed fingers III > IV > II > I (Fig. 5). Toes without expanded discs; base of inner metatarsal tubercle and outer metatarsal tubercle ovoid; subarticular tubercles with round base, all subconical except for conical proximal subarticular tubercles; flat plantar supernumerary tubercles, longitudinally aligned; tarsal tubercle absent; webbing between toes absent; relative lengths of toes IV > III > V > II > I (Fig. 5).

Skin on dorsum bearing numerous round tubercles, those on scapular region aligned to

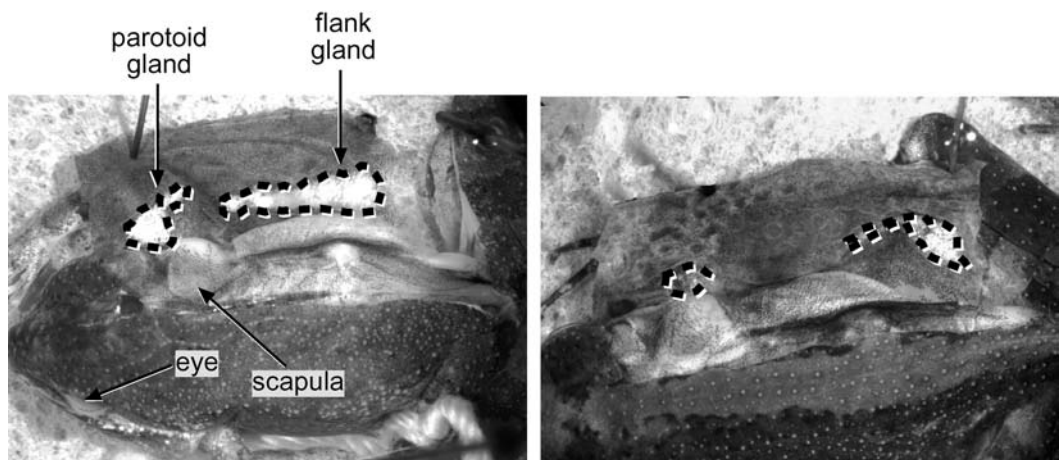


FIG. 4.—Dorsal view of dissected specimens showing flank and parotoid glands. The skin has been uplifted and its internal surface is showing. Left: *Physalaemus randi*, QCAZ 19579, SVL = 17.98 mm; right: *P. montubio*, QCAZ 19530, SVL = 21.96.

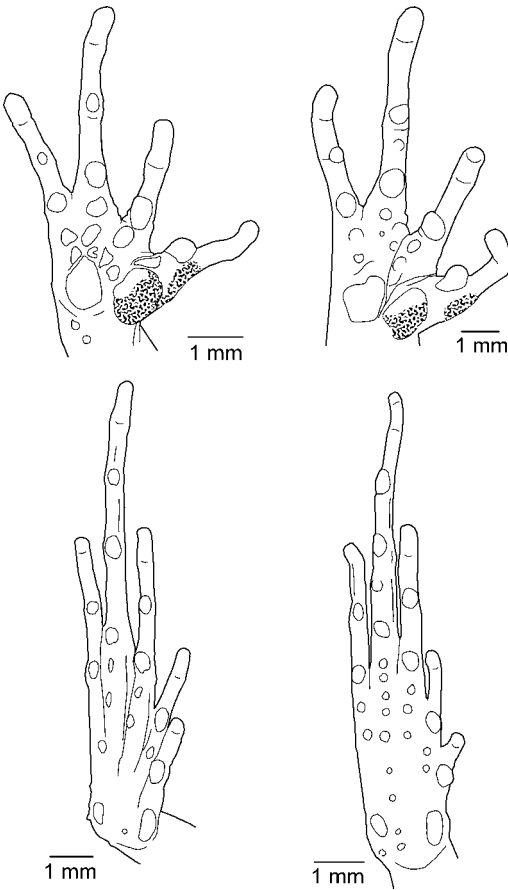


FIG. 5.—Ventral views of the hand and foot of the holotype of *Physalaemus randi* (left), QCAZ 19563 (adult male from Cerro Masvale, Ecuador) and holotype of *P. montubio* (right), QCAZ 19524 (adult male from Puerto Rico, Ecuador).

form a V-shaped mark with apex anterior (Fig. 6); skin on venter smooth. Tongue longer than wide; vomerine odontophores absent. Vocal slits present, parallel to margins of mandible. Deflated vocal sac forming folds on gular region and between posterior margin of tympanum and arm insertion.

Color of holotype in preservative.—Dorsum grayish brown with irregular dark patches; interorbital and intercanthal regions brown, with darker interorbital band; dorsal tubercles slightly lighter than background; margins of inverted V on scapular region black, light gray inside; cream middorsal line from posterior half of sacral region to vent; dorsal surfaces of arms and hindlimbs brown with dark brown transversal bars on exposed surfaces. Venter

cream posteriorly, with increasingly numerous minute brown spots towards throat, few spots between arms; undersides of head dark gray, becoming lighter posteriorly; cream midventral stripe from jaw margin to anterior half of abdomen, ill-defined towards end; ventral surfaces of limbs cream with numerous minute brown spots on outer edge; sides of head dark gray with two cream suborbital marks; flanks dark gray, with light brown flank glands.

Color of holotype in life.—(based on color photograph) Dorsum grayish brown with dark marks; margins of inverted V on scapular region black, light gray inside; interorbital and intercanthal regions brown; white labial line below eye and tympanum, tympanum dark gray; dark gray flanks; arms tan orange with darker forearms; exposed surfaces of thighs brown; dark brown transversal bars in exposed surfaces of forelimbs and hindlimbs. Dark brown iris.

