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*Copeia*, 1984(4), pp. 902–921

## Leptodactylid Frogs of the *Physalaemus pustulosus* Group

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**Within the leptodactylid frog genus *Physalaemus*, four species comprise a monophyletic group: *P. petersi* (with *P. freibergeri* designated as a junior synonym), *P. pustulatus*, *P. pustulosus* and *P. coloradum*, a new species from the Pacific lowlands of Ecuador. *Physalaemus petersi* and *P. pustulosus* seem to be sister-species, as do *P. pustulatus* and *P. coloradum*. The monophyly of the genus *Physalaemus* is questionable.**

THE 33 nominal species of small toad-like leptodactylids of the genus *Physalaemus* were placed in four species groups by Lynch (1970). Four species were recognized in the *Physalaemus pustulosus* group—*P. freibergeri* in Bolivia, *P. petersi* in the Amazon basin, *P. pustulatus* on the Pacific lowlands of Ecuador and *P. pustulosus* in Mexico, Central America, and northern South America. Lynch (1970) suggested that the nominal species *P. paraensis* and *P. schereri* were synonyms of *P. petersi* and that *P. stentor* was a synonym of *P. pustulosus*, although he provided no evidence to support these conclusions.

While studying specimens of *Physalaemus* that we collected on the Pacific lowlands of Peru and Ecuador, we discovered that two distinct taxa occurred in that region. Comparisons of the trans-Andean specimens with members of the *P. pustulosus* group from elsewhere in the range of the group resulted in this review. Our purposes are to: 1) define the *Physalaemus pustulosus*

group, 2) define the species in the group, 3) allocate the various names to known taxa, 4) describe a new species from trans-Andean Ecuador and 5) discuss the phylogenetic relationships of the species in the group.

### MATERIALS AND METHODS

We examined 1,471 preserved specimens, 76 cleared and stained skeletal preparations and 12 lots of tadpoles. Abbreviations for museum specimens are: AMNH = American Museum of Natural History, CAS-SU = California Academy of Science (Stanford University Collection), CM = Carnegie Museum, FMNH = Field Museum of Natural History, KU = University of Kansas Museum of Natural History, MCZ = Museum of Comparative Zoology, Harvard University, UMMZ = University of Michigan Museum of Zoology, USNM = National Museum of Natural History. Audiospectrograms

were made from tape recordings on a Model 7029A Sona-Graph (Kay Electric Co.). In the diagnoses, measurements are maximum snout-vent lengths. Statistical analyses were done using BMDP statistical software (Dixon, 1981).

*Specimens examined and locality records.*—The following abbreviations are used: (A) = alizarin skeleton, (A-A) = alizarin-alcian skeleton, (D) = dry skeleton, (L) = larvae, (Y) = young.

### *Physalaemus coloradorum*

Specimens examined listed in species description.

### *Physalaemus petersi*

Bolivia: **Cochabamba**: 6.5 km N Chipiriri, 260 m, KU 135513-16; **La Paz**: "Tumupassa," UMMZ 64122; "Iximias" (probably Ixiamas), UMMZ 64123(5); **Santa Cruz**: Buenavista, 500 m, AMNH 22632-33, 34068, 34065-66, UMMZ 63882(12), 66513(7), 66550, 66593, 66612. Brazil: **Amazonas**: Igarape Belém, nr. Rio Solimões, ca. "70 km E Leticia," AMNH 97080-209, 97211-323; Igarape Puruzinho, at Rio Madeira, USNM 202601-06; **Pará**: 65.5 km SW of Itaituba, Parque Nacional da Amazonia (Rio Tapajós), USNM 241212; ca. 75 km SW Itaituba, Parque Nacional da Amazonia (Rio Tapajós), USNM 241211; ca. 66 km SW Itaituba, Parque Nacional da Amazonia (Rio Tapajós), USNM 241210; IPEAN, 3 km E Belém, KU 128267; IPEAN, 5 km E Belém, KU 127994 (Y), 127320-37, 127319 (A-A). Colombia: **Amazonas**: Petuna, Rio Loreto-yacu, KU 153313; Puerto Nariño, KU 153314; **Putumayo**: San Antonio, Rio Guamé, 400 m, KU 140314; Umbria, 400 m, FMNH 61792. Ecuador: **Esmeraldas**: Alto Tambo, 10 km NW Lita on railroad, ca. 500 m, USNM 196855-55a (locality in error, see text); **Morona-Santiago**: Ashuara village on Rio Macuma, 300 m, ca. 10 km above Rio Morona (ca. 83 km ESE Macas), AMNH 94720-49, 94750 (11 Y); Cusume, Rio Cusume, 320 m (60 km airline SE Macas, 2°40'S, 77°42'N), AMNH 93802; Macas, Rio Yuquipa, USNM 196857; Miazal, USNM 196858, 196856-56a; **Napo**: 3 km from Santa Cecilia Turnoff toward Quito, 340 m, KU 149388-90; Puerto Libre, Rio Aguariño, 570 m, KU 122548-52; Rio Misahualli, Upper Rio Napo, USNM 196859, 196859a-f; Santa Cecilia, 340 m, KU 104629, 158501, 152407, 149384-7, 149383 (A-A); 146192-3, 122547; **Pastaza**: Oriente, Canelos, MCZ 17931-33; Puyo, FMNH 172637, UMMZ 127889, USNM 196866; 2.5 km SE Puyo, 960 m, USNM 196861; Puyo, 3,300 ft., USNM 196867-67a, 196865; Puyo, below Rio Shuriyacu, USNM 196860; Puyo, 9 km E "Veracruz," UMMZ 127890; 25 km N Puyo, USNM 205033-34; 3 km SSE Puyo, 975 m, USNM 196863-63a; 5 km SSE Puyo, Hacienda Madrid, 960 m, USNM 196862; Mera, 1,100 m, KU 178269-70; Mera, 1,140 m, KU 121357-8 (L), 121356 (Y), 121355 (L), 120290 (A), (A), 120280-89; Veracruz, 950 m, KU 121359 (L); Veracruz, ca. 10 km E Puyo, 990 m, USNM 196864, 196864a-d. Peru: **Cuzco**: Pilcopata, 750 m, KU 138979; **Huánuco**: Finca Panguana, Rio Llullapichis, 4-5 km upstream from Rio Pachitea, ca. 200 m, KU 154900-02; Rio Llullapichis, 4-5 km upstream from Rio Pachitea, 200 m, KU 171906 (A-A), 171903-05; **Loreto**: Pampa Hermosa, Rio Cushabatay, AMNH 42666; headwaters Rio Utoquinia, AMNH 42907; Domo Santa Clara, Orellana, USNM 127183; Monte Alegre, Rio Pachitea, AMNH 43020; Pebas, Ampiyacu River, MCZ 25598 (paratype of *E. schereri*); Pebas, Rio Ampiyacu, CAS-SU 6316, 6319 (paratypes of *Eupemphix schereri*), 6317 (holotype of *Eupemphix schereri*); Rio Tambo, AMNH 42238; Yagua Indian Village, headwaters Rio Loretoyacu, 100+ km NW Leticia, AMNH 96360-94; Rio Cashiboya, Ollanta, AMNH 42301; **Madre de Dios**: 30 km (airline) SSW of Puerto Maldonado, Tambopata Reserve, Explorer's Inn, 280 m, 12°50'S, 69°17'W, USNM 222305-08, 222363 (L), 222364-68 (L); **Pasco**: Oxapampa, Nevati, 275 m, KU 144317-8.

Literature records are: Bolivia: **El Beni**: Rurrenabaque (Donoso-Barros, 1969). Brasil: **Amazonas**: Eirunepe and Tabatinga (B. Lutz and Kloss, 1952), Tapaua, Rio Purus (Heyer, 1977). Ecuador: **Pastaza**: Canelos and Sarayacu (Boulenger, 1882). French Guiana: Saul and Zidok (Lescure, 1976).

### *Physalaemus pustulatus*

Ecuador: **El Oro**: 3 km E Pasaje, 30 m, AMNH 104968; **Guayas**: Guayaquil, KU 154561-62, MCZ 7666 (holotype); Puna Island, CAS-SU 6408. Peru: **Lambayeque**: 7 km S Motupe, 130 m, KU 162369-75 (162375, A-A).

### *Physalaemus pustulosus*

Colombia: **Antioquia**: 1 km W Valdivia, 1,400 m, KU 132843-46; **Bolívar**: Tierra Alta, 70 m, KU 144958; Alto de Quimari, 500 m, KU 144959-65 (144965, A-A); **Magdalena**: El Rodadero de Gaira, 5 m, KU 169132-33; between Mamatoco and La Tigrera, UMMZ 45485, 45583; Minca, UMMZ 45487; Fundación, UMMZ 45580, 45582, 48201; Bolívar, UMMZ 54586; Don Diego, UMMZ 48196; "Santa Marta Region," UMMZ 48200; **César**: Valencia de Jesús, UMMZ 54587-88; **Tolima**: Mariquita, FMNH 81829. PANAMA: Isla Taboga, KU 115270-73, 172426, USNM 38946, 48518-19, 51957-59, 80326, 102757-60. Trinidad: Churchill-Roosevelt Hwy, vicinity "Milestone 11.5," USNM 166528; Maracás, USNM 166517-27; Botanical Garden, Port of Spain, USNM 15493-97, 15528-29; no specific locality, USNM 17776-78; Upper Tucker Valley, USNM 119054; St. Augustine, USNM 141534-44, CM 5461-62, 5484-86; Mt. St. Benedict, UMMZ 70779-80, CM 5457; Tunapuna, Mt. St. Benedict, CM 4888(9), 4891(4), 4892(4), 4895; Tunapuna, St. John's Rd, CM 4896(2); Guayaquayare, CM 5492. Tobago: **St. Paul Parish**: Louis D'or Land Settlement, USNM 195020-28; Windward Rd, vicinity of milestone 22 1/2, USNM 195029, 195108-10. Venezuela: **Monagas**: 8 km WSW Caripito, KU 117115-21; **Sucre**: 7 km SE Carupano, 275 m, KU 132823-42; Guaraúnos, 10 m, KU 150800-13, 166640-47; **Táchira**: 7.5 km SW Punta de Piedra, 120 m, KU 166583; **Bolívar**: 13 km S, 1 km E Puente Cuyuni, 140 m, KU 166584-98, 167804 (L), 167805 (Y); **Miranda**: 1 km SW Araguaia, 90 m, KU 166599; **Sucre**: 7 km S Guaraúnos, Rio Sabacual, 10 m, 166600-39, 167680-746 (A); **Araguaa**: Turiamo Rd., KU 185695-96.

