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A New Species of *Pristimantis* (Anura: Strabomantidae) from the Eastern Slope of the Cordillera Oriental, Arauca, Colombia

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ABSTRACT: We describe a new species of *Pristimantis* from one of the most isolated regions of Colombia, at elevations of 700–800 m in the Tame River basin at the eastern slope of the Cordillera Oriental in Colombia (Department of Arauca). This locality has been in the grasp of guerrilla groups and right-wing paramilitaries, and as a consequence, this region has been historically inaccessible or risky for researchers. The new species is a diurnal forest dweller, similar to *Pristimantis savagei* and *P. vilarsi*. It is distinguished from its congeners by having finely shagreened dorsum skin, areolate ventral skin, moderate tympanic membrane size (length = 37.2–58.8% of eye length), long hind limbs (tibia length = 53.6–63.6% of snout–vent length), and an advertisement call composed of a short single note, while lacking ridges on scapula, tubercles on upper eyelid and heel, and basal webbing in toes. In addition to the new species described herein, we demonstrate that subarticular tubercles display more variation than what is commonly described in taxonomic studies of terraranan frogs.

Key words: Field surveys; Forested slopes of the Andes; Landfrogs; Subarticular tubercles; Tame; Terrarana

FORESTED slopes of the Andes are famous for being one of the most species-rich ecosystems on earth, and also one of the ecosystems most inadequately surveyed. This situation has drawn the attention of those concerned about biodiversity, given that the forested slopes of the Andes are disappearing at alarming rates (Gentry 1992; Lutz et al. 2013). The forested slopes of the Andes hold one of the highest diversities of amphibians in the world (Gascon et al. 2007). Nonetheless, our knowledge about their amphibian fauna remains deficient, while continuous amphibian declines are reported throughout tropical America (Blaustein and Dobson 2006; Gascon et al. 2007). There are three main factors limiting the study of the amphibian diversity in the forested slopes of the Colombian Andes. First, funding sources for field research in poorly known areas are scanty; second, a large percentage of amphibian holotypes and comparative collections are held in North American and European museums and universities; and third, there are few experts and trained personnel capable of describing species (Gascon et al. 2007).

The difficulty in studying species in the Colombian Andes is even more accentuated if we consider groups such as the speciose genus *Pristimantis* (~546 species; Frost 2019), which is a taxonomically difficult group given that many species closely resemble one another morphologically. Indeed, there are many undescribed species from the genus *Pristimantis* sitting in museum collections, waiting for description, at least in Colombian museum collections. One of the areas with the highest diversity of *Pristimantis* frogs is the Andean Cordilleras of Colombia, especially the Cordillera Occidental (Lynch and Ruiz-Carranza 1996; Lynch 1998). In contrast, compared with the cordilleras Central and Occidental, the Cordillera Oriental is considered less species rich in terms of *Pristimantis* frogs. However, fewer comprehensive field surveys have been

carried out the Cordillera Oriental (mainly on the eastern flank).

Thus, it is expected that the exploration of previously unvisited and poorly known areas in the Cordillera Oriental will result in the discovery of new species of *Pristimantis* frogs. In support of this, during 12 d in March 2013, we participated in a multidisciplinary Colombian scientific expedition to the eastern slopes of the Colombian Cordillera Oriental. The goal was to explore an unvisited and isolated region, the piedmont in the Tame River basin, where armed conflict has made this one of the most violent regions in Colombia. During our surveys, we registered 15 species of amphibians (González et al. 2015), of which one species of *Pristimantis* caught our attention because of its large vocal sac extending onto the chest and the male advertisement call behavior. We observed males calling at night from large rocks rather than from the forest vegetation. Here, we provide bioacoustic and morphological evidence that lead us to propose this taxon as a new species of the genus *Pristimantis* from the Cordillera Oriental of Colombia.

MATERIALS AND METHODS

The definition and terminology used in the diagnosis and description sections are, as far as possible, in accordance with the broadly used descriptions of terraranan frogs given by Lynch and Duellman (1997) and Duellman and Lehr (2009). Subarticular tubercles notation follows Lynch and Duellman (1997) and Ospina-Sarria and Duellman (2019). The diagnosis section is composed of a series of 14 standardized diagnostic characters that are slightly modified in content from those used in Lynch and Duellman (1997) and Duellman and Lehr (2009). Sexual maturation was determined by examination of gonads and secondary sex characters. Measurements were made to the nearest 0.1 mm with dial calipers with aid of a dissecting microscope. Abbreviations are as follows: SVL = snout–vent length, HL = head length, IOD = interorbital distance. Lengths of toes III and V were determined by adpressing both toes against

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toe IV, and lengths of fingers I and II by appressing the fingers against each other.

All recordings were edited with Audition CS6 for MacOS X and analyzed with the software Raven Pro v1.5 for MacOS X (Cornell Laboratory of Ornithology, Ithaca, NY). The terms and definitions for the acoustic parameters follow Köhler et al. (2017). Institutional abbreviations are: AMNH (American Museum of Natural History, Division of Vertebrate Zoology); ICN (Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional de Colombia, Bogotá); KU (Biodiversity Institute, University of Kansas). Field numbers are reported for specimens not yet deposited in permanent collections as follows: JDL (John Douglas Lynch). All specimens examined are listed in the Appendix.

SPECIES DESCRIPTION

Pristimantis terrapacis sp. nov.
(Table 1; Figs. 1A, 2A, 3)

Holotype.—ICN 58486, an adult male from the Rio Tame, Vereda Sabana de la Vega, 713 m elevation (6°22'N, 71°54'W; datum = WGS84), Departamento de Arauca, Colombia, one of the series collected by J.J. Ospina-Sarria on 17 and 22 March 2013.