Etymology.—The specific name *randi* is a noun in the genitive case and is a patronym for A. Stanley Rand, who has contributed to *Physalaemus* collections in western Ecuador, and most importantly, was a pioneer in behavioral studies of *Physalaemus*. His extensive research, in collaboration with M. J. Ryan, has greatly enriched the understanding of animal communication systems.

Variation.—There is extensive variation in the dorsal coloration of preserved specimens (Fig. 6). Most of the variation pertains to (1) number and distribution of dark marks, (2) hue of the background coloration, varying from light gray (QCAZ 19584; Fig. 6) to dark gray or dark brown (QCAZ 19575), (3) abundance and arrangement of tubercles (all lighter than the background), and (4) relative longitude of the cream-dorsal line, which is continuous or interrupted and varies between being restricted to the sacral region (e.g., holotype) and almost reaching the head (e.g., QCAZ 19580). In some individuals (e.g., QCAZ 19584; Fig. 6), the lighter area in the occipital region, limited by rows of tubercles forming an inverted V, is absent.

Ventral surfaces of all preserved specimens have a cream background with dark markings. The color of the markings varies from light gray (QCAZ 19581) to dark gray (QCAZ 19566). In some, the markings are restricted to the head (QCAZ 19586, QCAZ 19581) or



FIG. 6.—Dorsal views of adult *Physalaemus randi* showing variation in dorsal patterns. Left to right: QCAZ 19584 (female), QCAZ 19575 (male), QCAZ 19563 (male, holotype), QCAZ 19580 (male). All from Cerro Masvale (Provincia Manabí, Ecuador).

absent only in the posterolateral margins of the abdomen (QCAZ 19591). Variation between the extremes is continuous. On the abdomen, dark markings may be arranged in well-defined large spots (QCAZ 19591) or in diffuse speckled patterns (QCAZ 19576). Relative length of the midventral cream stripe, beginning at the tip of the snout, varies from being restricted to the head (QCAZ 19580) to extending to two-thirds of the SVL (QCAZ 19589).

The lateral head coloration varies extensively between light gray and dark gray or dark brown. In the dark-brown colored QCAZ 19591, the suborbital cream stripes are thin, well defined, with the posterior stripe extended below the tympanum and the parotoid gland. In addition, two ill-defined light brown labial bars are present anteriorly. In the light gray QCAZ 19586, the two suborbital cream stripes are fused into a single wide band. In QCAZ 19580, the loreal and suborbital areas are cream except for a light brown labial stripe; the canthal region is dark brown. One individual (QCAZ 19578) has black canthal stripes.

Live specimens from 11 km N Cerro Masvale, on the road to Virgen de Fátima (QCAZ 23461, 23523) had an orange mid-dorsal line running from the posterior half of the sacral region to the vent; the lighter zone between the dark V-shaped mark on the scapular region was also orange.

Morphometric data pertains only to adults. In the type series, the largest male has a SVL of 18.65 mm, and the largest female 19.71 mm; mean male SVL = 17.10 mm ($n = 35$, $SD = 0.74$), mean female SVL = 18.52 mm ($n = 5$,

$SD = 0.87$). Snout–vent length is significantly different between the sexes ($t = 3.93$, $df = 38$, $P = 0.0003$). Snout–vent length is not significantly different between males of Cerro Masvale and Puerto Inca ($t = 1.53$, $df = 31$, $P = 0.14$). The smallest specimen of each sex in the type series ($n = 40$) are the only two collected in El Piedrero, a locality 40 km E of Cerro Masvale. Descriptive statistics of morphometric measurements for two populations are given in Table 1.

All morphometric variables (Table 1) show a significant positive relation with SVL (simple regressions; ANOVA $P < 0.03$, $df = 37$). The relation was not significant between SVL and flank gland length ($F = 2.24$, $df = 10$, $P = 0.16$) and between SVL and parotoid gland length ($F = 0.05$, $df = 10$, $P = 0.83$). Flank gland length is not correlated with parotoid-flank length ($F = 0.41$, $df = 10$, $P = 0.53$). Total gland length (flank + parotoid) varies between 17.4% of SVL (QCAZ 19775 from Cerro Masvale) and 44.4% of SVL (QCAZ 19591 from Cerro Masvale). In all specimens, parotoid and flank glands are distinct from each other.

Distribution and ecology.—*Physalaemus randi* has been recorded in western Ecuador (Provincia del Guayas) from sea level to 150 m (Fig. 7). In the lowlands of western Ecuador, south of 1° latitude, precipitation is extremely seasonal, with higher precipitation in February–April (Lynch and Duellman, 1997). Among the known localities, annual precipitation ranges between 1031–2202 mm with only 0–45 mm during the three driest months of the year (July–September at Cerro Masvale); mean annual temperature ranges between

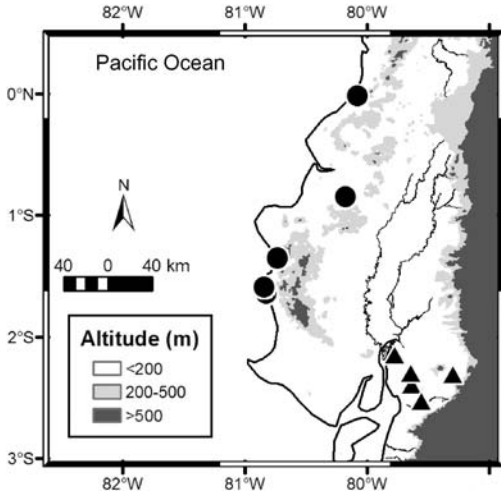


FIG. 7.—Known records of *Physalaemus randi* (triangles) and *P. montubio* (circles).