Literature records are:—Venezuela: **Bolívar**: 38 km S El Dorado (Heatwole, Solano, and Heatwole, 1965); El Manteco, Upata (Hoogmoed and Gorzula, 1979); **Táchira**: La Fria (Rivero, 1961); **Mérida**: Santa Elena (Rivero, 1961); **Monagas**: Caripito (Rivero, 1961); **Guárico**: El Sombrero, 160 m (Rivero, 1961); Espino, 200 m (Rivero, 1961); **Araguaa**: Maracay (A. Lutz, 1927; Rivero, 1961); **Miranda**: Ocumare del Tuy (Rivero, 1961); **Araguaa**: Pie del Cerro, 810 m (Rivero, 1961); **Carabobo**: Puerto Cabello, 5 km (Boettger, 1893; Rivero, 1961); **Miranda**: Santa Lucía, 300 m (Rivero, 1961); Turgua, 20 km (Alemán, 1952). **Guyana**: Rupununi Savannas (Hoogmoed, 1979). **Colombia**: Following records from Cochran and Goin (1970): **Antioquia**: Casabe; Chigorodo; San Pedro; **Atlántico**: Barranquilla; Palmar de Varela, Ponederia; **Sucre**: Coloso, E of Tolviejo, 250 m; Hda. La Aguada 22 km from San Onofre; Sincelejo; Tolviejo; **César**: Curumani; **Chocó**: Truando; **Córdoba**: Rio Manso, trib. of upper Rio Sinú; **Cundinamarca**: Apulo; 1 km E Girardot; San Javier, La Mesa; **Guajira**: 30 km S Castilletes; Piojo, 100 m; **Magdalena**: Ciénaga, Casa Blanca; Finca El Arnanar, Bonda; Larilla; **Norte de Santander**: Astillero, Rio Zulia; Finca Miramonte, 15-20 km N Camp Tibú, Catatumbo; **Santander**: Quebrada "La Lechera" Vélez; San Gil; **Tolima**: Honda, 3,400'. Also known from the Rio Truando, Chocó (type locality, Cope, 1864). Additionally we have examined all Middle American material (>700 specimens) used by Freeman (1967), but for the sake of brevity we do not list it here.

*Additional skeletal material.*—*P. albonotatus*—KU 92987 (A). *P. biligoni-gerus*—KU 80811(A), 93010 (A), 84768-76 (D). *P. centralis*—KU 92993 (A). *P. cuvieri*—KU 92999 (A), 186758 (D). *P. enesefae*—KU 166582 (A-A). *P. ephippifer*—KU 93005 (A), 127432-34 (A-A), 127472 (A-A). *P. gracilis*—KU 93016. *P. maculiventris*—KU 93022 (A). *P. nanus*—KU 93025 (A). *P. nattereri*—KU 92844 (A), 92845 (D). *P. pustulosus*—KU 41031 (D), 42774-77 (A-A), 61928-31 (A-A), 68269-72 (A), 108357-59 (A-A), 184956 (A), 186815 (A). *P. signiferus*—KU 93933 (A).

### SYSTEMATICS

We propose that the *P. pustulosus* group is a monophyletic unit composed of four species: *P. pustulosus*, *P. petersi* (*P. freibergeri* is a junior

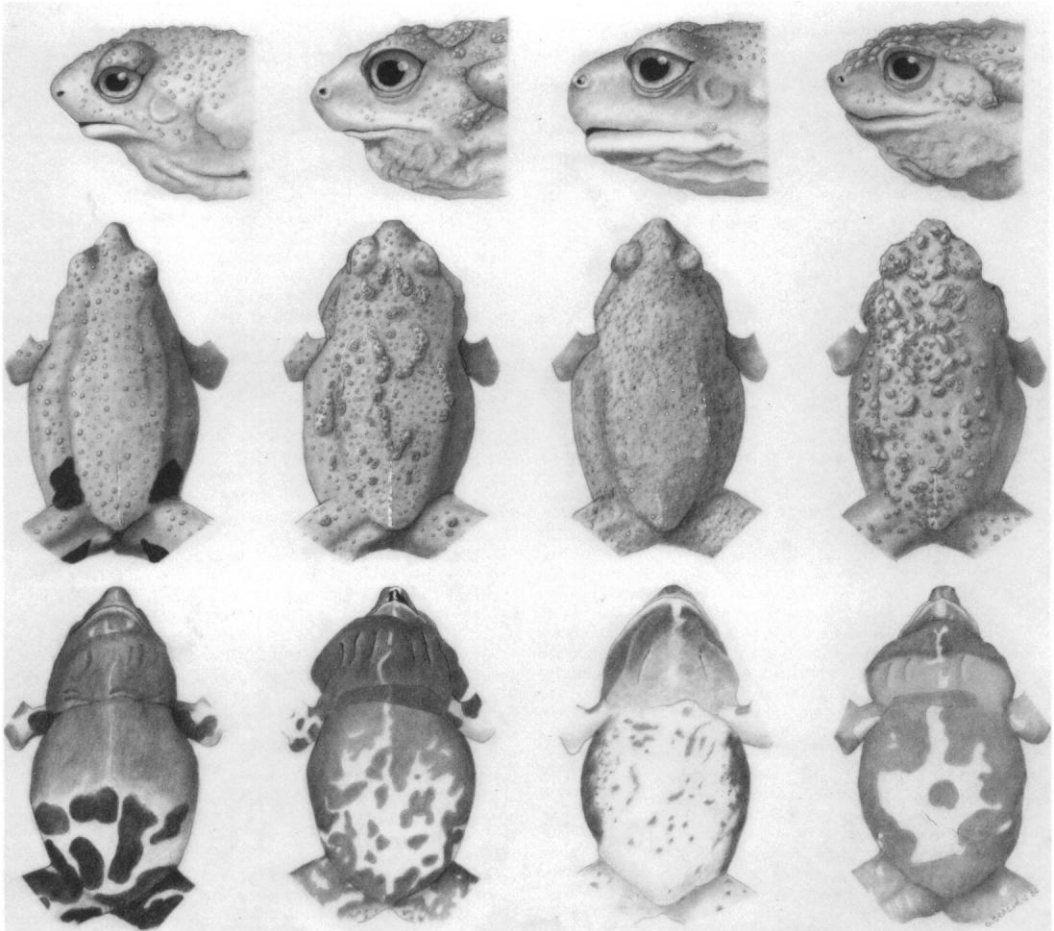


Fig. 1. Lateral (top), dorsal (middle), and ventral (bottom) views of adult male *Physalaemus*. From left to right: *P. petersi* (KU 120287), *P. pustulosus* (KU 96404), *P. pustulatus* (KU 162373) and *P. coloradum* (KU 117786). Not drawn to scale.

synonym), *P. pustulatus* and a new species described below. The group is defined by four shared derived features, any of which distinguishes its members from other species of *Physalaemus*: warty, tubercular skin, the presence of a parotoid gland, the presence of an elliptical flank gland and thin dentigerous processes of the vomers. The group contains the same nominal taxa that were included by Lynch (1970), plus one new species described herein.

Other diagnostic characters that are not unique to the group are the small, non-compressed metatarsal tubercles and the lack of inguinal glands. Features used by Lynch (1970) to define the group that are no longer valid are:

first finger longer than second, and lack of maxillary and premaxillary teeth.

*Physalaemus coloradum*, sp. nov.

Figs. 1, 2

*Holotype*.—KU 178271, an adult male from Santo Domingo de los Colorados, 580 m, Provincia Pichincha, Ecuador (0°15'S, 79°09'W) obtained on 9 June 1977 by Thomas J. Berger and John D. Lynch.

*Paratypes*.—All from Ecuador (29 ♂♂, 10 ♀♀, 6 juveniles): except for Río Cupa, all localities are in Provincia Pichincha; AMNH 114829, KU

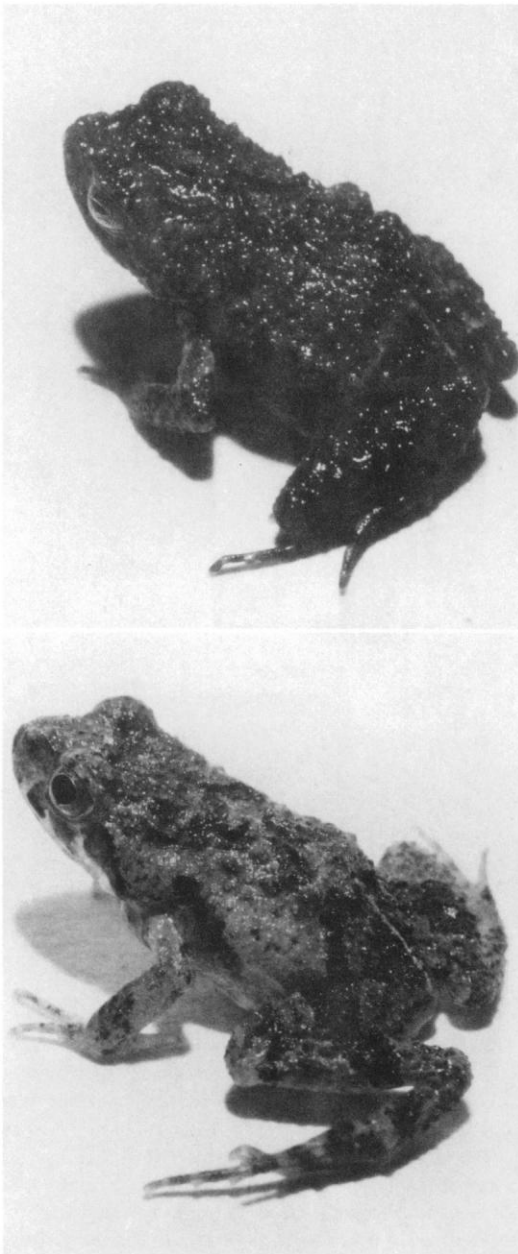


Fig. 2. Photographs of *P. coloradorum* (top, AMNH 89749, male paratype, 19.7 mm SVL) and *P. pustulatus* (bottom, AMNH 104968, juvenile male, 18.5 mm SVL). Photos by Charles W. Myers.

109138, 117780–91, 178272–73, USNM 196868, 241213–15 from Santo Domingo de los Colorados, 580 m; MCZ 98203 from 2 km N, 1 km E of Santo Domingo de los Colorados,

570 m; MCZ 97882–84 from 3 km SE of Santo Domingo de los Colorados, 550 m; USNM 212256 from 6 km E of Santo Domingo de los Colorados; AMNH 89749–50, KU 146194–96 from the Río Baba, 5–10 km SSW of Santo Domingo de los Colorados, 500 m; AMNH 111556, MCZ 90372–83, 92085 from Tinalandia, 15 km SE of Santo Domingo de los Colorados, 800 m; USNM 196869 from Río Cupa, Provincia Esmeraldas.

*Other specimens.*—KU 117792–93 (alizarin-alcian skeletons), KU 118136, (alizarin skeleton) and KU 118108 (larvae), same data as KU 117780–91.

*Diagnosis.*—A small species (♂ 24.1 mm, ♀ 25.7 mm; Table 1) of the *P. pustulosus* group having teeth on the maxilla and premaxilla, elongate gland posteriorly on flank, snout subacuminate with anterior margin of lip at the level of the margin of the nostrils, tympanic annulus granular, tympanum recessed and smooth, no tarsal tubercle and pattern of tubercles on dorsum consisting of scattered small tubercles and larger tubercles, some coalesced to form ridges.