Paratypes.—12 adult males collected with the holotype: ICN 58478, ICN 58479, ICN 58480–81, ICN 58482–84, ICN 58485, ICN 58487–90.

Diagnosis.—*Pristimantis terrapacis* is diagnosed by the following combination of characters: (1) skin of dorsum finely shagreen; ventral skin areolate; discoidal fold present, well anterior to the groin; dorsolateral folds absent; (2) tympanic membrane differentiated, round; its length 36.8–58.8% of eye length in 13 males; prominent tympanic annulus, its upper edge covered by supratympanic fold, which extends from posterior corner of orbit along upper edge of temporal region and distinctly curved toward the insertion of the arm; (3) snout moderately long, subacuminate in dorsal view, rounded in profile and lacking of papilla; canthus rostralis straight in dorsal view, rounded in profile; (4) upper eyelid smooth, narrower than IOD (41.6–52.9% IOD); interocular tubercle absent; cranial crest absent; (5) choanae small, ovoid; partially concealed by palatal shelf of maxillary arch; dentigerous processes of vomers prominent, triangular in outline, separated medially by a distance equal to the width of the visible dentigerous process, positioned posterior to level of choanae, each dentigerous process of vomers bearing five to six teeth; (6) males with vocal slits and large vocal sac extending onto chest; nuptial pads present on thumbs; (7) finger I slightly shorter than finger II; discs and circumferential grooves present on all fingers; discs truncate, except on finger I, which is round; disc of finger I smaller than that of finger II and this in turn smaller than discs on fingers III and IV; (8) fingers with lateral fringes; palmar tubercle partially divided distally; thenar tubercle oval, slightly smaller than palmar tubercle; supernumerary tubercles low, restricted to the proximal segments of the digits; subarticular tubercles present, except hyperdistals that are absent; subarticular tubercles low, with rounded base and larger than supernumerary tubercles; (9) antebrachial tubercle present; other ulnar tubercles absent; (10) heel and outer edge of tarsus lacking tubercles; inner tarsal fold present, very short, extending along one-fifth distal of

TABLE 1.—Selected meristic, mensural (mm), and proportional (percentages) data from the type series of *Pristimantis terrapacis* (values are given as range [mean \pm 1 SD]).

Trait	Male (n = 13)
Snout–vent length	24.4–34.3 (28.5 \pm 2.4)
Head width	9.8–13.6 (11.8 \pm 1.1)
Head length	9.0–13.0 (11.2 \pm 1.2)
Interorbital distance	5.8–7.7 (6.7 \pm 0.5)
Upper eyelid width	2.9–3.6 (3.1 \pm 0.2)
Eye diameter	3.8–4.9 (4.2 \pm 0.4)
Eye–nostril distance	3.0–4.0 (3.6 \pm 0.4)
Internarial distance	2.4–3.0 (2.6 \pm 0.2)
Tympanum diameter	1.4–2.0 (1.75 \pm 0.2)
Tibia length	14.3–18.4 (16.7 \pm 1.2)
Foot length	11.6–15.4 (13.7 \pm 1.3)
Head length/snout–vent length	36.8–45.2
Head width/snout–vent length	39.4–42.6
Eye diameter/head length	36.3–41.3
Eye–nostril distance/eye diameter	74.4–102.6
Upper eyelid width/interorbital distance	41.6–52.9
Interorbital distance/head width	52.3–61.2
Internarial distance/interorbital distance	37.7–42.8
Tympanum diameter/eye diameter	36.8–58.8
Tibia length/snout–vent length	53.6–63.6
Foot length/snout–vent length	43.6–53.0

tarsus; (11) elongate inner metatarsal tubercle, its length twice its width; low, conical outer metatarsal tubercle one-fifth size of inner metatarsal tubercle; subarticular tubercles present, except hyperdistals that are absent; subarticular tubercles projecting, with elongate base and larger than supernumerary tubercles; supernumerary plantar tubercles restricted to the proximal segments of digits II–IV (absent in digits I and V); (12) toes bearing prominent lateral fringes, toe webbing absent; toe III much shorter than toe V; toe III extending to proximal edge of the penultimate subarticular tubercle of toe IV; toe V reaching midway between penultimate and distal subarticular tubercles of toe IV; discs and circumferential grooves present on all toes; discs of toes III–V equal to disc on finger II and larger than discs of toes I and II; (13) color in life: the dorsum is pale gray or orange-tan with brown marking consisting of an interorbital bar, canthal and postorbital stripes poorly defined, and small spots on the body; labial bars and brown transverse bars on the limbs are poorly defined; flanks pale tan with faint gray diagonal marks; groin and anterior surfaces of thighs cream brown; posterior surfaces of the thighs black with greenish yellow flecks; throat white and belly surfaces yellow; iris coppery bronze with a median horizontal red streak; (14) SVL in adult males 24.4–34.3 mm (mean \pm 1 SD = 28.5 \pm 2.4 mm; n = 13).