24.4 and 25.8 C (El Piedrero and 10 miles E from Guayaquil, respectively). Cerro Masvale is part of a private natural reserve adjacent to a national protected area, Reserva Ecológica Manglares–Churute.

Localities are in the following vegetation types (as defined by Cerón et al., 1999): Lowland Deciduous Costa Forest (10 miles E from Guayaquil, 11 km N Cerro Masvale, Puerto Inca), Lowland Semideciduous Costa Forest (Cerro Masvale), and Lowland Evergreen Costa Forest (El Piedrero). All individuals collected in 2002 were found in artificial open areas. At Cerro Masvale, frogs were breeding in the vicinities of buildings, pastures, and agricultural lands. At 11 km N Cerro Masvale males were calling from a flooded rice field. At Puerto Inca males were calling from flooded grassland next to a banana plantation.

Reproductive activity is nocturnal. Choruses of males were found in Cerro Masvale, 11 km N Cerro Masvale, and Puerto Inca (20 February 2002, 21–25 March 2003) during the rainy season. Males call from small ponds and ditches while floating in a few centimeters of water, usually concealed by vegetation. Amplexus and egg deposition take place at the same sites where choruses call. As in most other Leptodactylinae, *P. randi* constructs floating foam nests. The nest is constructed during amplexus: while the female deposits the egg masses, the male beats them with his legs. At some ponds at Cerro Masvale, calling males

were abundant (>1 individual/m²), and some of them called within 20 cm of each other.

Call.—One male in a chorus at Cerro Masvale (QCAZ 19752, call QCAZ (S) 19752; SVL = 17.23 mm) was recorded at 2025 h on 20 February 2002 while calling next to a ditch, partly submerged in 0.5 cm of water, among vegetation (water temperature 25.4 C, air temperature 24.8 C). The call is a single note with up to six harmonics. The note has two components: a sequence of 14 to 15 amplitude-modulated pulses followed by a nearly pure tone “whine” with a downward frequency sweep (Fig. 2). Both components have approximately the same duration (first component lasts on average 49.7% of the call; range 44.5–56.0, $n = 17$). The fundamental frequency of the first component is higher than that of the second component. In a sequence of 17 calls, the dominant frequency of the first component is either in the first harmonic ($n = 9$, mean frequency = 1.314 KHz) or the second ($n = 8$, mean frequency = 2.885 KHz). In the second component, the dominant frequency is always the first harmonic. Each note sweeps downward in frequency by about 0.5 KHz. Call parameters for QCAZ 19752 are shown in Table 2. Similar call structure was recorded for QCAZ 23462 (call QCAZ (S) 23462, SVL = 18.76 mm) at the same locality on 21 March 2003 at 2025 h (water temperature 27.9 C, air temperature 27.5 C; Table 2). However, in this individual the dominant frequency is always the fundamental for both components. The first component lasts on average 50.0% of the call (range 44.4–58.0, $n = 16$).

The advertisement call of *P. randi* is shorter and has a higher frequency than that of *P. pustulatus*. The call of *P. pustulatus* consists of a frequency-modulated tone, similar to the “whine” component of the call of *P. pustulosus* (Fig. 3; Ryan, 1985). Call parameters for *P. pustulatus* (Fig. 3, Table 2) were measured from a recording of a male in a chorus at Puerto Rico (QCAZ 19518, call QCAZ (S) 19518; SVL = 25.85 mm) at 2040 h in 17 February 2002. The male was calling partly submerged in water (water temperature 26.8 C, air temperature 24.0 C).

Remarks.—*Physalaemus randi* is assigned to the *P. pustulosus* group based on the presence of four synapomorphies (Cannatella et al., 1998): (1) presence of flank glands, (2)

presence of parotoid glands, (3) warty skin, and (4) dentigerous process of the vomer thin and spikelike.

Physalaemus montubio sp. nov.

Holotype.—QCAZ 19524 (field no. SCPUCE 4820), an adult male from Ecuador, Provincia de Manabí, Puerto Rico (1.639° S, 80.830° W), 30 m, collected by D. C. Cannatella, L. A. Coloma, A. Holloway, and S. R. Ron on 18 February 2002.

Paratopotypes.—QCAZ 19375–80, 19511, 19515–17, 19519–22, 19526–27, 19530–33, 19549–50, 19552, 19555–57, adult males; 19512, 19525, adult females, collected by D. C. Cannatella, L. A. Coloma, A. Holloway, and S. R. Ron on 17–18 February 2002.

Paratypes.—Ecuador: Provincia de Manabí: Río Cuaque, in the road to Recinto 10 de Agosto (0.014° S, 80.073° W), 20 m, QCAZ 19383–86, adult males, collected by F. Ayala on 15 February 2002; Río Cuaque, in the road between Pedernales and El Carmen, 100 m, KU 218219, adult female, collected by D. Kizirian, F. Campos, J. J. Wiens, and L. A. Coloma on 31 December 1989; Puerto Cayo, QCAZ 14729, adult male, collected by R. Gattelli on 9 February 2000; Río Chico near Salango, QCAZ 12340–41, 12362, adult males, 12339, adult female, collected by F. Campos and M. J. Barragán on 4 July 1998; Calceta, QCAZ 3728, adult female, collected by G. Onore on 2 February 2002.

