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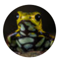
Article *in* Zootaxa · October 2021

DOI: 10.11646/zootaxa.5047.5.3



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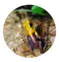

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Zootaxa 5047 (5): 531–546
https://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5047.5.3
http://zoobank.org/urn:lsid:zoobank.org:pub:1675F37F-6DA9-4D88-BBBF-2B95D3DAEE62

A new species of Andean golden poison frog (*Andinobates*, Dendrobatidae) from the Eastern Andes of Colombia

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Abstract

A new species of *Andinobates* (Dendrobatidae) is described from the East Andes of Colombia, just 37 km away from the Colombian capital, Bogotá. *Andinobates supata* **sp. nov.**, represents the second known species of yellow *Andinobates*, and can be distinguished from the other, *Andinobates tolimensis*, by an unique combination of ventral and dorsal color patterns. Our phylogenetic analyses, based on ≈ 1120 bp from two mitochondrial markers (16S rRNA and cytochrome b) showed that this new taxon is sister to a clade formed by *A. cassidyhornae*, *A. bombetes*, *A. opisthomelas*, *A. tolimensis* and *A. virolinensis*. The new species appears to be restricted to a handful of small forest fragments (<10 ha) distributed in no more than 5 km^2, between 1800–2000 m elevation, where the human activity is high. In addition, more than 90% of the original forest has been logged at the type locality, and its watersheds receive considerable agrochemical discharges. Altogether, the evidence suggests that this new species should be listed as Critically Endangered and should receive immediate attention regarding basic research and urgent conservation measures.

Key words: *Andinobates supata* **sp. nov**., *Andinobates bombetes* group, poison frogs, Eastern Andes, Colombia

Resumen

Una nueva especie de *Andinobates* (Dendrobatidae) es descrita para los Andes Orientales de Colombia, a solo 37 km de la capital colombiana, Bogotá. *Andinobates supata* **sp. nov.**, es una de las dos especies conocidas de *Andinobates* amarillos, y puede separarse del otro, *Andinobates tolimensis*, por una combinación única de patrones de coloración ventral y dorsal. Los análisis filogenéticos con ≈ 1120 pb de dos marcadores mitocondriales (ARNr 16S y citocromo b) revelaron que este nuevo taxón está relacionado con un clado formado por *A. cassidyhornae*, *A. bombetes*, *A. opisthomelas*, *A. tolimensis* y *A. virolinensis*. Esta nueva especie parece estar restringida a un puñado de pequeños fragmentos de bosque (<10 ha) distribuidos en no más de 5 km^2, entre 1800-2000 m de altitud, donde la actividad humana es alta. Asimismo, más del 90% del bosque original se ha talado en la localidad tipo y sus cuencas hidrográficas reciben considerables descargas de agroquímicos. En conjunto, la evidencia sugiere que esta nueva especie debería incluirse como En Peligro Crítico y debería recibir atención inmediata con respecto a la investigación básica y las medidas de conservación urgentes.

Accepted by E. Twomey: 10 Sept. 2021; published: 4 Oct. 2021

Introduction

The tropical Andes harbor exceptional biodiversity and endemicity (Myers *et al.* 2000). Within this region, more than 30,000 plant species (> 15,000 endemic), 569 mammal species (75 endemic), 1,728 bird species (584 endemic), 610 reptile species (275 endemic), 1,155 amphibian species (664 endemic), and 380 freshwater fish species (131 endemic) have been reported (Mittermeier *et al.* 2004). Moreover, multiple species of vertebrates (e.g. Acevedo *et al.* 2013; Avendaño *et al.* 2015; Carantón-Ayala & Certuche-Cubillos 2010; Grant & Myers 2013), invertebrates (e.g. Campos 2010; Rabeling *et al.* 2016), and plants (e.g. Diazgranados & Sánchez 2017; Pedraza-Peñalosa 2015) from the Northern Andes have been described recently. These mountains are also considered one of the most endangered environments in the neotropics due to intensive agricultural activities and human settlements (Morales & Armenteras 2013). The area covered by pastures increased by 26–53% in the past 60 years, and the annual deforestation rate is around 1.5% (Viña *et al.* 1999). At least 44 species of frogs are presumably threatened due to habitat destruction in the Colombian Andean forests (Rueda-Almonacid *et al.* 2004). Moreover, mid-elevation tropical Andes provide almost perfect conditions for growth and infection of the frog pathogenic fungus *Batrachochytrium dendrobatidis* (Ron 2005; La Marca *et al.* 2005; Puschendorf *et al.* 2006; Stuart *et al.* 2004), which is among the main causes of population declines in frogs, and in some cases has resulted in the extinction of many local amphibian populations (Ruiz *et al*. 2008; Bustamante *et al.* 2005; La Marca *et al.* 2005; Rueda *et al.* 2004). The combination of high diversity and strong threats render the Andean mountains an ecosystem in critical need of knowledge and conservation of amphibians.