Comparisons.—*Pristimantis terrapacis* differs from the other species in the genus by having a large vocal sac extending onto the chest, moderate tympanic membrane size (length 36.8–58.8% of eye length), canthal and postorbital stripes poorly defined, skin of dorsum finely shagreen, ventral skin areolate, finger I slightly shorter than finger II, inner tarsal fold present, very short, extending along one-fifth distal of tarsus, subarticular tubercles projecting on the foot, supernumerary plantar tubercles restricted to the proximal segments of the digits II–IV (absent in digits I and V); long hind limbs (tibia length = 53.6–63.6% of SVL in males), advertisement call composed of a short single note, and by lacking of heel tubercles, tarsal tubercles, supra-anal

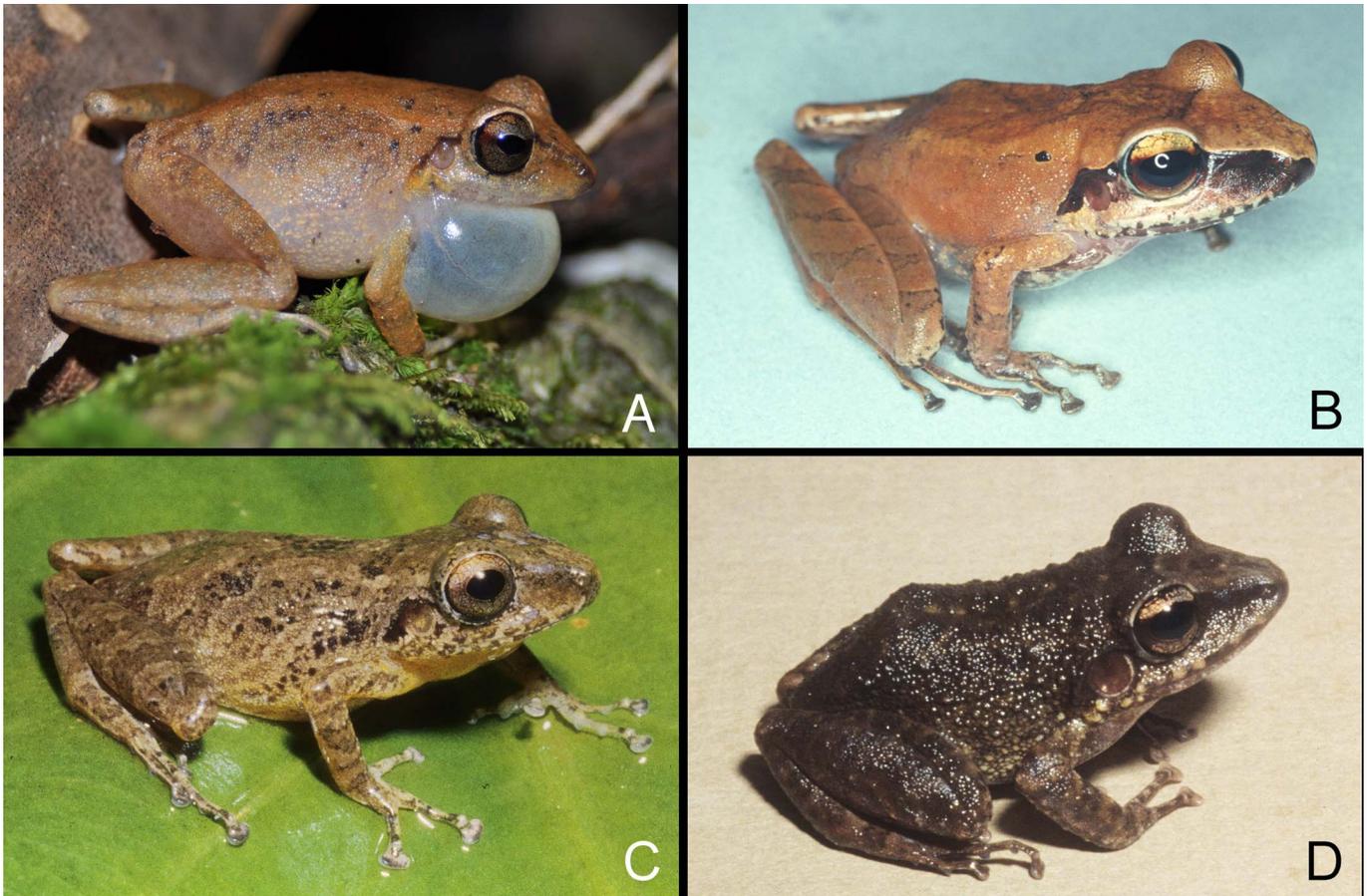


FIG. 1.—Living specimens of *Pristimantis terrapacis* (A; holotype, ICN 58486 adult male, snout–vent length = 30 mm), *P. incertus* (B; KU 166376), *P. savagei* (C; ICN 14989, adult male), and *P. vilarsi* (D; JDL 19875, adult male). A color version of this figure is available online.

tubercles, hyperdistal tubercles, dorsolateral folds and ridges in scapula region, and toe webbing. It is most similar to *P. savagei* (Pyburn and Lynch 1981) and *P. vilarsi* (Melin 1941) by having dorsal skin finely shagreen, snout subacuminate in dorsal view, rounded in profile, tympanic membrane and tympanic annulus prominent, only antibranchial tubercle evident, inner tarsal fold present, very short, extending along one-fifth distal of tarsus, and coloration pale gray or orange-tan with brown marking consisting of an interorbital bar, canthal and postorbital stripes, and small spots on the body (Fig. 1A,C,D). *Pristimantis terrapacis* differs from *P. savagei* by having areolate ventral skin and by lacking ridges on scapula, tubercles on upper eyelid and heel, and basal webbing in toes instead of ventral skin smooth, ridged on scapula, small tubercles on upper eyelid (Fig. 2A,C) and heel, and basal webbing in toes in *P. savagei* (Pyburn and Lynch 1981). Besides, *P. terrapacis* has an advisement call composed of a series of well-spaced, single-note calls with duration ranging from 0.054 to 0.076 s (mean \pm 1 SD = 0.066 ± 0.009 s; $n = 6$; Fig. 5) rather than an advisement call composed of 7–34 notes per call with duration ranging from 0.6 to 3.2 s in *P. savagei* (Pyburn and Lynch 1981). From *P. vilarsi*, *P. terrapacis* is distinguished in having moderate tympanic membrane size (length = 36.8–58.8% of eye length; Figs. 1A, 2A), skin of dorsum finely shagreen, ventral skin areolate, and long hind limbs (tibia length = 53.6–63.6% of SVL in males) instead of a large tympanic membrane size

($\geq 60\%$ of eye length; Figs. 1D, 2D), skin of dorsum smooth with scattered tubercles, ventral skin smooth, and shorter hind limbs (tibia length = 49.8–55.1% of SVL in males) in *P. vilarsi* (Lynch 1994; Duellman and Lehr 2009).