Diagnosis.—A member of the *P. pustulosus* group as defined by Cannatella et al. (1998); see Remarks. *Physalaemus montubio* is characterized by (1) mean SVL 20.59 mm in males (18.67–22.56; $n = 38$), 22.62 mm in females (SVL 21.58–24.16; $n = 4$); (2) skin on dorsum bearing numerous round or subconical tubercles; (3) snout subacuminate in dorsal view, rounded in profile; (4) vomerine odontophores absent; (5) maxillary teeth present; (6) parotoid glands present, mean length = 1.96 mm (SD = 0.65; 5.0–16.6% of SVL; $n = 20$); (7) flank glands present, mean length = 3.6 mm (SD = 1.8; 4.5–31% of SVL; $n = 20$); (8) tarsal tubercle absent; (9) nuptial pads present; (10) finger I shorter than II; (11) tympanic annulus evident, concealed dorsally; tympanic membrane not tuberculate; (12) dentigerous process of the vomer thin and spikelike; (13) stalk

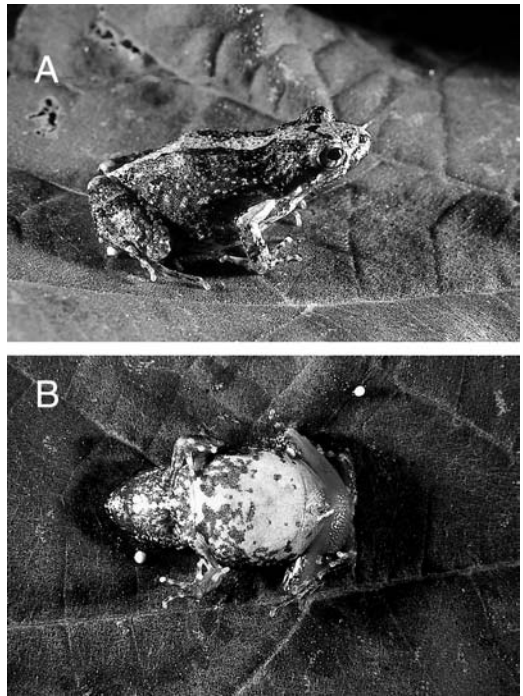


FIG. 8.—Dorsolateral (A) and ventral (B) views of *Physalaemus montubio*, QCAZ 19512 (adult female from Puerto Rico, Ecuador).

of the alary process of the hyoid very narrow; (14) anterior process of hyale well developed and prominent.

Physalaemus montubio (Fig. 8) differs from the larger *P. pustulosus*, and *P. petersi* by the absence of a tarsal tubercle and the presence of teeth on the maxilla and premaxilla. *Physalaemus coloradorum* has a different advertisement call (Ryan and Rand, 2001), more tuberculated skin than *P. montubio*, and a nearly vertical loreal region (slope gradually towards the lips in *P. montubio*). The ranges of adult size of *P. montubio* and *P. pustulatus* do not overlap (male SVL range 18.67–22.56 mm and 25.17–29.88 [$n = 31$], respectively). Additionally, *P. pustulatus* has an advertisement call approximately five times longer with a lower dominant frequency (Table 2, Figs. 2 and 3). *Physalaemus montubio* is most similar to *P. randi*. The species differ markedly in at least four parameters of their advertisement calls (i.e., call duration, call repetition rate, rise time, and number of pulses at the beginning of the call; see *P. randi* diagnosis for details; Table 2, Fig. 2). *Physalaemus montubio* has

a greater SVL and proportionally shorter flank and parotoid glands than *P. randi* (Fig. 4; see *P. randi* Diagnosis).

Description of holotype.—Adult male, 22.55 mm SVL, foot length 10.91 mm, tibia length 10.57 mm, femur length 10.46 mm, arm length 4.91 mm, head length 7.43 mm, head width 7.82 mm, eye-nostril distance 2.35 mm, dorsum width 8.77 mm, body as wide as head except on scapular region where it is 1.3 mm wider; diameter of eye 2.2 times the diameter of tympanic annulus; tympanic membrane and tympanic annulus barely evident; tympanic annulus rounded; supratympanic fold absent; head slightly convex between orbits and intercanthal region; snout rounded in profile and in dorsal view; nostrils slightly elevated anteriorly, internarial region concave; canthus rostralis rounded; loreal region convex with concave depression from posterior border of nostril to anteroventral border of orbit.

Fingers without expanded discs; nuptial pad present, brown, covering posterior two thirds of thenar tubercle and extending to base of thumb (Fig. 5). Base of palmar tubercle ovoid and slightly pointed anteriorly, smaller than base of ovoid thenar tubercle; subarticular tubercles conical with round base; flat supernumerary palmar tubercles present. Webbing between fingers absent; relative lengths of adpressed fingers III > IV > II > I (Fig. 5). Toes without expanded discs; base of inner metatarsal tubercle ovoid, larger than ovoid base of outer metatarsal tubercle; inner metatarsal tubercle more prominent than outer metatarsal tubercle; subarticular tubercles with round base, all conical except for subconical distal subarticular tubercles of fingers III, IV, and V; flat plantar supernumerary tubercles, longitudinally aligned; tarsal tubercle absent; webbing between toes absent; relative lengths of toes IV > III > V > II > I (Fig. 5).

Skin on dorsum bearing numerous, minute, round tubercles, more abundant in sacral region; skin on venter smooth. Tongue longer than wide; vomerine teeth and odontophores absent. Vocal slits present, parallel to margins of mandible. Deflated vocal sac forming folds on gular region and extending posteriorly to proximal end of the arm.