The absence of a tarsal tubercle and the presence of maxillary and premaxillary teeth immediately distinguish *P. coloradorum* from the larger (♂ 31 mm, ♀ 35 mm) *P. petersi* and *P. pustulosus*, both of which also have the first finger noticeably longer than the second. The first finger is equal in length to the second in *P. coloradorum* and *P. pustulatus*. *P. pustulatus* differs from *P. coloradorum* by being larger (♂ 28.1 mm, ♀ 28.3 mm) and by having an elongate row of small glands on the flank, a round snout with the anterior margin of the lip at the level of the anterior edge of the nostrils, nontuberculate tympanic annulus, and a pattern of tubercles on the dorsum consisting of many small tubercles with large tubercles forming a pair of rows diverging posteriorly in the scapular region.

*Description.*—Size small; snout–vent length in 29 males 18.0–24.1 mm ( $\bar{x}$  = 20.4  $\pm$  SD 1.11), in 10 females 22.3–25.7 mm ( $\bar{x}$  = 23.6  $\pm$  1.00). Snout in dorsal view subacuminate, narrow; snout in lateral profile subacuminate, extending well beyond margin of lip; anterior edge of lip at level of posterior margin of nostrils; snout longer than length of eye; interorbital area level; canthus rostralis rounded, tuberculate; loreal region barely concave; lips not flared; tympanum small (less than half diameter of eye), re-

TABLE 1. SUMMARY STATISTICS FOR SNOUT-VENT LENGTH (SAMPLES 1-9 OF *P. pustulosus* ARE INDICATED IN FIG. 4).

Species (♂♂, ♀♀)	Mean $\pm$ SD Range		t-test probability
	Males	Females	
<i>P. coloradorum</i> (29, 10)	20.4 $\pm$ 1.11 18.0-24.1	23.6 $\pm$ 1.00 22.3-25.7	<0.0001
<i>P. petersi</i> (7, 2)	30.6 $\pm$ 1.03 28.4-31.6	— 32.2-35.8	—
<i>P. pustulatus</i> (8, 2)	26.2 $\pm$ 1.34 24.0-28.1	— 26.2-28.3	—
<i>P. pustulosus</i>			
9. W. Darién (22, 10)	26.0 $\pm$ 1.39 24.0-28.8	27.7 $\pm$ 1.66 25.4-30.8	0.0129
4. Cuyuni (8, 8)	26.3 $\pm$ 0.94 25.0-27.5	29.2 $\pm$ 1.70 26.4-31.2	0.0018
1. Tobago (12, 1)	26.6 $\pm$ 1.18 24.2-28.1	— 28.1	—
2. Trinidad (47, 11)	27.1 $\pm$ 1.42 24.0-29.8	30.4 $\pm$ 1.84 27.4-33.1	0.0001
7. Isla Taboga (7, 7)	27.6 $\pm$ 0.73 26.4-28.5	28.8 $\pm$ 2.27 25.6-31.9	0.2229
6. Bolívar-Antioquia (9, 2)	27.7 $\pm$ 1.19 26.5-29.9	— 27.8-31.2	—
5. Magdalena (5, 6)	28.6 $\pm$ 2.36 24.9-30.7	29.0 $\pm$ 2.15 26.1-31.1	0.7996
8. E. Darién (9, 9)	28.7 $\pm$ 1.54 25.8-31.0	31.4 $\pm$ 3.26 24.0-34.6	0.0405
3. Guaraúnos (47, 0)	30.3 $\pm$ 1.03 28.6-32.8	— —	—

cessed, smooth; tympanic annulus granular; supratympanic fold short, consisting of two or three granules, terminating posteriorly in large, triangular, glandular area; large tubercle at angle of jaws.

Forelimbs slender; row of tubercles on ventrolateral edge of forearm; fingers slender, 1 = 2 = 4 < 3; webbing and fringes absent; subarticular tubercles large, subconical; supernumerary tubercles small, subconical, present only on proximal segments; palmar tubercle large, broadly ovoid; prepollical tubercle large, elongately ovoid; nuptial excrescences on inner surfaces of thumbs in males, finely spinous, pale brown. Hind limbs short; tibia 48.5% of snout-vent length; foot 10.0% of snout-vent length; ventral surface of tarsus having many small tubercles but no distinct, large tarsal tubercle; outer metatarsal tubercle small, conical; inner

metatarsal tubercle elliptical; toes long, slender, 1 < 2 < 5 < 3 < 4; subarticular tubercles large, subconical; supernumerary tubercles numerous on proximal segments, minute; toes webbed basally; fringes absent.

All dorsal surfaces bearing small tubercles; large tubercles on head and body. Some coalesced to form canthal, interorbital, postorbital, occipital, scapular, and paravertebral ridges. Flank gland elongate, narrowly elliptical, on upper part of posterior two-thirds of flank. Skin on venter smooth. Anal opening directed posteriorly at upper level of thighs, lacking sheath or folds. Choanae small, round, widely separated; tongue elongate, widest posteriorly, free posteriorly for about one-third its length. Vocal slits parallel to rami of jaw; vocal sac median, subgular, when inflated extending laterally well beyond sides of head.

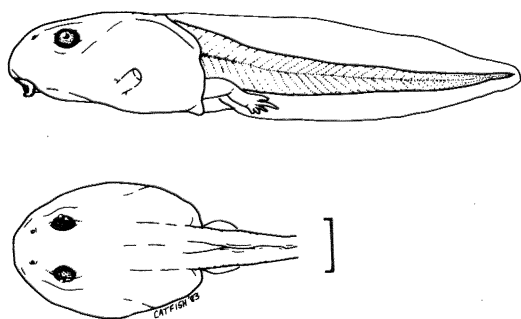


Fig. 3. Lateral and dorsal views of the larva of *P. coloradorum* (KU 118108). Scale equals 2 mm.

Color in preservative: Dorsum of head and body dark grayish brown with or without darker interorbital bar and darker chevron-shaped mark in scapular region; cream middorsal line present from sacrum posteriorly. Upper lip with or without faint grayish white diagonal bars. Flanks uniformly dark brown; limbs brown with dark brown bar on each segment, except upper arm. Venter dark brown with tendency for mid-ventral white streak on throat and chest; belly mottled with white; ventral surfaces of limbs brown.

Color in life: Dorsum brown with or without orange-brown middorsal stripe posteriorly; forelimbs orange-brown with dark brown markings; hind limbs orange-brown with dark brown to black bars; posterior surfaces of thighs brown with few cream flecks; venter black, heavily mottled with white or bluish white, becoming dark brown on flanks and hind limbs; iris pale grayish brown or dull bronze with fine black reticulations.

*Measurements of holotype (in mm).*—Snout–vent length 20.0, tibia length 9.7, foot length 10.0, head length 8.1, head width 7.9, eye 2.7, eye–nostril 2.0, tympanum 1.2.

*Tadpoles.*—A series of *Physalaemus* tadpoles was collected from a shallow puddle at the edge of a field at Santo Domingo de los Colorados on 4 March 1968. Because *P. coloradorum* is the only species of the genus known from this region, we assign these tadpoles to that species. The lot (KU 118108) consists of six larvae, two of which are in very poor condition. The other four are at stages 37 to 39 (Gosner, 1960); the SVL of these ranges from 7.2 to 8.3 and the

total length from 15.6 to 20.3 mm. A tadpole at stage 38 has a SVL of 7.2 mm and total length of 19.3 mm (Fig. 3).

Body widest at midbody (at level of spiracle), wider than deep; snout short, rounded in lateral view; eyes small, close together, oriented dorsolaterally; nostrils closer to eyes than to tip of snout, directed almost dorsally; spiracle sinistral, directed posterodorsally, its opening at about midlength of body. At midlength of tail, caudal fins slightly deeper than slender caudal musculature; tail rounded at tip; dorsal fin not extending onto body. Mouth anteroventral, barely wider than internarial distance; upper lip bare medially; one row of labial papillae laterally; lower lip bearing one continuous row of papillae; moderately deep lateral fold bearing two or three rows; beaks slender, broad, serrate; two upper and three lower rows of denticles; second upper row interrupted medially.

In life, pale gray; tail transparent, flecked with light brown (Field notes of J. D. Lynch, 4 March 1968). In preservative, dorsal surface of body brown; ventral surface transparent; fins transparent; caudal musculature pink, both flecked with brown.

*Etymology.*—The specific name is a patronym for the Colorado Indians who live in the area inhabited by this species of *Physalaemus*.

*Remarks.*—Foam nests have been observed in temporary ponds. Breeding occurs at least from 4 March to 9 June. The photograph of “*P. pustulatus*” on page 492 of Lynch (1970) is actually *P. coloradorum*.

*Distribution.*—This species is known from a rather limited area on the Pacific lowlands and foothills of the Andes (to elevations of 800 m) in western Ecuador (Fig. 4). The distance between the northernmost locality (Río Cupa) and the southernmost locality (Río Baba) is only 110 km. The Río Baba is a tributary of the Río Palenque, on which about 35 km south of the southernmost locality is the Centro Científico Río Palenque. Extensive field work at the Centro Científico and at Quevedo, some 50 km further south, has not revealed the presence of *Physalaemus*. All of the localities from which *P. coloradorum* is known lie in the vegetation zones of humid tropical forest (Río Cupa) or very humid tropical forest (all others), according to Holdridge’s (1964) classification (Mapa Ecológico . . . Ecuador, 1963). There is a hiatus of