Pristimantis incertus (Lutz 1927), a distinctive species, has also been compared with *P. savagei* and *P. vilarsi* (Figs. 1B, 2B). *Pristimantis terrapacis* differs from *P. incertus* in having finger I slightly shorter than finger II, toe III extending to proximal edge of the antepenultimate sub-articular tubercle of toe IV, and canthal stripe poorly defined (Figs. 1A, 2A) rather than finger I equal to II (Rivero 1961), toe III not reaching the antepenultimate sub-articular tubercle of toe IV, and canthal stripe well defined in *P. incertus* (Figs. 1B, 2B). Among species of *Pristimantis* in eastern flanks of the Cordillera Oriental in Colombia, exclusively *P. carrangerorum* (Lynch 1994) and *P. medemi* (Lynch 1994) share subacuminate snout in dorsal view and rounded in profile, areolate ventral skin, only antibranchial tubercle evident, short inner tarsal fold, supernumerary plantar tubercles restricted to the proximal segments of the digits II–IV (absent in digits I and V), long hind limbs, and the absence of supra-anal tubercles and cranial crests. However, *P. carrangerorum* differs from *P. terrapacis* by having ridges in scapula region and small, nonconical tubercle on the heel, and small tubercles on upper eyelid (Lynch 1994), which are absent in *P. terrapacis*. From *P. medemi*, *P. terrapacis* differs by having skin of dorsum finely



FIG. 2.—*Pristimantis terrapacis* (A; holotype, ICN 58486, adult male, snout–vent length [SVL] = 30 mm), *P. incertus* (B; KU 166383, adult male, SVL 25 mm), *P. savagei* (C; KU 187009, adult male, SVL = 21.6 mm), and *P. vilarsi* (D; KU 207529, adult male, SVL = 24 mm). A color version of this figure is available online.

shagreen, upper eyelid smooth, finger I slightly shorter than finger II, discs on outer fingers, and discs on fingers III and IV smaller than tympanic annulus rather than dorsum finely tuberculate with scattered larger tubercles, upper eyelid bearing only small tubercles, first finger slightly longer than second, and discs on outer fingers as wide as tympanum in *P. medemi* (Lynch 1994). Other species that superficially resemble *P. terrapacis* from northeastern South America are *P. chiastonotus* (Lynch and Hoogmoed 1977), *P. gutturalis* (Hoogmoed et al. 1977), and *P. zeuctotylus* (Lynch and Hoogmoed 1977). However, *P. terrapacis* differs by

having a very short inner tarsal fold, extending along one-fifth distal of tarsus (inner tarsal is absent in those species; Hoogmoed et al. 1977; Lynch and Hoogmoed 1977). In addition, *P. terrapacis* differs from *P. chiastonotus* by lacking dorsolateral folds (dorsolateral folds present in *P. chiastonotus*; Lynch and Hoogmoed 1977). *Pristimantis terrapacis* differs from *P. gutturalis* by having skin of dorsum finely shagreen and upper eyelid smooth rather than skin of dorsum finely shagreen with large pustules interspersed, which are much larger on upper eyelid in *P. gutturalis* (Hoogmoed et al. 1977). Finally, *P. terrapacis* is distin-