Color of holotype in preservative.—Dorsum grayish brown with irregular dark patches; two

faint dark longitudinal stripes from sacral region to posterior edge of orbits; dorsal tubercles lighter than background; light gray middorsal line from posterior two-thirds of sacrum to vent; dorsal surfaces of forearms and hindlimbs brown with dark brown transversal bars on exposed surfaces, arms light brown. Venter cream posteriorly with few scattered minute brown spots; brown blotches present on anterior half of venter except on proximity of armpits; ventral surfaces of head dark brown; light brown medial stripe from jaw tip to scapular region; ventral surfaces of hindlimbs and arms cream with numerous minute brown spots on outer edge, ventral surfaces of forearms brown becoming cream towards the inner edge; sides of head brown with light brown area below the orbit and tympanum; flanks dark gray ventrally, light gray dorsally.

Color in life.—(KU 218219, adult female from Río Cuaque). Dorsum light brown with darker blotches on sides and on limbs. Venter off-white near abdomen with light brown speckling. Pelvic region, throat, and underside of legs not pigmented. Iris bronze. Dark brown stripe posterior to eye. Upper lip white (L. A. Coloma field notes, 31 December 1989).

Etymology.—The specific name *montubio* is a noun in apposition derived from the Ecuadorian word “montubio” that refers to the people who inhabit the country side of the lowlands of western Ecuador. Because of its tolerance of habitat disturbance, *Physalaemus* are well known by montubios who refer to them as “ranas bullangueras” (noisy frogs) due to their loud advertisement calls.

Variation.—There is continuous variation in the number and shape of the dorsal tubercles (Fig. 9). The tubercles can be scattered and predominantly rounded (QCAZ 19520) or abundant and subconical (QCAZ 19530). The background coloration varies from light gray (QCAZ 12341, 19555) to dark gray or dark brown (QCAZ 19532). A lighter middorsal band is present in some individuals (QCAZ 19512, QCAZ 19522). Dorsolateral light-gray bands are present in QCAZ 19557. There is extensive variation in the number and distribution of dark marks. Representative states within the variation of these continuous characters are shown in Fig. 9.

Ventral surfaces of preserved specimens have a cream background with dark markings.

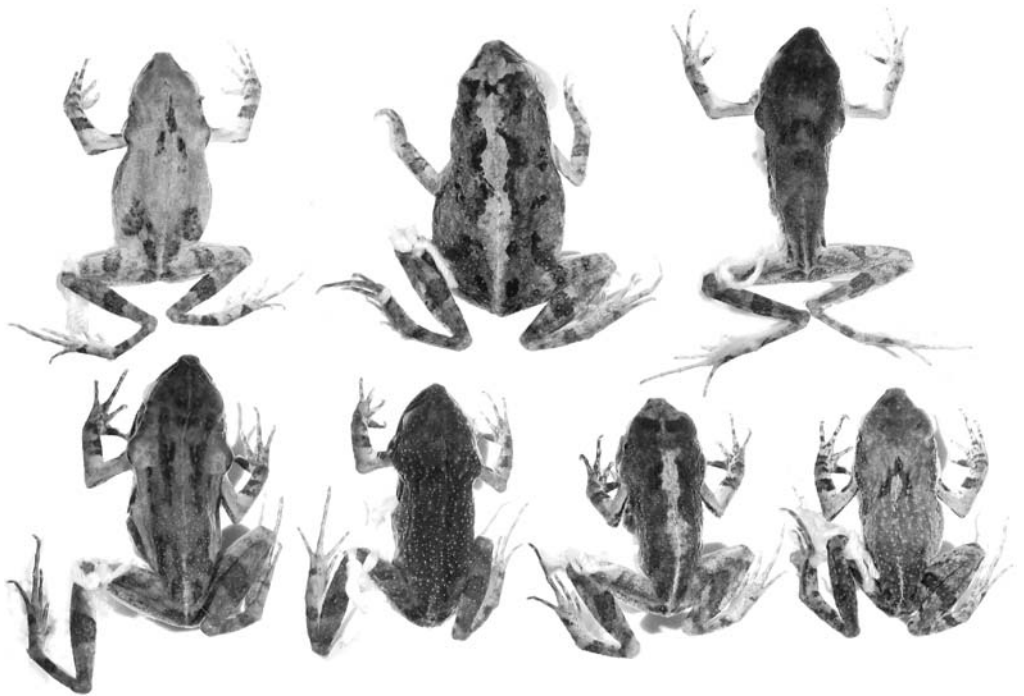


FIG. 9.—Dorsal views of adult *Physalaemus montubio* showing variation in dorsal patterns. Upper row (left to right): QCAZ 12341 (male, Río Chico), QCAZ 19512 (female, Puerto Rico), QCAZ 19520 (male, Puerto Rico). Lower row (all males, Puerto Rico): QCAZ 19524, QCAZ 19530, QCAZ 19552, QCAZ 19555. All from Provincia de Manabí, Ecuador.

Coloration varies mainly in: (1) the hue of the markings, varying from light gray (QCAZ 19512) to dark brown (QCAZ 19516); and (2) the distribution of the markings, which can be almost completely restricted to the head (QCAZ 19520) or the chest (QCAZ 12339) or present in all the venter (QCAZ 19516). Variation between extreme states is continuous. In the abdomen, dark marks can be arranged in well-defined large spots (QCAZ 19555) or in diffuse speckled patterns (QCAZ 14729). In all specimens (except QCAZ 12362 and 19519) a midventral cream to light brown stripe, starting on the head, is present. The extent of the stripe varies from being restricted to the head (QCAZ 19522) to reaching up to 2/3 of SVL (QCAZ 12340). The stripe varies from discrete (QCAZ 12340) to ill defined (QCAZ 19525).