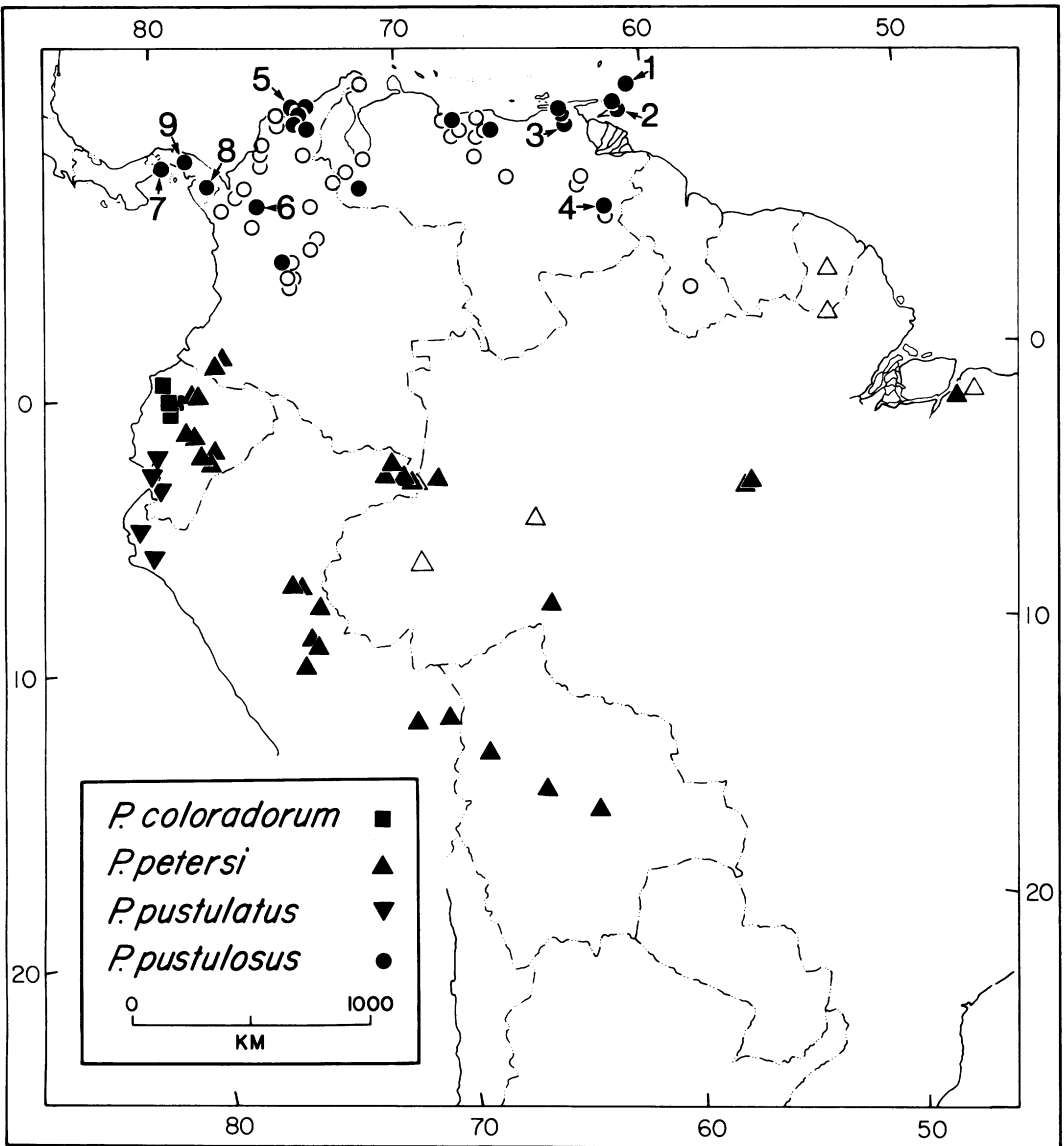


Fig. 4. Distribution of the *P. pustulosus* group in South America. Numbered localities are discussed in the text under the account of *P. pustulosus*, and in Table 1. Open symbols represent literature records.

about 215 km between the ranges of *P. coloradorum* and *P. pustulatus* in very dry tropical forest (Holdridge, 1964) at Guayaquil.

*Physalaemus petersi* (Jiménez de la Espada)  
Fig. 1

*Engystomops petersi* Jiménez de la Espada, 1872;  
type locality "Oriente en el Ecuador."

*Eupemphix paraensis* Müller, 1923; type locality  
"Peixeboi (an der Bragancabahn), Staat Para,  
Nord-Brasilien."

*Eupemphix schereri* Myers, 1942; holotype CAS-  
SU 6317 from "Pevas, at the mouth of the  
Ampiyacu River, Amazonian Peru," Depart-  
amento Loreto.

*Eupemphix freibergi* Donoso-Barros, 1969; ho-  
lotype Donoso-Barros collection (Univ. Con-

cepción, Chile) 745 from "Runerrabaque, Rio Beni, Bolivia," (misspelling of Rurrenabaque, Departamento El Beni). New Synonymy.

*Diagnosis.*—A large species (♂♂ 31.6 mm, ♀♀ 35.8 mm; Table 1) of the *P. pustulosus* group lacking teeth on the maxilla and premaxilla, having an elongately ovoid gland medially on the flank, snout acuminate with anterior margin of lip at a level posterior to the nostrils, tympanic annulus usually well defined at least ventrally, tympanum smooth, tarsal tubercle large, and pattern of tubercles on dorsum consisting of small tubercles with scattered larger tubercles tending to form diverging rows in the occipital and scapular regions in less than one-fourth of the specimens.

The presence of a tarsal tubercle and absence of maxillary teeth immediately distinguishes *P. petersi* from *P. coloradum* and *P. pustulatus* both of which are smaller (♂♂ 28.1 mm, ♀♀ 28.3 mm) and have the first finger equal in length to the second. The first finger is noticeably longer than the second in *P. petersi* and *P. pustulosus*, the only other cis-Andean species. *P. pustulosus* differs from *P. petersi* by having a more elongate gland on the flank, a subacuminate snout with the anterior margin of the lip at the level of the posterior margin of the nostrils, a tuberculate tympanic membrane, and a pattern of tubercles on the dorsum consisting of randomly scattered large and small tubercles or the large tubercles forming longitudinal rows or chevrons. Furthermore, *P. pustulosus* lacks the large black inguinal spots characteristic of *P. petersi*.

*Variation.*—Intraspecific variation in coloration and dorsal tuberculation is exhibited in this species. For purposes of comparison, we have used Ecuadorian frogs from Mera (N = 11) and the Santa Cecilia area (N = 17), Peruvian specimens from the Río Pachitea (N = 6) and Tambopata (N = 4), Bolivian frogs from Chipiriri (N = 4) and Buenavista (N = 6), and Brazilian specimens from Igarape Belém (N = 30) and Belém (N = 18). A larger sample of frogs from Igarape Belém (N = 345) was employed for the study of the frequency of two color morphs. There is minor variation in the disposition of the dorsal tubercles, and noteworthy variation in the dorsal and ventral coloration. Only adult specimens from Belém, Brazil, were used for statistics of SVL (Table 1).

The dorsal tuberculation in all frogs consists of small regularly distributed dorsal tubercles with larger tubercles scattered irregularly, but

rarely forming a pattern. However, in all populations 10 to 20% of the frogs exhibit faint interorbital, occipital, or scapular rows of tubercles. These patterns never approach the degree of tuberculation seen in the other species of the group, nor is the variation as impressive as in *P. pustulosus* (Freeman, 1967).

The dorsal and flank coloration in preservative varies from pale gray or tan with diffuse darker markings to uniform dark brown. At Santa Cecilia the frogs have a gray to gray-brown dorsum. At Mera the frogs are brown dorsally, except for three specimens that have a distinctly pale snout and flanks (hereafter referred to as the pale morph). Frogs from Belém are mostly brown, although some are gray-brown; a few have darker mottled areas on the gray (no pale morphs). The frogs from Igarape Belém are uniformly brown dorsally; 52 of 345 specimens were the pale morph. The frogs from the Río Pachitea are brown to dark brown (none pale). At Tambopata the frogs are pale gray to gray-brown, with darker mottling in two of the four (no pale morphs). The frogs from Chipiriri, Bolivia, are brown with darker brown markings (no pale morphs). Frogs from Buenavista are pale brown to brown, with darker mottling in some (no pale morphs).

More pronounced variation is exhibited in the ventral coloration. Frogs from Mera, Ecuador, have dark brown throats and chests; large, discrete black-brown blotches are present on the off-white abdomen. A midventral pale line is distinct in most, but indistinct in others. Frogs from Santa Cecilia have gray to brown chests and throats; the abdominal blotches are smaller and more numerous, and the midventral line more distinct, than in the frogs from Mera.

The throats and chests are brown in the frogs from the Río Pachitea; dark blotches are few and more diffuse than in the Ecuadorian specimens. The midventral line is scarcely evident or absent. Frogs from Tambopata have a pale gray-brown throat and chest; as in the other Peruvian frogs, the abdominal blotches are few or absent, and the midventral line indistinct. The throat and chest are tan in the frogs from Chipiriri; the blotches are few and diffuse, and the midventral line indistinct. Some of the frogs from Buenavista appear faded; the chin and chest are pale to dark brown. The ventral blotches are few, small and diffuse, or absent in some frogs. The midventral line is barely evident.



At Belém the throat and chest are gray-tan to brown; the blotches are discrete and larger than those of the frogs from Santa Cecilia, but not as large as those from Mera. The midventral line is absent in most, but barely evident in a few. The frogs from Igarape Belém have a pale gray or tan throat and chest, and a few are brown. The blotches are gray to dark brown, similar in size to those in frogs from Santa Cecilia; the midventral stripe is distinct in a few but indistinct in most.

Coloration in life has been summarized from field notes of various collectors. Belém, Brazil (M. L. Crump): Dorsum dark grayish brown with orange middorsal line posteriorly in some; forelimbs golden brown with brown bars; hind limbs brown with black bars. Flanks orange-brown. Chin, throat, chest and anterior part of belly dark brown with white flecks on chest; posterior part of belly, groin, and anterior and ventral surfaces of thighs pale gray with black and pale blue bold mottling.

Santa Cecilia, Ecuador (W. E. Duellman): Dorsum dull brown with tips of tubercles red or orange and in some individuals small, dark brown spots; limbs brown with dark bars. Flanks creamy yellow anteriorly, becoming orange posteriorly in larger frogs, with large black spots. Throat and chest dark gray with minute white flecks and usually a median cream line; posterior part of belly and ventral surfaces of thighs white or gray with bold black mottling. Iris dull bronze.

Mera, Ecuador (J. D. Lynch): Dorsum brown with tips of tubercles red; brown with dark brown bars edged with black. Flanks orange. Throat and chest dull yellowish brown; belly and hidden surfaces of thighs black with white or bluish white spots.

Chipiriri, Bolivia (T. H. Fritts): Dorsum dark tan with irregular brown marks and faint beige middorsal line posteriorly; limbs tan with dark brown bars. Flanks reddish orange. Throat and chest dark gray with median white line; belly greenish white with black spots; inguinal region and thighs mottled black and bluish white. Iris bronze.

Close inspection of color transparencies of living frogs reveals the presence of orange-tipped tubercles in specimens from Belém, Chipiriri and Santa Cecilia and red-tipped tubercles in specimens from Mera and some specimens from Santa Cecilia. Donoso-Barros (1969) noted in the type description of *Eupemphix freibergi*

that in that species "los tuberculos mas prominentes presentan puntos rojos mas claros."

*Tadpoles.*—Tadpoles of this species from Mera, Ecuador, were described by Duellman (1978). A striking feature is the paired elliptical glands located at midlength of the body (see Comparisons).

*Remarks.*—Foam nests float on the surfaces of temporary pools in which the tadpoles develop. Peters (1955) noted that the type locality was probably in Napo-Pastaza province. Jiménez de la Espada (1875:163), in his second and more detailed account of the species, cited "Archidona, provincia Oriental del Ecuador, cerca de las orillas del rio Napo" as the source of the two specimens he examined, most likely the type material.

Boulenger (1882) confused some specimens from Amazonian Ecuador (Sarayacu and Canelos) with *P. stentor*, a species named from Isla Taboga, Panama, and a name considered to be a junior synonym of *P. pustulosus*. Gorham (1966) implied that there was some confusion about the type locality of *P. stentor*, but it is clear from the itinerary of Espada and the illustration of *P. stentor* (Jiménez de la Espada, 1875) that the type locality is not in error.

We examined USNM 196855 from the province of Esmeraldas on the Pacific slopes of Ecuador. The specimen is correctly identified, but we consider the locality data to be in error, because *P. petersi* does not occur west of the Andes.