This exceptional amphibian diversity is highlighted by the Neotropical poison frogs (Dendrobatidae), which are well-known for their diversity of chemical defenses, bright coloration, and reproductive strategies. Within this family, the genus *Andinobates* currently contains 15 species, most occurring between 1300 and 2300 m elevation in the Andes of Colombia: *Andinobates bombetes* (Myers & Daly 1980), *A. cassidyhornae* Amézquita *et al.* (2013), *A. daleswansoni* and *A. dorisswansonae* (Rueda *et al.* 2006), *A. opisthomelas* (Boulenger 1899), *A. tolimensis* (Bernal *et al.* 2007), *A. virolinensis* (Ruiz-Carranza & Ramírez-Pinilla 1992), and Ecuador: *A. abditus* (Myers and Daly 1976). The remaining species are from the Pacific region of Colombia and Panama lowlands: *A. altobueyensis* and *A. fulguritus* (Silverstone 1975), *A. claudiae* (Jungfer *et al.* 2000), *A. geminisae* Batista *et al.* (2014), *A. minutus* (Shreve 1935), *A. victimatus* Márquez *et al.* (2017) and *A. viridis* (Myers & Daly 1976). Species of this genus are characterized by their small size, fused vertebrae 2 and 3, and the absence of limb reticulation, among other traits (Brown & Twomey *et al.* 2011). Five new species of *Andinobates* (formerly *Ranitomeya)* from the Colombian Andes have been described in the last fifteen years: *A. dorisswansonae* and *A. daleswansoni* (Rueda *et al*. 2006), *A. tolimensis* (Bernal *et al*. 2007). *A. cassidyhornae* (Amézquita *et al.* 2013) and *A. victimatus* (Marquéz *et al.* 2017).

In the course of amphibian surveys to investigate new populations of the highly threatened harlequin toads (*Atelopus* spp) in the Eastern Colombian Andes, we found a population of a tiny golden-yellow poison frogs (genus *Andinobates*), less than 37 km from the capital, Bogotá. Here we describe this new species that differs from these and other *Andinobates* by a unique combination of morphological and molecular evidence that support its species status. We also give preliminary information on its natural history, which we have accumulated in the course of our field work.