Lateral head coloration varies extensively between light gray (QCAZ 12339) to dark gray or dark brown (QCAZ 19532). In specimens with darker coloration, the suborbital cream stripes are short and ill defined. In specimens with lighter coloration, a single cream wide

band is present below the orbit. One or two additional cream to light brown labial bars may be present anteriorly (QCAZ 19549).

In the type series, the largest male has a SVL of 22.56 mm, and the largest female, 24.16 mm; male mean SVL = 20.59 mm ($n = 38$, $SD = 1.26$), female mean SVL = 22.62 mm ($n = 4$, $SD = 1.14$). Small sample size of females prevents analysis of intersexual differences in size. However, available data suggest that females are larger than males. The smallest female (SVL 21.58 mm, QCAZ 19525) is larger than 80% of the males ($n = 38$). Among 18 adult males, combined gland length (flank + parotoid) varies from 13.7% of SVL (QCAZ 19530 from Puerto Rico) to 44.9% (QCAZ 19386 from Río Cuaque). In all specimens, parotoid and flank glands are distinct from each other.

Distribution and ecology.—*Physalaemus montubio* has been recorded in western Ecuador (Provincia de Manabí) from sea level to 200 m (Fig. 7). At the known localities, annual precipitation ranges between 156–1115 mm (Río Chico and Calceta, respectively) with

only 0–33 mm falling during the three driest months of the year (Puerto Rico and Calceta, respectively; at Puerto Rico, the driest months are September–November); mean annual temperature is 24.7–26 C (Río Cuaque and Calceta).

Localities are in the following vegetation types (as defined by Cerón et al., 1999): Lowland Evergreen Costa Forest (Río Cuaque), Lowland Semideciduous Costa Forest (Calceta), and Lowland Dry Shrub (Puerto Cayo, Puerto Rico, and Río Chico). All individuals collected in 2002 were found by night in artificial open areas.

Reproductive activity is nocturnal. In Puerto Rico, frogs were breeding near buildings, pastures, and in other cleared areas. Choruses were heard in March 1999, February 2002, and March 2003, during the rainy season. Most individuals were congregated around small temporary pools that filled after heavy rains. Males called while floating in a few centimeters of water. At Puerto Rico, a large aggregation was found in a stream pool 50 m away from the Pacific Ocean. Dozens of males were calling among aquatic plants. Interestingly the chorus was synchronized into two antiphonal “voices.” Other species calling and breeding on the same pond were *Bufo marinus* and the hylids *Trachycephalus jordani* and *Scinax quinquifasciatus*. Amplexus and egg deposition take place at the same sites where choruses call. Amplexant pairs were observed to make floating foam nests. To do so, the male beats the egg masses with his legs as they are discharged by the female.

In 1999 and 2002, *P. montubio* was breeding syntopically with *P. pustulatus* at Puerto Rico. At some pools, males of both species were calling simultaneously. Coloma and Ron (2001) published a color photograph of a calling male of *P. montubio* from Puerto Rico.

Call.—One male (QCAZ 19517, call QCAZ (S) 19517; SVL = 20.85 mm) in a chorus at Puerto Rico, was recorded at 2025 h on 17 February 2002 while calling partly submerged in 2 cm of water, on a roadside pool (water temperature 27.4 C, air temperature 24.2 C). The call consists of a single, short note that begins with two to five amplitude-modulated pulses followed by a nearly pure tone with a downward frequency sweep (Fig. 2, Table 2). The mean duration of the first component is

18.6% of the call (range 11.7–24.9, $n = 13$). The call has a rich harmonic structure (Fig. 2). In the second component of the call, the dominant frequency is always in the first harmonic. In the pulsed component, the dominant frequency is either the first harmonic (mean frequency = 1.369 KHz, $n = 6$) or the second (mean frequency = 3.098 KHz, $n = 7$). The holotype, QCAZ 19524, (call QCAZ (S) 19524; SVL = 22.55 mm) was recorded at 0005 h on the same night and locality. The call is similar to that of QCAZ 19517 but with more discrete pulses at the beginning of the call. In the pulsed component of the call, the dominant frequency is always in the second harmonic (mean frequency = 2.689 KHz, $n = 15$). The mean duration of the first component is 25.1% of the call (range 20.6–31.7, $n = 15$). Other call parameters are shown in Table 2.

Remarks.—*Physalaemus montubio* is assigned to the *P. pustulosus* group based on the presence of four synapomorphies (Cannatella et al., 1998): (1) presence of flank glands, (2) presence of parotoid glands, (3) warty skin, and (4) dentigerous process of the vomer thin and spikelike.

Morphometric comparisons between P. randi, and P. montubio.—Measurements of eight morphometric variables are given in Table 1. In the PCA, the first three principal components account for 59.3% of the variation (Table 3). Principal Component I describes a gradient based mainly on tibia and femur length. Principal Component II describes a gradient based on arm length and dorsum width. Overall, *P. montubio* and *P. randi* overlap widely in morphometric space (Fig. 10).

DISCUSSION

According to the phylogeny presented by Cannatella et al. (1998), the *P. pustulosus* group is supported by at least four morphological synapomorphies: (1) presence of flank glands, (2) presence of parotoid glands, (3) warty skin, and (4) dentigerous process of the vomer thin and spikelike. *Physalaemus montubio* and *P. randi* have not been included in any phylogenetic analysis previously. Nevertheless, its inclusion in the group is supported by the presence of all these morphological synapomorphies.

Two basal clades are defined in the Cannatella et al. (1998) phylogeny, one distributed in

TABLE 3.—Character loading and percentage of explained variance for Principal Components (PC) I–III for eight morphometric variables. To remove the effect of “size,” linear regressions were performed between all variables and snout-vent length (SVL). The PC analysis was applied to SVL and the residuals from the regressions with the other variables.