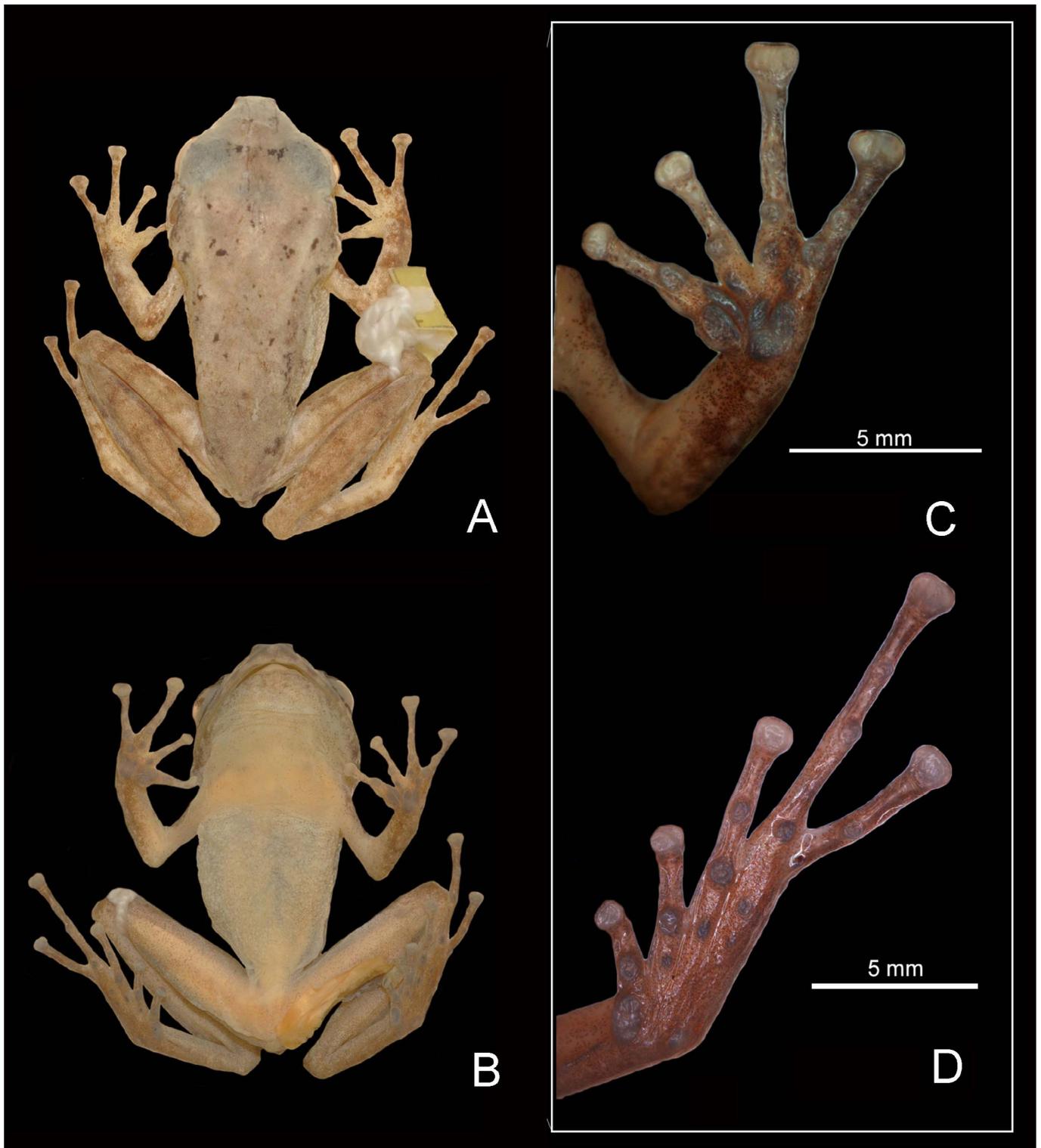


FIG. 3.—*Pristimantis terrapacis* (A; holotype, ICN 58486, adult male, snout-vent length = 30 mm). Dorsal and ventral views of body (A, B). Palmar view of hand and plantar view of foot showing subarticular tubercles (C, D). A color version of this figure is available online.

guished from *P. zeuctotylus* by having palmar tubercle partially divided distally and dorsal skin lacking dorsolateral folds rather than palmar tubercle not bifid and dorsal skin having dorsolateral folds in *P. zeuctotylus* (Lynch and Hoogmoed 1977).

Description of the holotype.—An adult male with head wider than body; head width 40.0% of SVL; HL 43.3% of SVL; snout moderately long, subacuminate in dorsal view, rounded in profile; snout lacking papilla at its tip; eye-nostril distance 85.1% of diameter of eye; nostrils not protuberant,

directly lateral at level of lower jaw. Canthus rostralis straight in dorsal view, rounded in profile, not elevated; loreal region depressed; top of head flat, lacks tubercle between upper eyelids; upper eyelid smooth, its width 44.2% of IOD; supratympanic fold distinctly curved toward the insertion of the arm; tympanic membrane present; upper edge of tympanic annulus covered by supratympanic fold; two rounded postrictal tubercles present. Choanae small, ovoid, partially concealed by palatal shelf; dentigerous processes of vomers prominent, each process bearing four teeth; tongue wider than long, its posterior margin not notched, posterior third not adherent to floor of mouth; paired vocal slits, longitudinal, lateral to base of tongue; large median subgular sac extending onto chest.

Skin on dorsum finely shagreen (Fig. 3A); skin on belly, throat, and ventral surfaces on the flanks areolate (Fig. 3B); discoidal fold present, well anterior to groin; dorsolateral folds absent; cloacal sheath short; no tubercles in the cloacal region. Antebrachial tubercle present; other ulnar tubercles absent; palmar tubercle divided distally (Fig. 3C); thenar tubercle oval, slightly smaller than palmar tubercle; subarticular tubercles low, with rounded base, one on thumb and second finger and two on third and fourth fingers, and larger than supernumerary tubercles; supernumerary tubercles low, restricted to the proximal segments of the digits; fingers having lateral fringes; relative lengths of fingers I < II < IV < III, all fingers having terminal ventral pads well defined by circumferential grooves; disc on thumb round, slightly smaller than finger II; discs on fingers III and IV truncate and much smaller than tympanic annulus; white nonspinous nuptial pads are present on the dorsolateral surface of the base of the thumb. Moderately robust hind limbs; when hind limbs flexed perpendicular to axis of body, heels overlap; tibia length 58.0% of SVL; foot length 48.3% of SVL; heel and outer edge of tarsus lacking tubercles; inner tarsal fold present, very short, extending along one-fifth distal of tarsus; inner metatarsal tubercle elongate, its length twice its width; conical outer metatarsal tubercle one-fifth size of inner metatarsal tubercle; toes bearing lateral fringes and discs (about as wide as long) on expanded pads; webbing absent; relative lengths of toes I < II < III < V < IV, toe III much shorter than toe V, toe III extending to proximal edge of the penultimate subarticular tubercle of toe IV, toe V reaching midway between penultimate and distal subarticular tubercles of toe IV, all toes having terminal ventral pads well defined by circumferential grooves; discs of toes III and IV equal to disc on finger IV and larger than disc of toes I and II; subarticular tubercles projecting (Fig. 3D), with elongate base, one on toes I and II, two on toes III and V, and three on toe IV; supernumerary plantar tubercles low, restricted to the proximal segments of the digits II–IV (absent in digits I and V).

Measurements of holotype (mm).—SVL 30, tibia length 17.4, foot length 14.5, HL 13.0, head width 12.0, IOD 7.0, internarial distance 2.9, width of upper eyelid 3.1, diameter of eye 4.7, eye–nostril distance 4.0.