Materials and methods

Specimens were collected in the municipality of Supatá, Cundinamarca, in the Eastern Andes (Cordillera Oriental) of Colombia (Fig. 1). All specimens used in this study were euthanized and preserved following the standard techniques and procedures proposed by McDiarmid (1994) and Cortez *et al.* (2006). Following Brown & Twomey *et al.* (2011) and Márquez *et al.* (2017), 19 body measurements were taken on adults using a Mitutoyo digital caliper (0.01 mm): Snout-to-vent length (SVL); tibia length, taken from the heel to the outer surface of the flexed knee (TL); greatest body width, taken under the axillae (GBW); head width, taken between the angles of the jaws (HW); inter orbital distance (IOD); head length, sagittal distance from the tip of the snout to the angle of the jaw (HL); distance from the tip of the snout to the center of the naris (TSCN); distance from the center of the naris to the anterior edge of the eye (NED); inter-narinal distance (IND); eye diameter (ED); horizontal diameter of the tympanum (HDT); distance from the corner of the mouth to the edge of the tympanic ring (MTD); hand length, measured from the proximal edge of the large medial palmar tubercle to the tip of the longest (third) finger (HaL); width of the third finger disc (W3FD); width of the first finger below the disc (W3F); width of the third toe disc (W3TD); width of the third toe below the disc (W3T); width of the fourth toe disc (W4TD); width of the fourth toe below the disc (W4T). For tadpoles and following McDiarmid & Altig (1999), we measured the total length (ToL); head-to-body length (HBL); mid-body width (BW); mid-body height (BH); tail length (TaL); mid-tail height (TH); tail muscle width at the base of the tail (TMW); tail muscle height at the base of the tail (TMH); maximal tail muscle width (MTMW). The body mass of live individuals was measured using a digital balance (0.1 g resolution). The preserved individuals were sexed by direct inspection of gonads and other secondary sexual traits such as vocal slits in males. Morphological and anatomical terminology follows Grant *et al.* (2006). Museum abbreviations denote Museo de Historia Natural, Pontificia Universidad Javeriana, Bogotá, Colombia (MUJ).

Molecular and phylogenetic analyses. We extracted genomic DNA from toe-clippings of three individuals of *A. supata* **sp. nov.**, and one individual of *A. tolimensis*, both from their type localities, using QIAGEN DNeasy extraction kits. Fragments of two mitochondrial loci, 16S rRNA (16S; ≈ 420 bp) and cytochrome b (Cytb; 700 bp), were amplified as detailed by Amézquita *et al.* (2013), and Sanger-sequenced in both directions, using an ABI 3500 Genetic Analyzer. The obtained chromatograms were assembled and visually checked using Geneious v5.1 (Drummond *et al.* 2010). These sequences were uploaded to GenBank, under accession numbers KT364459–KT364468 (Table 1.)

We aligned our sequences with those from 10 other *Andinobates* species and *Ranitomeya ventrimaculata* (used as outgroup) available in GenBank (Table 1) using MUSCLE (Edgar 2004). Bayesian (Rannala & Yang 1996) and maximum likelihood (ML; Felsenstein 1981) mitochondrial phylogenies were inferred from a concatenated alignment of both loci, excluding sites with more than 25% of missing data. The best partitioning strategy and DNA evolution models for each locus were simultaneously chosen using PartitionFinder (Lanfear *et al.* 2012). We performed two replicate Bayesian MCMC runs with four chains for 10,000,000 generations, sampling every 1,000 in MrBayes 3.2.1 (Ronquist *et al.* 2012). Convergence was assessed using Tracer v1.5 (Rambaut & Drummond 2007), and the first 2,500,000 generations were discarded as burnin. RAxML 7.7.3 (Stamatakis 2006) was used to infer the ML genealogy, under the GTR+Γ model and the partitioning strategy mentioned above. One thousand boostrap pseudoreplicates were performed to assess nodal support.

In addition, we calculated average inter- and intraspecific Kimura two-parameter (K2P; Kimura 1980) distances between concatenated mtDNA sequences of species belonging to the *bombetes* species group (Brown & Twomey *et al.* 2011) using MEGA 5 (Tamura *et al.* 2011). One individual of *Andinobates bombetes* was excluded from this analysis, since its Cytb sequence was ≈400 bp shorter than those of other individuals.

Bioacoustic analyses. To characterize the mate-recognition signal of the new species, we recorded advertisement calls of five males in the field, under natural conditions. Recordings were taken during the day, from 7 am to 5 pm. We positioned a Shure BG 4.1 unidirectional microphone at no less than 50 cm in front of a calling male. The microphone was connected to a Marantz PMD 660 digital recorder. Immediately after recording, we measured the male's dorsal body temperature using an Oakton infrared (InfraPro 1. ST20) thermometer. Males were then photographed next to a standard 20 cm ruler, which was used as a scale to measure snout-to-vent length. Digital vocalization recordings were analyzed on Raven Pro 1.4 (Cornell Laboratory of Ornithology, NY, USA) by measuring temporal call traits on oscillograms and spectral call traits on power spectra (window: Blackman window, frame length: 15.5 ms, filter bandwidth: 106 Hz).