Variable	Size-free morphology		
	PC I	PC II	PC III
SVL	<0.00001	<0.00001	1.000
Residual dorsum width	0.545	-0.604	<0.00001
Residual tibia length	0.778	0.177	<0.00001
Residual femur length	0.706	-0.137	<0.00001
Residual arm length	0.426	0.607	<0.00001
Residual head length	0.603	0.304	<0.00001
Residual head width	0.579	-0.516	<0.00001
Residual eye-nostril distance	0.299	0.486	<0.00001
Eigenvalue	2.37	1.378	1.000
%	39.6	17.2	12.5

Central America, northern South America, and the Amazon basin (containing *P. petersi*, and *P. pustulosus*) and the other in western Ecuador and northwestern Peru (containing all remaining species of the group). Synapomorphies for the latter clade are: (1) absence of a tarsal tubercle, (2) narrow stalk of the alary process of the hyoid, and (3) insertion of petrohyoideus anterior muscle along edge of hyoid plate (Cannatella et al., 1998). Although character (3) has not been assessed in *P. montubio* and *P. randi*, characters (1) and (2) indicate their inclusion in the northwestern South American clade.

Numerous publications on sexual selection and call evolution of the *P. pustulosus* group have included species from western Ecuador (e.g., Rand et al., 1992; Ryan and Rand, 1990, 1993, 1995; Ryan et al., 2003). In all those accounts (except Ryan, 1990) and in Cannatella et al. (1998) there has been confusion on the assignment of specimens and calls to *P. pustulatus*. The confusion probably arose from the poor condition of the type material of *P. pustulatus*. The holotype (MCZ 7666 from “Guayaquil”) was collected in 1913 and has a SVL of 20.77 mm. The internal organs had been removed, and the frog lacks nuptial pads and vocal slits. The holotype closely resembles larger *P. pustulatus* specimens from Guayaquil (KU 154561–62) indicating that it is a conspecific juvenile. Because of the condition of the holotype, much larger specimens of *Physalae-*

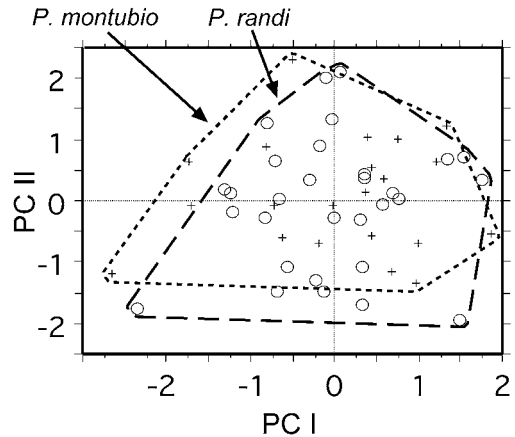


FIG. 10.—Axes I and II from Principal Components Analysis based on snout-vent length and seven size-corrected morphological variables for 21 specimens of *Physalaemus montubio* from Puerto Rico (+), and 30 of *P. randi* from Cerro Masvale and Puerto Inca (o).

mus pustulatus collected in Portoviejo (Provincia de Manabí, Cannatella et al., 1998) were mistakenly referred to an undescribed species, frequently referred as *P. sp. C* in the literature (e.g., Cannatella et al., 1998; Tárano and Ryan, 2002). *Physalaemus pustulatus* has also been recorded in Puerto Rico (Provincia de Manabí, QCAZ 19355), Patricia Pilar (Provincia de Los Ríos, QCAZ 19607), Isla Puná (Provincia del Guayas, CAS 5408), and Cerro Blanco (Provincia del Guayas, QCAZ 23427). It is not established yet if morphologically similar specimens from northwestern Peru, referred to as “*P. caicai*” by Ryan and Rand (2001) or “*P. sp. B*” by Cannatella et al. (1998), deserve to be considered a separate species from *P. pustulatus*. Conversely, calls and specimens from southern Ecuador (Provincia de El Oro, Pasaje) thought to belong to *P. pustulatus* (e.g., Ryan, 1996; Ryan and Rand, 2001) belong either to *P. randi* or to a closely related undescribed species. Further analysis of molecular and morphological data is necessary to determine their taxonomic status.

RESUMEN

Describimos dos nuevas especies del género leptodactílido *Physalaemus* de las tierras bajas del occidente del Ecuador. Las nuevas especies pertenecen al grupo de especies *P. pustulosus*. Se diferencian de otras especies del grupo, excepto *P. coloradum*, por su

tamaño más pequeño. Se distinguen de *P. coloradorum* por tener una piel dorsal menos tuberculada y región loreal más aplanada. Las nuevas especies se diferencian entre sí marcadamente en sus cantos de anuncio. Aunque los rangos se sobrelapan, el tamaño de su cuerpo y el largo relativo de sus glándulas del flanco y parotoideas también es significativamente diferente. En general, las nuevas especies se parecen mucho entre sí en patrones de coloración y forma del cuerpo; su diagnóstico es difícil en base a caracteres morfológicos.