Distribution and ecology.—*Pristimantis terrapacis* is known only from the type locality in the riparian forest of the Tame River basin and in the vicinity of the montane forest with streams (Fig. 4). The forest cover of the riparian and montane forest is composed of large exposed rocks, rocky streambeds, and shrubby areas with grass and steep hillsides.

The males were calling at night from rocks or from the ground, near the river and small streams. Females were not seen. In the type locality *P. terrapacis* occurs in sympatry with *P. frater* (Werner 1899).

The recording is composed of a series of well-spaced, single-note calls heard as drawn-out “tics.” The single-note calls are 0.054–0.076 s in duration (mean \pm 1 SD = 0.066 \pm 0.009 s; n = 6), with intercall intervals of 2.48–3.88 s in duration (mean \pm 1 SD = 3.04 \pm 0.74 s; n = 4). The call is initiated with an abrupt rise in frequency from 1419 to 5376 Hz (Fig. 5).

Etymology.—The specific epithet is a noun in apposition, derived from the Latin *terra* (land) and *pacis* (the peace). Over 40 yr, the municipality of Tame as well as the Department of Arauca have been one of the battlefields of the Colombian armed conflict. Tame is considered one of the most violent municipalities—if not the most violent in Colombia. We name this species to reflect a strong desire that the municipality of Tame be a land of peace.

DISCUSSION

Our objective was to describe a new species of *Pristimantis* from the Cordillera Oriental of Colombia, one of the many species of *Pristimantis* undescribed from Colombia. To increase the knowledge of amphibian species in Colombia, it is necessary to generate a seed grant system to support field surveys, which must be complemented with a program of research grants focused on accelerating the naming process of the known but yet undescribed species currently sitting in Colombian museum shelves.

It is most important to compare *P. terrapacis* with *P. savagei* and *P. vilarsi* because these are the only known species from the eastern flank of the Cordillera Oriental of Colombia that resemble *P. terrapacis* in having dorsal skin shagreen, small spots on the body, and a pale gray or orange-tan color pattern with brown marking consisting of an interorbital bar and canthal and postorbital stripes. Nonetheless, these species can be readily separated. Two of the most clear-cut morphological differences between *P. terrapacis* and *P. savagei* and *P. vilarsi* are the projecting subarticular tubercles under toes and the large subgular vocal sac that remains well distended in preservative (Figs. 1A, 3B–D). Projecting subarticular tubercles under the toes are common in species of terrestrial habitus—*Eleutherodactylus coqui* Thomas 1966, *Haddadus binotatus* (von Spix 1824), *Niceforonia mantipus* (Boulenger 1908), *Oreobates quixensis* Jiménez de la Espada 1872, and *O. saxatilis* (Duellman 1990); however, they are uncommon in the genus *Pristimantis*, where some species are terrestrial, but most are arboreal (Lynch and Duellman 1997). Conversely, large subgular vocal sacs are broadly distributed in the genus *Pristimantis* and also in other terraranan frogs of arboreal habitus—*Pristimantis brevifrons* (Lynch 1981), *P. ptochus* (Lynch 1998), *Diasporus gularis* (Boulenger 1898), and *D. quidditus* (Lynch 2001). Additional direct evidence must be gathered for a clear understanding of the causal explanation related to the finding of both character states in *P. terrapacis*.

Subarticular Tubercles in Terraranan Frogs

Subarticular tubercles occur under the joints between phalanges in fingers and toes in frogs. In the case of