Results

Molecular and phylogenetic analyses. Our final alignment was composed of 1111 base-pairs (411 bp from 16S. and 700 from Cytb), partitioned by gene and for Cytb, also by codon position. The GTR+Γ model was chosen for 16S and the first position of Cytb, and the K2P+I and HKY+I were chosen for the second and third positions of Cytb, respectively. MrBayes runs converged well before the pre-established burnin (2,500,000 generations), with a final split frequency standard deviation of 0.0031. All individuals of *Andinobates supata* **sp. nov**, were placed in a single, well-supported clade, nested within the *bombetes* group (Fig. 2). Our phylogeny broadly corresponds with the results from previously published work (Brown & Twomey *et al.* 2011; Amézquita *et al.* 2013), except that the current analysis places *A. cassidyhornae* and *A. opisthomelas* as sister taxa (Bayesian posterior probability 0.95; ML bootstrap support 63), and *A. bombetes* as their sister. *Andinobates dorisswansonae* appeared as the sister taxon of the rest of the *bombetes* group.

TABLE 1. Localities and GenBank accession numbers of the specimens used in molecular analyses.

Species	Locality	Study	GB 16S	GB Cytb
A. bombetes	Colombia, Quindío, Barbas, Hacienda Lusitania	Santos *et al.* 2009	EU342669	JN 635880
A. bombetes	Colombia, Quindío, Barbas, Hacienda Lusitania	Santos & Cannatella. 2011	HQ290981	HQ290558
A. bombetes	Colombia, Quindío, Filandia	Brown & Twomey *et al.* 2011	JN635869	-
A. cassidyhornae	Colombia, Antioquia, Reserva Mesenia-Paramillo	Amézquita *et al.* 2013	JQ936636	JQ936622
A. cassidyhornae	Colombia, Antioquia, Reserva Mesenia-Paramillo	Amézquita *et al.* 2013	JQ936637	JQ936623
A. cassidyhornae	Colombia, Antioquia, Ciudad Bolivar	Amézquita *et al.* 2013	JX879710	JX879720
A. cassidyhornae	Colombia, Antioquia, Ciudad Bolívar	Amézquita *et al.* 2013	JX879714	JX879724
A. cassidyhornae	Colombia, Chocó, Carmen de Atrato	Amézquita *et al.* 2013	JX879712	JX879722
A. cassidyhornae	Colombia, Chocó, Carmen de Atrato	Amézquita *et al.* 2013	JX879713	JX879723
A. claudiae	Panamá, Bocas del Toro, Isla del Toro,	Santos & Cannatella. 2011	HQ290983	HQ290560
A. dorisswansonae	Colombia, Tolima, Falan	Brown & Twomey *et al.* 2011	JN635861	JQ936629
A. dorisswansonae	Colombia, Tolima, Falan	Brown & Twomey *et al.* 2011	JN635863	JQ936630
A. fulguritus	Colombia, Chocó, Bahía Solano, Sierra Mecana	Grant *et al.* 2006	DQ502106	DQ502538
A. opisthomelas	Colombia, Antioquia, Guatapé	Amézquita *et al.* 2013	JQ936633	JQ936619
A. opisthomelas	Colombia, Antioquia, Guatapé	Amézquita *et al.* 2013	JQ936634	JQ936620
A. opisthomelas	Colombia, Antioquia, Guatapé	Amézquita *et al.* 2013	JQ936635	JQ936621
A. opisthomelas	Colombia, Antioquia, Amalfi	Amézquita *et al.* 2013	JX879706	JX879716
A. opisthomelas	Colombia, Antioquia, Amalfi	Amézquita *et al.* 2013	JX879707	JX879717
A. opisthomelas	Colombia, Antioquia, Amalfi	Amézquita *et al.* 2013	JX879708	JX879718
A. minutus	Panamá, Cocle, El Copé, Parque Omar Torrijos	Grant *et al.* 2006	DQ502168	DQ502603
A. sp. Quibdó	Colombia, Chocó, Quibdó, La Troje	Santos *et al.* 2009	EU342670	JN635881
A. supata sp. nov.	Colombia, Cundinamarca, Supatá	Brown & Twomey *et al.* 2011	JN635865	KT364466