*Distribution.*—This species is widely distributed in the upper Amazon Basin, and it occurs to elevations of 1,140 m in the foothills of the Andes; in the lower Amazon Basin it is known only from the vicinity of Belém near the mouth of the Rio Amazonas (Fig. 4). It also occurs in the eastern Guianan region (Lescure, 1976). *Physalaemus petersi* seems to be primarily an inhabitant of rainforest, although some individuals have been found in clearings. Throughout most of its range, *P. petersi* does not occur in sympatry with any other species of *Physalaemus*. However, in the vicinity of Belém, Brazil, it occurs with *P. ephippifer* which is more abundant and has a broader ecological distribution than *P. petersi* (Crump, 1971). The range of *P. petersi* in Bolivia seems to be restricted to humid forested regions, but few specimens are known.

Apparently its range does not overlap those of species of *Physalaemus* characteristic of more open and seasonal environments to the east and south, where *P. cuvieri*, *P. biligonigerus*, and *P. nattereri* have been reported (Gans, 1960).

*Justification of synonymy.*—Failure to compare specimens with topotypic material of named taxa has resulted in a multiplicity of names that have been applied to this widespread species. Moreover, there has been confusion of the generic status of many species now placed in *Physalaemus*. Fortunately we could examine recently collected specimens from near the type localities of all of the nominal species. Our comparisons suggest the existence of only one species.

In his description of *P. freibergi*, Donoso-Barros (1969) stated that *P. petersi* had smooth dorsal skin, in contrast to the warty skin of *P. freibergi*, and used this as one of his principal diagnostic features. Lynch (1970) recognized *P. freibergi* as a distinct species, apparently on conclusions he drew from Donoso-Barros' poor drawing. The drawing shows a prominent tubercle on the tarsus, which Lynch interpreted to be a heel (rather than inner tarsal) tubercle, and thus unique in the *pustulosus* group. However, Donoso-Barros (1969:184) stated: "Un tuberculo tarsal trihedral prominente con un corto espolon," indicating the inner tarsal tubercle commonly found in species of *Physalaemus*.

Lynch (1970) considered the nominal taxon *schერი* to be synonymous with *petersi*, but did not examine specimens of the former. We examined the holotype and paratypes of *Eupemphix schერი* and compared them directly with specimens of *P. petersi*, and consider them to be conspecific. The specimens agree in all diagnostic features. In his description of the species, Myers (1942) considered *P. schერი* to be close to *P. petersi*. The differences he noted in *P. schერი* were the half obscured tympanum, the longer first finger, and the presence of smooth flat warts on the dorsum. Myers examined no material of *P. petersi* and apparently relied on Espada's 1872 description. Jiménez de la Espada's (1875) later and more complete account described the skin as smooth, yet glandular, the tympanum as "muy perceptible," and the first and second fingers "casi iguales."

The degree of exposure of the tympanum depends on mode of preservation and the size of the animal, because the supratympanic fold

may partially hide the tympanum in larger animals. Both descriptions indicate the presence of warty (glandular) areas on the dorsum, and the comparison of finger lengths is often subjective. The supposed differences between the species are not apparent when hundreds of specimens are compared.

*Physalaemus pustulatus* (Shreve)

Figs. 1, 2

*Edalorhina pustulata* Shreve, 1941; holotype MCZ 7666 from "Guayaquil," Provincia Guayas, Ecuador.

*Diagnosis.*—A moderate-sized species (♂ 28.1 mm, ♀ 28.3 mm; Table 1) of the *P. pustulosus* group having teeth on the maxilla and premaxilla, an elongate row of glands on the flank, snout round with anterior margin of lip at the level of the anterior margin of the nostrils, tympanic annulus well-defined at least ventrally, tympanum smooth and not recessed; tarsal tubercle absent, and pattern of tubercles on dorsum consisting of small tubercles with some larger tubercles forming rows that diverge posteriorly in the scapular region.

The absence of a tarsal tubercle and the presence of teeth on the upper jaw immediately distinguish *P. pustulatus* from *P. petersi* and *P. pustulosus*, both of which are larger (♂ 31 mm, ♀ 35 mm) and have the first finger noticeably longer than the second. The first finger is equal to the second in *P. pustulatus* and *P. coloradum*. *P. coloradum* differs from *P. pustulatus* by being smaller (♂ 24.1 mm, ♀ 25.7 mm) and by having a single elongate gland on the flank, a subacuminate snout with the anterior margin of the lip at the level of the posterior margin of the nostrils, a tuberculate tympanic annulus, and a pattern of small tubercles on the dorsum with many large tubercles coalesced to form ridges. *P. pustulatus* is much less "warty" than *P. coloradum*.

*Remarks.*—In living specimens from Motupe, Peru, the dorsum was olive-tan with dark, dull olive-green markings on the body and dark brown transverse bars on the limbs. A faint, creamy white labial stripe was present. The flanks were grayish-green. The venter was white with gray flecks on the chest; the anterior part of the vocal sac was dark gray. The ventral surfaces of the hind limbs were pink. The iris was

pale bronze with fine black reticulations. Field notes by Charles W. Myers on a specimen from Pasaje, Ecuador, indicate that the dorsum was grayish brown with black markings and limb bars. The flanks, suborbital area, upper arms, and anterior surface of the thighs were orange-brown. The throat was gray with a white line extending into some black spots on the chest; otherwise, the venter was white. The iris was bronze-brown, becoming gray below the pupil.

Despite differences in colors in life between northern and southern parts of range, structural features of specimens throughout the range are essentially the same. In preserved frogs the chest is more heavily pigmented in northern specimens (Guayaquil and Pasaje, Ecuador) than in southern specimens (Motupe, Peru).

At a locality 7 km south of Motupe, Departamento Lambayeque, Peru, on 2 March 1975, males were calling from shallow water in muddy ditches in scrub savanna. On 3 March 1975, many foam nests were observed floating on the water in roadside ditches between Motupe and Olmos, 27 km N of Motupe.

The photograph of "*P. pustulatus*" (KU 117780) in Lynch (1970) is actually *P. coloradum*.

**Distribution.**—*Physalaemus pustulatus* occurs on the coastal lowlands (up to elevations of 130 m) of southern Ecuador and northern Peru (Fig. 4). In this region it inhabits dry environments, including very dry tropical forest in the north and subtropical desert in the south (Tosi, 1960; Holdridge, 1964).

*Physalaemus pustulosus* (Cope)  
Fig. 1

*Paludicola pustulosa* Cope, 1864; type locality "New Grenada, on the River Truando," Colombia.

*Bufo stentor* Jiménez de la Espada, 1872; type locality "Isla de Taboga," Panama.

*Eupemphix trinitatis* Boulenger, 1889; type locality "Trinidad."

*Bufo atrigularis* Werner, 1899; type locality "Arima auf Trinidad."

*Eupemphix ruthveni* Netting, 1913; holotype UMMZ 45582 from "Fundacion, Colombia," Departamento Magdalena.

**Diagnosis.**—A large species (♂♂ 32.8 mm, ♀♀ 34.6 mm; Table 1) of the *Physalaemus pustulosus* group

lacking teeth on the maxilla and premaxilla, having an elongately elliptical gland medially on the flank, snout subacuminate with the anterior margin of the lip at the level of the posterior edge of the nostrils, tympanic annulus not evident externally, tympanum tuberculate, tarsal tubercle large, and pattern of tubercles on dorsum consisting of randomly scattered large and small tubercles or the large tubercles forming longitudinal rows or chevrons.

The presence of a tarsal tubercle and absence of maxillary teeth immediately distinguish *P. pustulosus* from *P. coloradum* and *P. pustulatus*, both of which are smaller (♂♂ 28.1 mm, ♀♀ 28.3 mm) and have the first finger equal in length to the second. The first finger is noticeably longer than the second in *P. pustulosus* and *P. petersi*. *Physalaemus petersi* differs from *P. pustulosus* by having a more ovoid gland on the flank, an acuminate snout with the anterior margin of the tip at a level posterior to the nostrils, a smooth tympanic membrane, and a pattern of tubercles on the dorsum consisting of small tubercles and scattered large tubercles tending to form diverging rows in occipital and scapular regions in some specimens. Furthermore, *P. petersi* has a large black spot or mottling in the inguinal region, a character absent in *P. pustulosus*.

**Distribution.**—In South America, *P. pustulosus* occurs along the Caribbean lowlands from northwestern Colombia eastward nearly to the mouth of the Río Orinoco; it also occurs in the Cauca and Magdalena valleys in Colombia, in the llanos of Venezuela, in savannas in Guyanan Venezuela and Guyana, and on the islands of Trinidad and Tobago (Fig. 4). In Middle America the species is widely distributed in the lowlands from central Veracruz and southern Oaxaca, Mexico, through Panama, including Isla Taboga. The species primarily inhabits open thorn scrub forests and savannas at elevations of less than 300 m but also enters rainforests. At widely scattered localities from Mexico to South America it reaches elevations in excess of 1,000 m; in South America these are at 1,400 m at 1 km W of Valdivia, Antioquia, Colombia, and at 1,100 m at Turgua, Miranda, Venezuela (Alemán, 1952). In the Venezuelan llanos and savannas, *P. pustulosus* occurs sympatrically with *P. enesefae*, a smaller species (♂♂ 28 mm, ♀♀ 32 mm) that has a noticeably different call produced by males from secluded sites at the margins of temporary ponds.

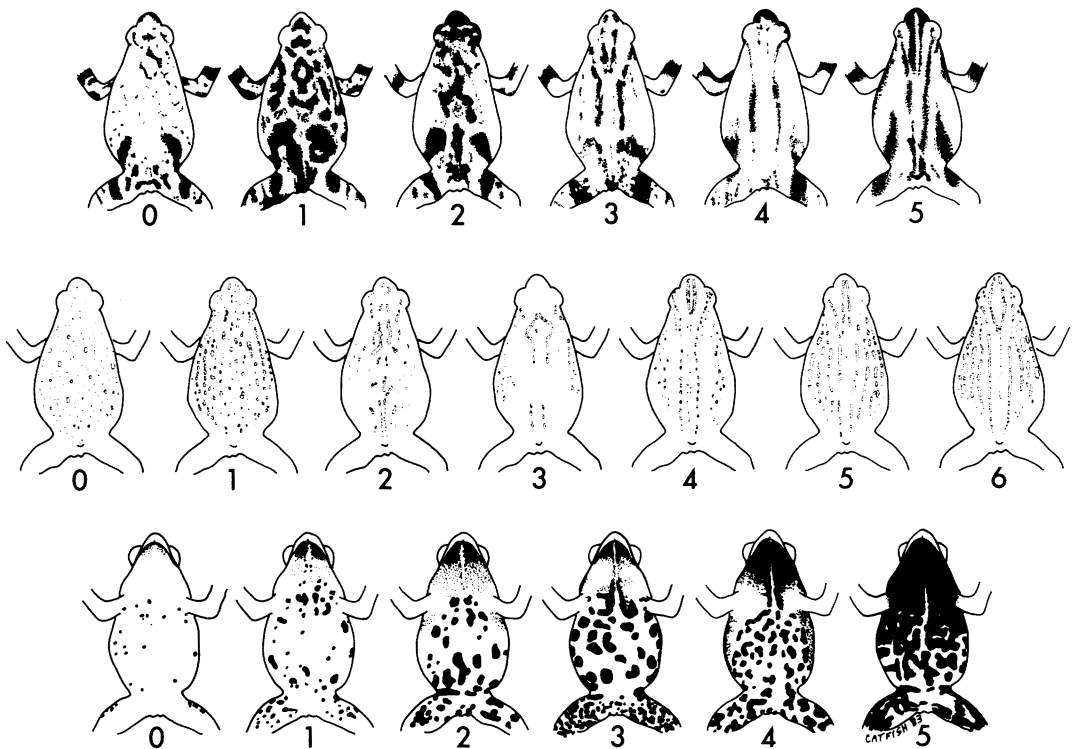


Fig. 5. Coded states of dorsal coloration (top), dorsal pustule pattern (middle) and ventral coloration (bottom) for *P. pustulosus*. Redrawn from Freeman (1967).