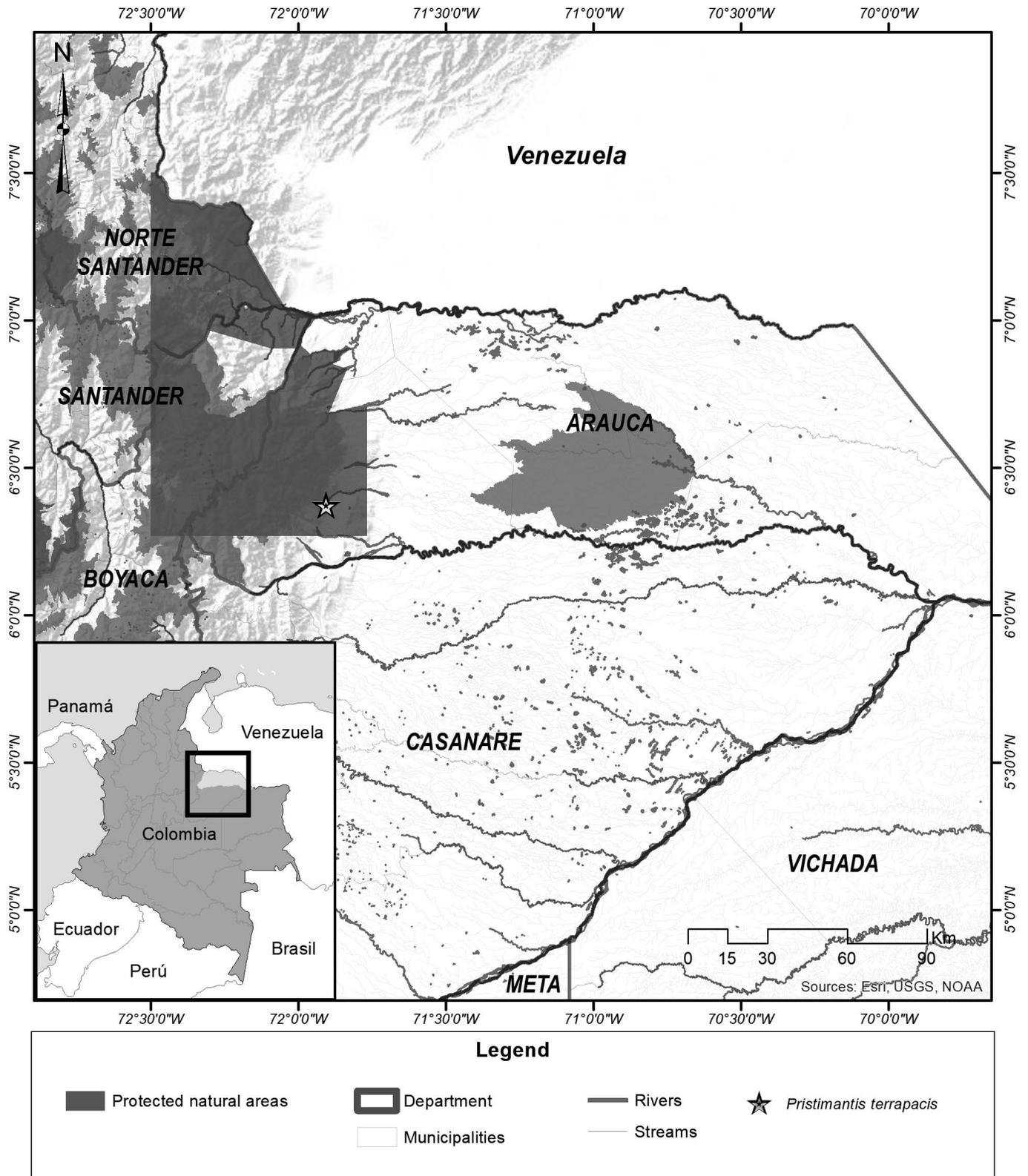


FIG. 4.—Map of northeastern Colombia (inset) showing the type locality of *Pristimantis terrapacis* (star).

terranean frogs, most genera have subarticular tubercles, and the only exceptions known so far occur in the genus *Brachycephalus* Fitzinger 1826 and in the monotypic genus *Geobatrachus* Ruthven 1915, in which the subarticular

tubercles are absent. When subarticular tubercles are present, they appear under fingers and toes at the same time; their distribution does not show evidence of independence. Nevertheless, when the elevation of subarticular

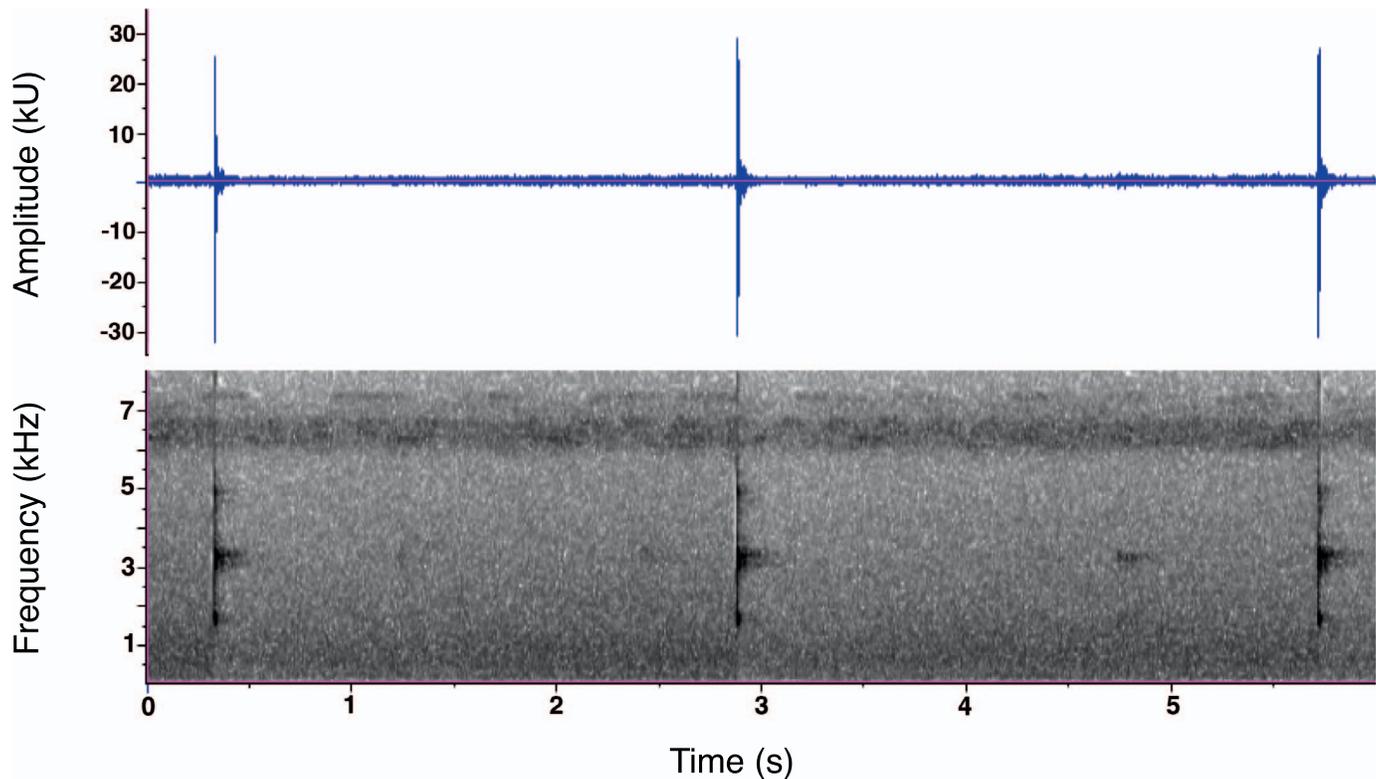


FIG. 5.—Three calls (= single notes) of *Pristimantis terrapacis*, from male holotype calling above a large rock at the type locality. Specimen (ICN 58486) recorded 22 March 2013, at air temperature of 19°C. A color version of this figure is available online.