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LITERATURE CITED

- CANNATELLA, D. C., AND W. E. DUELLMAN. 1984. Leptodactylid frogs of the *Physalaemus pustulosus* group. *Copeia* 1984:902–921.
- CANNATELLA, D. C., D. M. HILLIS, P. T. CHIPPIINDALE, L. WEIGT, A. S. RAND, AND M. J. RYAN. 1998. Phylogeny of frogs of the *Physalaemus pustulosus* species group with an examination of data incongruence. *Systematic Biology* 47:311–335.
- CERÓN, C., W. PALACIOS, R. VALENCIA, AND R. SIERRA. 1999. Las formaciones naturales de la Costa del Ecuador. Pp. 55–78. In R. Sierra (Ed.), *Propuesta Preliminar de un Sistema de Clasificación de Vegetación para el Ecuador Continental*. Proyecto INEFAN/GERF-BIRF y Ecociencia, Quito, Ecuador.
- CHARIF, R. A., S. MITCHELL, AND C. W. CLARK. 1995. *Canary 1.12 User's Manual*. Cornell Laboratory of Ornithology, Ithaca, New York, U.S.A.
- COLOMA, L. A., AND S. R. RON. 2001. Megadiverse Ecuador: Amphibians, Reptiles, Birds, and Mammals. Serie de Divulgación del Museo de Zoología. Centro de Biodiversidad y Ambiente, Pontificia Universidad Católica del Ecuador, Quito, Ecuador.
- DUELLMAN, W. E. 1970. *Hylid frogs of Middle America*. Monograph of the Museum of Natural History University of Kansas 1:1–753.
- ESRI. 2001. ArcGis, version 8.2. Environmental Systems Research Institute, Inc., Redlands, California, U.S.A.
- GREENFIELD, M. D., AND A. S. RAND. 2000. Frogs have rules: selective attention algorithms regulate chorusing in *Physalaemus pustulosus* (Leptodactylidae). *Ethology* 106:331–347.
- LYNCH, J. D., AND W. E. DUELLMAN. 1997. Frogs of the genus *Eleutherodactylus* in western Ecuador: systematics, ecology, and biogeography. Special Publication Natural History Museum University of Kansas 23:1–236.
- MINITAB. 1995. *Users Guide: Release 10.51 Xtra*. Minitab Inc. State College, Pennsylvania, U.S.A.
- RAND, A. S., AND M. J. RYAN. 1981. The adaptive significance of a complex vocal repertoire in a neotropical frog. *Zeitschrift für Tierpsychologie* 57:209–214.
- RAND, A. S., M. J. RYAN, AND W. WILCZYNSKI. 1992. Signal redundancy and receiver permissiveness in acoustic mate recognition by the Túngara frog, *Physalaemus pustulosus*. *American Zoologist* 32:81–90.
- RYAN, M. J. 1980. Female mate choice in a Neotropical frog. *Science* 209:523–525.
- . 1985. *The túngara frog: a study of sexual selection and communication*. University of Chicago Press, Chicago, Illinois, U.S.A.
- . 1990. Vocal morphology of the *Physalaemus pustulosus* species group (Leptodactylidae): morphological response to sexual selection for complex calls. *Biological Journal of the Linnean Society* 40:37–52.
- . 1996. Phylogenetics in behavior: some cautions and expectations. Pp. 1–21. In E. P. Martins (Ed.), *Phylogenies and the Comparative Method in Animal Behavior*. Oxford University Press, New York, U.S.A.
- RYAN, M. J., J. H. FOX, W. WILCZYNSKI, AND A. S. RAND. 1990. Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. *Nature* 343:66–67.
- RYAN, M. J., AND A. S. RAND. 1990. The sensory basis of sexual selection for complex calls in the Túngara frog, *Physalaemus pustulosus* (sexual selection for sensory exploitation). *Evolution* 44:305–314.
- . 1993. Sexual selection and signal evolution—the ghost of biases past. *Philosophical Transactions of the Royal Society of London (Biology)* 340:187–195.
- . 1995. Female responses to ancestral advertisement calls in túngara frogs. *Science* 269:390–392.
- . 2001. Feature weighting in signal recognition and discrimination by túngara frogs. Pp. 86–101. In M. J. Ryan (Ed.), *Anuran Communication*. Smithsonian Institution Press, Washington, D.C., U.S.A.
- RYAN, M. J., W. RAND, P. L. HURD, S. M. PHELPS, AND A. S. RAND. 2003. Generalization in response to mate recognition signals. *The American Naturalist* 161:380–394.
- SIMMONS, J. E. 2002. Herpetological collecting and collections management. *Herpetological Circular* 31:1–153.
- TÁRANO, Z., AND M. J. RYAN. 2002. No pre-existing biases for heterospecific calls traits in the frog *Physalaemus enesefae*. *Animal Behaviour* 64:599–607.
- VITT L. J., S. S. SARTORIUS, T. C. S. AVILA-PIRES, M. C. ESPÓSITO, AND D. B. MILES. 2000. Niche segregation among sympatric Amazonian teiid lizards. *Oecologia* 122:410–420.

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APPENDIX I

Examined Specimens

Physalaemus coloradorum.—Ecuador: Pichincha: 1 km NW from La Florida, 1003 m, QCAZ 19373–74, 19439–41

Physalaemus petersi.—Bolivia: Cochabamba: 6.5 km N Chipiriri, 260 m, KU 135513–16. Ecuador: Orellana: Estación Científica de la Universidad Católica del Ecuador, Parque Nacional Yasuní, 240 m, QCAZ 14733–38.

Physalaemus pustulatus.—Ecuador: Provincia de Manabí: Puerto Rico, 10 m, QCAZ 19355, 19513–14, 19518,

19523, 19537, 19541–42, 19545–48, 19551, 19553–54. Provincia de Los Ríos: Patricia Pilar, 200 m, QCAZ 19538–40, 19605–14, 19745–48. Provincia del Guayas: Guayaquil, MCZ 7666 (holotype). Provincia del Guayas: Isla Puná, CAS 5408. Provincia del Guayas: Cerro Blanco, QCAZ 23427.