*Tadpoles*.—The tadpoles of this species have been described from Darién, Panama (Breder, 1946) and Trinidad (Kenny, 1969).

*Variation*.—We examined frogs of this species from throughout the range in Middle America and northern South America. We selected the following samples of adults from combined localities, which are numbered in Fig. 4: 1) Tobago ( $N = 13$ ). 2) Trinidad ( $N = 59$ ); 3) Guaraúnos and Río Sabacual, 7 km S Guaraúnos, Estado Sucre, Venezuela ( $N = 47$ ); 4) 13 km S of Río Cuyuni, Estado Bolívar, Venezuela ( $N = 16$ ); 5) Fundación (type locality of *ruthveni*) and other localities in the lowlands of Departamento Magdalena, Colombia ( $N = 11$ ); 6) three localities in the departments of Antioquia and Bolívar in north-central Colombia ( $N = 11$ ); 7) Isla Taboga, Panama ( $N = 14$ ); 8) Río Mono and Río Jaque, eastern Darién, Panama ( $N = 18$ ); 9) El Real and Río Chucunaque, western Darién, Panama ( $N = 32$ ). Each specimen was sexed, and the following data were taken: 1) snout–vent length, 2) ventral color pattern, 3)

dorsal color pattern, 4) pattern of pustules on dorsum. The patterns of coloration and pustules were coded in the manner described by Freeman (1967) (Fig. 5).

Contingency table analyses were performed on pairwise combinations of the ventral coloration, dorsal coloration, pustule pattern and sex variables. Each population was analyzed separately, and all populations were combined for an overall analysis. Association was significant ( $P < 0.05$ , Pearson's chi-square) for the following: Population 6 (sex vs pustules), Population 7 (sex vs dorsum), Populations 7 and 9 (sex vs venter), Populations 2, 3, 4, 6, 8 and 9 (dorsum vs pustules). When all samples were combined, the following associations were significant: sex vs pustules, sex vs venter and dorsum vs pustules.

Within populations the highly significant association of dorsal coloration with pustule pattern is because the dorsal pustules are pigmented; thus, by a priori delineation of character states the two variables are generally correlated.

In the combined analysis, the association of

sex with dorsal pustule pattern was significant at  $P = 0.01$ ; 42.6% of the females had states 0, 1, or 2 (less pustular), whereas only 23.5% of the males did. Conversely, 76.5% of the males had states 3, 5 or 6 (more pustular), as opposed to only 57.4% of the females.

The association of sex with ventral coloration was highly significant ( $P < 0.001$ ); 88.9% of the females, but only 47.6% of the males, have states 4 or 5.

Snout-vent length varies among the 9 localities (Table 1). Males are smallest ( $\bar{x} = 26.0$  mm) in Population 9 (western Darién) and largest ( $\bar{x} = 30.3$ ) in Population 3 (Guaraúños, Venezuela). Although these populations are near the extremes of the range of the sites studied, a geographical cline is not evident because frogs from eastern Darién (Population 8) are among the largest, and frogs from Cuyuni, Venezuela (Population 4) are among the smallest.

An analysis of variance on the SVL of males of all populations yielded a highly significant test ( $P \ll 0.0001$ ), indicating that the means of the groups are not equal. An a posteriori Student-Neuman-Keuls test (Sokal and Rohlf, 1981) shows that the mean SVL of the following subsets did not differ from one another (Table 1): Populations 9, 4, and 1; Populations 4, 1, 2, 7 and 6; Populations 2, 7, 6 and 5; Populations 7, 6, 5 and 8. Omitting Population 5 from the analysis yielded one less subset, but the results were otherwise the same. Population 3 (Guaraúños, Venezuela) differed from the others and is the largest in mean SVL. The mean SVL of 31 other males collected in amplexus at this site is 32.8. Measurements of freshly killed frogs were taken, and the range of SVL was 31–35 mm. We attribute the difference to preservation artifacts.

Within a population the males are generally smaller than females (Table 1). The mean SVL's of the 31 amplexant pairs (32.8, males; 35.8, females) were significantly different at  $P < 0.0001$ . Pearson's correlation coefficient between the SVL of amplexant males and females is  $-0.157$ ,  $0.50 > P > 0.20$ .

**Remarks.**—Lynch (1970) provisionally allocated the nominal species *Bufo stentor* to the synonymy of *P. pustulosus*. Our examination of topotypic material from Isla Taboga and the figure of *B. stentor* in Jiménez de la Espada (1875) supports Lynch's suggestion that the two nominal taxa are conspecific. Our characterization of *P. pustulosus* as edentate is based on the examination

of more than 500 specimens, from every country where the species occurs.

#### COMPARISONS

**Advertisement calls.**—Males of all four species have greatly distensible subgular vocal sacs that extend well beyond the lateral margins of the lips when inflated. Males of three species (*P. petersi*, *P. pustulatus* and *P. pustulosus*) call while floating on the surface of temporary pools, even from water that has accumulated in hoof prints. Males of *P. coloradorum* call from secluded sites in, or at the edge of, temporary pools—roots of partially submerged clumps of grass and under leaves and debris partially submerged in water.

The complex call of *P. pustulosus* has been described in detail by Drewry et al. (1982), and the biological significance of variation in the call was discussed by Ryan (1983). We present data for one individual of each of the other three species in comparison with the calls of two individuals of *P. pustulosus* (Fig. 6).

The calls of all species consist of a well-modulated note in which the first two harmonics are emphasized more than the others. The dominant frequency is the second harmonic in *P. pustulatus* and the first harmonic in the other species. All harmonics decline in frequency in the duration of the note. The beginning and ending frequencies of the dominant frequency and durations of the notes are: *P. coloradorum* 1,000 to 750 Hz, 0.10 sec; *P. petersi* 700 to 400 Hz, 0.06 sec; *P. pustulatus* 1,700 to 1,200 Hz, 0.12 sec; *P. pustulosus* 900–1,000 to 500–600 Hz, 0.13–0.14 sec. Note repetition rates probably are dependent on temperature, level of sexual excitement, and number of other males (Drewry et al., 1982). Note repetition rates (calls per minute) from recordings are: *P. coloradorum* 7, *P. petersi* 3, *P. pustulatus* 7 and *P. pustulosus* 7–20. The call of the latter species differs from the others by commonly having one or more secondary notes, at least the first of which is produced simultaneously with the latter part of the primary note.

**Osteology.**—In addition to the four species of the *P. pustulosus* group, alizarin, alizarin-alcian, and dried skeletons of the following species of *Physalaemus* were examined: *P. albonotatus*, *P. biligonigerus*, *P. centralis*, *P. cuvieri*, *P. enesefae*, *P. ephippifer*, *P. gracilis*, *P. maculiventris*, *P. nanus*, *P. nattereri* and *P. signiferus*. The skulls of *P.*

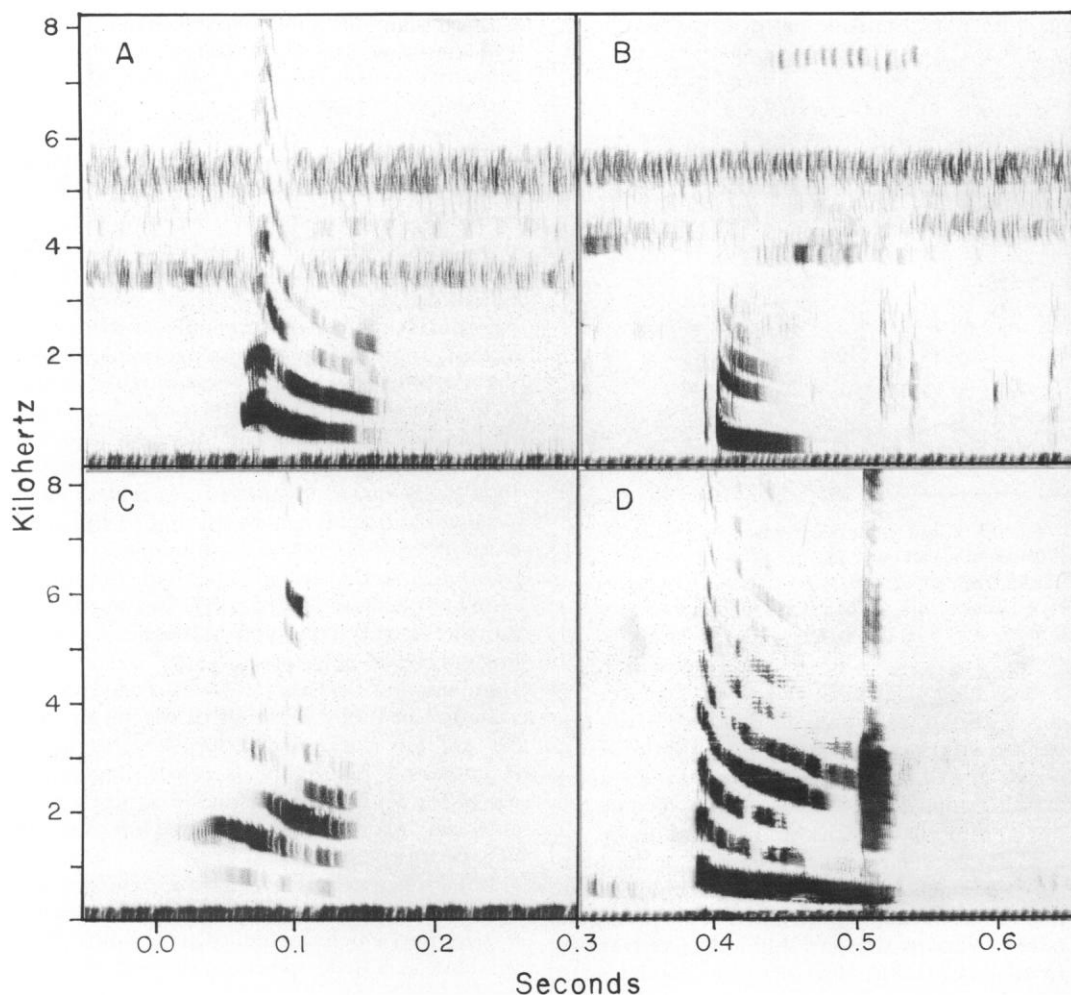


Fig. 6. Audiospectrograms of advertisement calls of species of the *pustulosus* group. A) *P. coloradorum* (recorded at Santo Domingo de los Colorados, Ecuador, by R. W. McDiarmid), B) *P. petersi* (KU 128267, KU Tape 967, 26 C), C) *P. pustulatus* (KU 162369, KU Tape 1220, 27 C), D) *P. pustulosus* (KU 108380, KU Tape 806, 29 C). Narrow band (45 Hz) analysis.