tubercles under fingers and toes is coded, as was found in *P. terrapacis*, there is evidence of independence in their distribution. Other species having subarticular tubercles low under fingers and subarticular tubercles projecting under toes are *Craugastor megacephalus* (Cope 1875 [1876]), *C. opimus* (Savage and Myers 2002), *N. mantipus*, and *P. thectopternus* (Lynch 1975). Thus, variation associated with the subarticular tubercles must be coded in three characters: (1) presence/absence of subarticular tubercles, (2) elevation of subarticular tubercles under fingers, and (3) elevation of subarticular tubercles under toes. It is clear that the subarticular tubercles display more variation than what is commonly assumed (see also Lynch 1998; Ospina-Sarria and Duellman 2019).

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RESUMEN: Describimos una nueva especie de *Pristimantis* de uno de los lugares más apartados de Colombia, las elevaciones medias de la cuenca del río Tame en la vertiente oriental de la Cordillera Oriental en Colombia (Departamento de Arauca). Esta localidad ha estado al alcance de grupos guerrilleros y paramilitares de derecha, como consecuencia esta región ha sido históricamente inaccesible o altamente riesgosa para los investigadores. La nueva especie es diurna, habitante de los bosques de galería y es similar a *Pristimantis savagei* y *P. vilarsi*. La nueva especie se distingue de todos sus congéneres por tener el dorso finamente granular, vientre areolado, membrana timpánica de tamaño moderado (longitud = 37.2–58.8% de la longitud del ojo), extremidades posteriores largas (longitud de la tibia = 53.6–63.6% de SVL), un canto de anuncio compuesto por una sola nota corta y por carecer de crestas escapulares, tubérculos en párpado superior y talón y membradas basales en los dedos de los pies. Además de describir la nueva especie, en este artículo demostramos que los tuberculos subarticulares tienen una variación mucho mayor a la que comúnmente se describe en estudios taxonómicos enfocados en Terrarana.

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APPENDIX

Specimens Examined

- Brachycephalus ephippium*.—BRAZIL: RIO DE JANEIRO: AMNH 77354.
- Brachycephalus didactylus*.—BRAZIL: RIO DE JANEIRO: AMNH 129471.
- Craugastor megacephalus*.—PANAMA: BOCAS DEL TORO: Rio Changena (KU 108426–27, 108429); Almirante (KU 79990).
- Craugastor opimus*.—PANAMA: DARIEN: Laguna (KU 76226). PANAMA: 4.8 km N community of Altos de Pacora on rd to Mandinga (KU 108435).
- Diasporus gularis*.—COLOMBIA: VALLE DEL CAUCA: Municipio Buenaventura, Estación Agroforestal Bajo Calima (ICN 45169).
- Diasporus quidditus*.—COLOMBIA: VALLE DEL CAUCA: Municipio Buenaventura, Estación Agroforestal Bajo Calima (ICN 45173).
- Eleutherodactylus coqui*.—PUERTO RICO: HUMACAO: 3.5 mi S El Verde (KU 79927, 79935).
- Geobatrachus walkeri*.—COLOMBIA: MAGDALENA: 10 km E El Campaño, W slope Cerro Kennedy (KU 169367, 169371).
- Haddadus binotatus*.—BRAZIL: SÃO PAULO: Paranapiacaba (KU 74197–98).
- Niceforonia mantipus*.—COLOMBIA: VALLE DEL CAUCA: 18 km from Cali on road to Buenaventura (KU 143970).
- Oreobates quixensis*.—ECUADOR: NAPO: Lago Agrio (KU 126233, 126235); 7 km S Rio Tiputini (KU 297257). SUCUMBIO: Limoncocha (KU 178249).
- Oreobates saxatilis*.—PERU: SAN MARTÍN: Ponga de Shilcayo, ca 4 km NNW Tarapoto (KU 212327); 27 km NE Tarapoto (KU 217329).
- Pristimantis carrangerorum*.—COLOMBIA: BOYACÁ: Municipio Pajarito, Inspección de Policía de Corinto, Quebrada La Rochita (ICN 5345), Finca El descanso, Quebrada La Limonita (ICN 9444).
- Pristimantis chiastonotus*.—BRAZIL: AMAPA: Serra do Navio (KU 140879–80).
- Pristimantis incertus*.—VENEZUELA: ARAGUA: Estación Biológica Rancho Grande (KU 166382–83).
- Pristimantis medemi*.—COLOMBIA: META: Quebrada Salinas, Las Salinas de Upín, Municipio de Restrepo (ICN 21213). CUNDINAMARCA: Municipio Medina, Vereda Choapal, 6–7 km NNE Medina, Carretera Medina a Gachalá (ICN 14596).

Pristimantis savagei.—COLOMBIA: META: Sierra de la Macarena, ca. 35 km WSW Vistahermosa (KU 187009).

Pristimantis thectopternus.—COLOMBIA: CAUCA: Road to coast from El Tambo (KU 143983).

Pristimantis vilarsi.—VENEZUELA: AMAZONAS: Puerto Ayacucho (KU 207529).

Pristimantis zeuctotylus.—GUYANA: RUPUNUNI: N Acarahy Mts, W New River (KU 69663). BRAZIL: AMAPA: Serra do Navio (KU 140881).

Strabomantis cornutus.—ECUADOR: NAPO: 2 km SSW Rio Reventador (KU 165222).

Strabomantis ruizi.—COLOMBIA: VALLE DEL CAUCA: Yotoco (KU 181993).