*pustulosus* and *P. ephippifer* were illustrated by Lynch (1971).

No skull bones are lacking in any of the species. In the *P. pustulosus* group the nasals and frontoparietals meet medially along the midline, except in male (but not female) *P. petersi*. The other species are similar except for *P. gracilis*, in which the medial edges of the nasals are rounded and do not touch.

In the *P. pustulosus* group, *P. petersi* and *P. pustulosus* lack teeth on the maxilla and premaxilla. Also, *P. maculiventris*, *P. nanus* and *P. nattereri* lack teeth. Lynch (1970) noted that the

teeth are lacking in *P. freibergi* (= *P. petersi*), *P. maculiventris*, *P. nanus*, *P. nattereri*, *P. obtectus*, *P. paraensis* (= *P. petersi*), *P. petersi*, *P. pustulosus*, *P. schereri* (= *P. petersi*), *P. signiferus* and *P. stentor* (= *P. pustulosus*). He examined alcoholic specimens as well as skeletons. Our data on alcoholic material support the observations of Lynch, except that the teeth are poorly developed, but present in *P. signiferus*.

None of the species has vomerine teeth. Lynch (1971) stated that prevomerine (=vomerine) teeth are present in some specimens of *P. bilinguigerus*. We examined 14 skeletons of this

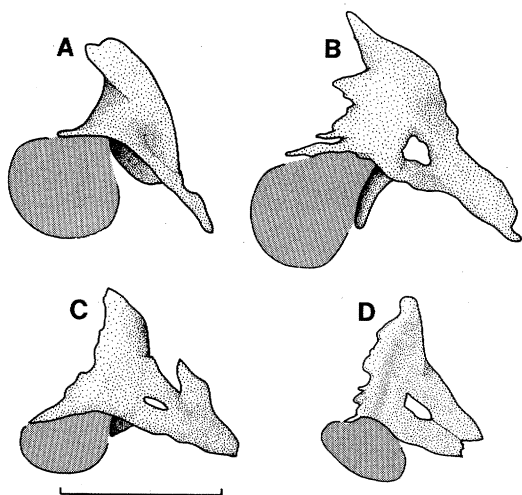


Fig. 7. Right vomers and choanae (shaded) of A) *P. pustulosus* (KU 68271, male), B) *P. centralis* (KU 92993, male), C) *P. ephippifer* (KU 127434, male) and D) *P. maculiventris* (KU 93022, male). Scale equals 1 mm.

species and found no vomerine teeth in the material that Lynch examined, or in additional material. The dentigerous processes of the vomers are long and thin in the *P. pustulosus* group, but not in the other species examined (Fig. 7).

In *P. pustulosus* and *P. coloradum* the pterygoid contacts the prootic; in the other species it does not reach the prootic. The pterygoid never overlaps the parasphenoid (contrary to Lynch, 1971:180). The occipital condyles are widely separated in all species, and all species possess columellae. The frontoparietals are not fused to the prootics, and the nasals do not contact the frontoparietals in any of the species examined.

Within the *P. pustulosus* group, the pterygoids are in contact with the palatines only in *P. pustulosus*. In the other species, the pterygoids are in contact with, or at least reach the level of the palatines in *P. biligonigerus*, *P. centralis*, *P. cuvieri* and *P. nattereri*. In all species of the *P. pustulosus* group the palatines contact the maxilla, except for some males of *petersi*. In *P. maculiventris*, *P. nanus* and *P. signiferus*, the palatines do not extend laterally to the maxilla but do reach the maxilla in the other species.

The pectoral girdle is fully arciferous in all species. The omosternum is thin and cartilaginous, although there is slight calcium deposition in some specimens of some species. There

is variation in the shape of the sternum within and among species. We recognize three rather subjective states: bifurcate, slightly bifurcate, and simple. No variation in sternum shape was observed in the following species, but in most only one skeleton was available: bifurcate: *P. albonotatus* (1), *P. biligonigerus* (2), *P. centralis* (1), *P. coloradum* (3), *P. nattereri* (2), *P. signiferus* (1); slightly bifurcate: *P. cuvieri* (1), *P. gracilis* (1), *P. enesefae* (1), *P. nanus* (1); simple: *P. maculiventris* (1), *P. pustulatus* (1). In *ephippifer* the sternum is simple in one specimen and bifurcate in four. In *petersi* the sternum is simple in two, slightly bifurcate in one, and bifurcate in one. In *P. pustulosus* the sternum is simple in four, slightly bifurcate in 13, and bifurcate in 67. Cei (1980) illustrated bifurcate sterna in *P. nattereri*, *P. biligonigerus*, *P. santafecinus*, *P. cuvieri*, *P. albonotatus* and *P. riograndensis*, slightly bifurcate sternum in *P. gracilis*, and simple sterna in *P. fernandezae* and *P. henseli*. The shape of the sternum has been used by Barrio (1965) as the only morphological character that diagnoses the sibling species *P. biligonigerus* and *P. santafecinus*. Duellman and Veloso (1977) also used sternal variation in their diagnoses of species of *Pleurodema*. The data on intraspecific variation in *P. pustulosus* (Fig. 8) and *P. petersi* suggest that use of sternal morphology as a diagnostic character when large sample sizes are not available may be unwise.

In all species there are eight procoelous presacral vertebrae. These are least well-ossified in *P. petersi*, in which the neural arches of the first vertebra in a male specimen do not meet medially.

Lynch (1971, character 50) described the tympanum as usually concealed, and visible externally in *P. pustulatus*. Our observations indicate that it is at least partially visible in most species (including *P. pustulatus*) but concealed in *P. maculiventris*, *P. henseli*, *P. olfersi* and *P. gracilis*.

Examination of the tympanic annulus in alizarin-alcian skeletons shows that *P. coloradum* has a much smaller tympanic annulus than other members of the group (Fig. 9).

**Hyoid apparatus.**—Alizarin-alcian blue preparations of *P. ephippifer* and *P. enesefae* and all species in the *P. pustulosus* group were examined. In addition, the following species were dissected: *P. petersi*, *P. pustulatus*, *P. albonotatus*, *P. biligonigerus* and *P. signiferus*. In *P. coloradum* and *P. pustulatus* the alary processes of the

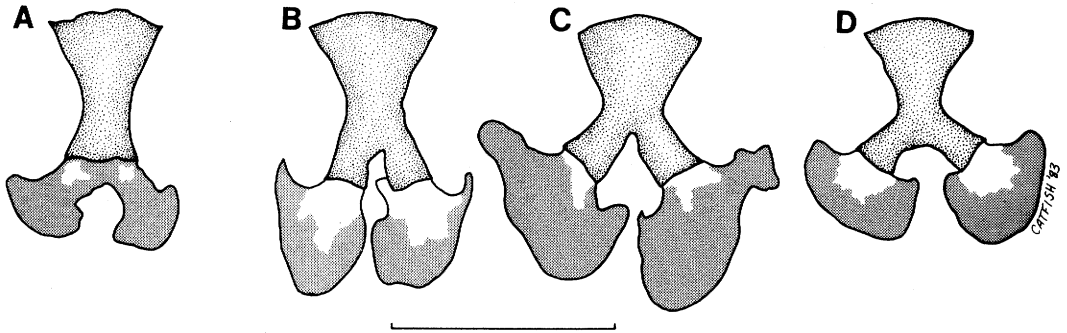


Fig. 8. Intraspecific variation in the sternum of male *P. pustulosus*: A) KU 61931, 27.7 mm SVL from El Salvador: San Salvador: San Salvador Instituto Tropical, B) KU 61928, 27.5 mm SVL from same locality, C) KU 108358, 27.7 mm SVL from Panama: Darién: El Real, D) KU 42776, 25.1 mm SVL from Nicaragua: Managua: 3 km N Sabana Grande. Scale equals 2 mm. Stippled areas = bone, shaded areas = cartilage and white areas = calcified cartilage.

hyoid plate are narrowly stalked. In *P. pustulosus*, *P. petersi* and the other species they are broad and wing-like.

Lynch (1971) stated that *Physalaemus* is characterized by the "myobatrachine pattern" of muscle insertion on the hyoid plate (character 37, p. 182). This means that the anterior petrohyoid muscle inserts on the midventral surface of the alary process, as opposed to the "cycloranine pattern," in which the insertion is on the lateral edge of the hyoid plate, as it is in the lymnodynastines (=cycloranine of Lynch, 1971). Heyer (1974) stated that in *P. albonotatus*, *P. biligonigerus*, *P. fuscomaculatus*, *P. nattereri* and *P. signiferus* the insertion of the anterior petrohyoid muscle is on the midventral surface ("myobatrachine pattern"). The other species that we examined have the myobatrachine pattern, and our data confirmed Heyer's observations. Trewavas (1933) reported the same condition in *Eupemphix* (= *Physalaemus*) *nana* and *Physalaemus cuvieri*.

Anterior processes of the hyale are poorly developed in some specimens of *P. pustulosus* and *P. petersi*, and well-developed in other specimens of these two, as well as in *P. pustulatus*, *P. coloradum* and the other species examined. The variation in *P. pustulosus* and *P. petersi* probably reflects the large samples of these two species. The posterolateral processes are long and narrow and the bony posteromedial processes are present in all species. Lynch (1971) figured the hyoid plate of "*P. pustulatus*." This may be a mistaken identification because the morphology of the hyoid plate in his illustration

differs substantially from the specimens we examined.

**Larvae.**—Tadpoles are available for three of the four species of the *P. pustulosus* group. The larvae of *P. petersi* are easily distinguished from those of *P. pustulosus* and *P. coloradum* (as well as all other species of *Physalaemus*) by the presence of paired elliptical glands on each side of the vertebral column at midlength of the body. These glands are homologous with similar glands seen in adults of the *P. pustulosus* group, but do not develop in larvae of *P. pustulosus* and *P. petersi* until after metamorphosis. Moreover, these glands are present in larvae with a body length of 2–3 mm. We are unaware of such glandular development in any other tadpole,

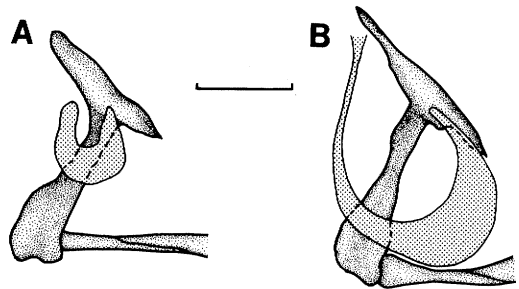


Fig. 9. Right squamosal and tympanic annulus (shaded of A) *P. coloradum* (KU 117793, male) and B) *P. pustulosus* (KU 108358, male). Scale equals 1 mm.



and this precocious development certainly merits further study.

The larvae of *P. petersi* are about twice the body length of larvae of the other two species in the same stage of development. The mottled pigments are the most widely distributed in *P. petersi*.

The larvae of *P. coloradum* and *P. pustulosus* are almost indistinguishable to the naked eye. Comparisons of these two have been based on *P. pustulosus* (KU 116713) from Darién, Panama, the region most proximate to *P. coloradum* for which larvae are available. The coloration of the two tadpoles is quite similar; the larvae of *P. pustulosus* appear to be slightly larger. A few subtle differences are present. The nostrils in the *P. coloradum* larvae are directed almost dorsally, whereas those in *P. pustulosus* are directed more laterally. The papillae of the lower lip appear to be longer in *P. coloradum* than in *P. pustulosus*. Also, the width of the oral disc is relatively greater in *P. coloradum* than in *P. pustulosus*. We have quantified this difference as follows: Four larvae of *P. coloradum* and 20 larvae of *P. pustulosus* at similar stages (37 to 39) were measured in arbitrary units under the microscope. The median ratio of oral disc width to body length for *P. coloradum* is 0.242 (0.229–0.258); that of *P. pustulosus* is 0.192 (0.171–0.221). The ranges are non-overlapping. A non-parametric Mann-Whitney U test (Sokal and Rohlf, 1981) for equality of the samples is significant at  $P = 0.002$ .

Geographic variation is evident in size and coloration of *P. pustulosus* larvae. Larvae from Río Sabacual, Venezuela (KU 167803) are larger and possess less pigment than the larvae from Darién, Panama. This corresponds to the adults; those from Darién are smaller and more darkly pigmented.

#### DISCUSSION

*Monophyly of the P. pustulosus group.*—Four characters possessed by all members of the *P. pustulosus* group but by no other *Physalaemus* are: 1) parotoid glands, 2) elliptical flank glands, 3) warty, pustular skin, and 4) thin dentigerous processes of the vomers. One might hypothesize that these are synapomorphies for the *P. pustulosus* group, because their occurrence is unique within the genus. However, if the *P. pustulosus* group is a primitive grade in the genus, these characters may be primitive rather than derived (Wiley, 1981). In order to avoid an error in

interpretation we have examined the character-states of appropriate outgroups: *Pseudopaludicola* and *Pleurodema*.

We have assumed that the genus *Physalaemus* is monophyletic. This position has been taken by Heyer (1974, 1975) who listed several derived characters for the genus. Heyer (1974) examined five species of *Physalaemus*, and considered the genus *Pseudopaludicola* to be the sister-group of that genus. *Pleurodema*, in turn, was the sister-group to *Physalaemus* + *Pseudopaludicola*. Heyer (1975) analyzed the intergeneric relationships of the family Leptodactylidae, treating *Physalaemus* as monophyletic. Of three cladograms presented, in the first two *Pseudopaludicola* was considered to be the sister-group of *Physalaemus*, but in the third (Heyer's preferred) cladogram *Pleurodema* was the sister-group. In that tree *Pseudopaludicola* was the sister-group to *Edalorhina*. Thus, the choice of *Pseudopaludicola* and *Pleurodema* as outgroups to *Physalaemus* is justified at this point (although we later suggest that *Pseudopaludicola* is derived from within the genus *Physalaemus*).

The thin dentigerous processes of the vomers are found only in the *P. pustulosus* group and not in other *Physalaemus*, *Pleurodema* or *Pseudopaludicola*. Although some *Pleurodema* and *Physalaemus* possess glands on various parts of the body (Lynch, 1971; Duellman and Veloso, 1977), only the *P. pustulosus* group has discrete parotoid and flank glands. The pustular skin of the *P. pustulosus* group is unique in *Physalaemus*. Some *Pleurodema* and *Pseudopaludicola* are warty, but these warts are different than the isolated pustules on the otherwise smooth skin of the *P. pustulosus* group. Thus, we consider these four states to be derived states unifying the four species in the *P. pustulosus* group of *Physalaemus*. The species *P. enesefae* and *P. ephippifer* are most like members of the *P. pustulosus* group in terms of overall similarity, especially in the bones, but we have not found derived characters that unite either of these species as a sister-taxon to the *P. pustulosus* group.

*Relationships within the P. pustulosus group.*—Given that the *P. pustulosus* group is monophyletic, what are the relationships of the four species? We suggest that *P. pustulosus* and *P. petersi* are sister-species, and that *P. coloradum* and *P. pustulatus* are also sister-species.

*Physalaemus pustulosus* and *petersi* both have the first finger noticeably longer than the second; this feature is unique among the 23 species

of *Physalaemus* that we examined, and is a derived state. Both species are edentate; four other species of the genus are edentate, but because of the corroborated monophyly of the *P. pustulosus* group we consider these to be homoplasious occurrences.

*P. pustulatus*–*P. coloradum* are united by the lack of a tarsal tubercle and narrow (rather than broad, wing-like) alary processes of the hyoid plate. The tarsal tubercle is absent in five other species of the genus, but because of the monophyly of the *P. pustulosus* group we consider these to be homoplasies. The presence of narrow alary processes of the hyoid is unique in the genus, and is a derived character-state.

Using this phylogeny as a framework we propose the following sequence of events, following the conceptual framework of vicariance biogeography (Wiley, 1981): Prior to the uplift of the Andes, there was a single species in northern South America that was ancestral to the *P. pustulosus* group. The uplift of the Andes in the late Tertiary yielded two species, one on each side of the cordillera. Subsequent speciation of the trans-Andean species gave rise to *P. coloradum* and *P. pustulatus*. The cis-Andean species differentiated into *P. petersi*, associated today with the Amazon drainage, and *P. pustulosus*, which was restricted to the drier Orinoco River drainage and Caribbean coastal regions and associated valleys. Following the closure of the Panamanian portal in the late Pliocene, *P. pustulosus* dispersed into Central America, eventually reaching southern Mexico.

*Monophyly of the genus Physalaemus*.—As noted above, Heyer (1974) considered *Physalaemus* to be a monophyletic group based on five derived states (his states 23, 26, 28, 65, 88). None of these is unique within the Leptodactylinae, according to Heyer's preferred tree (1974, Fig. 7). Each of the character-states 23, 26 and 28 arose three other times, 65 evolved four other times, and 88 arose one other time on the cladogram. Heyer's use of the monothetic method accounts in part for the large number of convergences (and no reversals), and has been criticized by Farris et al. (1982).

Rather than discuss the reliability of Heyer's characters or method of analysis, we suggest a relationship between some species of *Physalaemus* and *Pseudopaludicola*. Cei (1980) pointed out that the tadpoles of *Physalaemus fernandezae* and *P. henseli*, and *Pseudopaludicola falcipes* share a medially interrupted row of papillae on the

lower lip. The larvae of *Physalaemus cuvieri* also share this feature (pers. observ.). However, the tadpoles of the *P. pustulosus* group, *P. enesefae* and *P. ephippifer*, have complete rows like those reported for *P. biligonigerus*, and *P. nattereri* by Cei (1980). Lynch (1971) summarized data on the distribution of labial papillae among leptodactylid larvae and noted that all New World taxa for which data were available had uninterrupted rows on the lower lip. Thus, the occurrence of the interrupted state is unique in the Leptodactylidae (excluding myobatrachids) and a derived feature.

*Pseudopaludicola* is unique among the leptodactylines in lacking the posterolateral process of the hyoid plate (character-state 82, Heyer, 1974). The alary process is greatly expanded in the genus, as it is in *Physalaemus* and a few other leptodactylids. We interpret the "absence" of the posterolateral process as the fusion of that process with the broad, winglike alary process, producing a large plate (Trewavas, 1933). Thus, the condition in *Pseudopaludicola* is derived from the expanded alary process. Trewavas (1933) pointed out that *Eupemphix* (= *Physalaemus*) *nana* and *Pseudopaludicola falcipes* lack the omohyoid and the second posterior petrohyoid muscles, a derived state. These muscles are absent in some genera in other families, such as bufonids and microhylids, but this does not detract from their usefulness in suggesting relationships within the Leptodactylinae.

These data from the larvae and the hyoid plate are suggestive of a derivation of the species of *Pseudopaludicola* from within the genus *Physalaemus*, rendering the latter paraphyletic. There is little doubt that *Pseudopaludicola* is monophyletic, because all of the species possess a unique antibrachial tubercle. *Physalaemus*, on the other hand, has no unique synapomorphies, and we consider the monophyly of the genus as yet unresolved. Only a few of the species have been studied in detail, and well corroborated hypotheses about the phylogeny of the genus must await morphological and life history data on the poorly known species.

#### ACKNOWLEDGMENTS

For the loan of specimens, we are indebted to Pere Alberch, W. Ronald Heyer, Robert F. Inger, Arnold G. Kluge, Alan E. Leviton, C. J. McCoy and Charles W. Myers. We are grateful to Charles W. Myers for providing field notes and photographs, to Roy W. McDiarmid for a

tape recording of *Physalaemus coloradum*, and to Gretchen Bratcher for executing Fig. 1. Some of the material used herein was collected during the course of field work supported by grants from the National Science Foundation (DEB 74-02998, DEB 76-09986) to William E. Duellman, and by a National Science Foundation Graduate Fellowship to David C. Cannatella. We thank our field companions Thomas J. Berger, Juan R. León, John D. Lynch, John E. Simmons and Linda Trueb, for their help. Permits and/or logistic support were provided by Jorge Hernández-C. of Inderena in Bogotá and Miguel Moreno of the Museo Ecuatoriano de Historia Natural in Quito.

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*Copeia*, 1984(4), pp. 921–933

## Taxonomic Distinction of the Antilles *Gambusia puncticulata* Complex (Pisces: Poeciliidae) from the *G. yucatana* Complex of Mexico and Central America

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The *G. puncticulata* species group of Rivas (1963) was shown to be a monophyletic group separable from the remainder of the *G. affinis* species group of Rosen and Bailey (1963). The *G. puncticulata* species group (named the *G. puncticulata* complex by Fink, 1971a) was reviewed and found to consist of three subgroups. The first subgroup (I) is the *G. yucatana* complex occurring on the mainland of Mexico and Central America. The second and third subgroups, *puncticulata* (II) and *hubbsi* (III) forms, are sister groups within the *G. puncticulata* complex restricted to the Antilles. The *puncticulata* forms (group II) consist of the populations from Cuba, Jamaica and the Cayman Islands called *G. p. puncticulata* by Fink (1971a) and previously called *G. puncticulata*, *G. howelli*, *G. oligosticta* and *G. caymanensis*. The *hubbsi* forms (group III) consist of populations previously called *G. bucheri*, *G. baracoana*, *G. monticola* (Cuban), *G. manni* (Lake Cunningham, New Providence Island, Bahamas) and *G. hubbsi* (variable salinities, Bahamas).

THE *Gambusia puncticulata* complex was considered by Fink (1971a) to include six subspecies of *G. puncticulata*, instead of the eight nominal species previously included in the group by Rivas (1963). Included in Fink's complex was a new subspecies subsequently described by Ri-

vas (1971). As a result of Fink's study all populations from the mainland of Mexico and Central America were considered to be *G. p. yucatana*, and populations at the Cayman Islands, Cuba, Jamaica and the Bahama Islands were considered to be *G. p. puncticulata*. The