......continued on the next page

TABLE 1. (Continued)

Species	Locality	Study	GB 16S	GB Cytb
A. supata sp. nov.	Colombia, Cundinamarca, Supatá	Brown & Twomey *et al.* 2011	JN635867	KT364467
A. supata sp. nov.	Colombia, Cundinamarca, Supatá	This study	KT364460	KT364464
A. supata sp. nov.	Colombia, Cundinamarca, Supatá	This study	KT364461	KT364465
A. supata sp. nov.	Colombia, Cundinamarca, Supatá	This study	KT364459	KT364463
A. tolimensis	Colombia, Tolima, Falan	Brown & Twomey *et al.* 2011	JN635857	JQ936632
A. tolimensis	Colombia, Tolima, Falan	Brown & Twomey *et al.* 2011	JN635857	JQ936631
A. tolimensis	Colombia, Tolima, Falan	This study	KT364462	KT364468
A. virolinensis	Colombia, Santander, Virolín, Costilla de Fara	Brown & Twomey *et al.* 2011	JN635873	JQ936626
A. virolinensis	Colombia, Santander, Virolín, Costilla de Fara	Brown & Twomey *et al.* 2011	JN635871	JQ936627
A. virolinensis	Colombia, Santander, Socorro	Brown & Twomey *et al.* 2011	JN635875	JQ936625
A. virolinensis	Colombia, Santander Socorro	Brown & Twomey *et al.* 2011	JN635876	JQ936628
A. virolinensis	Colombia, Santander, Virolín, Costilla de Fara	Santos & Cannatella. 2011	HQ290994	HQ290571
Ranitomeya ventrimaculata	Ecuador, Francisco de Orellana, Parque Nacional	Santos & Cannatella. 2011	HQ290979	HQ290556

K2P distances between *Andinobates supata* **sp. nov.** and other species of the *bombetes* group (Table 2) ranged between 0.014 and 0.086, well within the range of between-species variation observed for the rest of comparisons (0.014–0.092), and around an order of magnitude greater than intraspecific distances (0.002–0.008), supporting the status of *A. supata* **sp. nov.** as a separate species of the *bombetes* group.

TABLE 2. Pairwise genetic (K2P) distances among seven species of the *Andinobates bombetes* group.

Species	Ad	As	Ac	Ab	Ao	At	Av
A. dorisswansonae	0.002						
A. supata **sp. nov.**	0.086	0.002					
A. cassidyhornae	0.087	0.023	0.001				
A. bombetes	0.089	0.020	0.024	0.008			
A. opisthomelas	0.089	0.019	0.020	0.022	0.008		
A. tolimensis	0.089	0.020	0.033	0.024	0.026	0.002	
A. virolinensis	0.092	0.014	0.025	0.019	0.019	0.017	0.003

Systematics

Andinobates supata **sp. nov.**

Figures 1, 2, 3, 4 (E-M) and 5. Table 1.

Andinobates sp. Lötters *et al.* 2007 (Figures 571–574)
Andinobates sp. “supatá” Brown & Twomey *et al.* 2011.
Andinobates sp. aff. *tolimensis* Brown & Twomey *et al.* 2011 (Figures 6–7)
“*Andinobates supatae”* Salazar, Márquez, Chaves-Portilla, Dorado-Correa & Amézquita; In Kahn *et al.* (2016), species account 290–294.

Holotype. Adult female (MUJ 6604), Colombia, Departamento de Cundinamarca, about 8 km south of the Municipio de Supatá, Vereda San Marcos (ca 5°3’N, 74°14’W, 1890–2000 m elevation), collected by Giovanni Chaves-Portilla, Erika Nathalia Salazar and José Gil-Acero on 3 February 2007.

Paratypes. Three adult males (MUJ 6605, 6607,6608), one adult female (MUJ 6609), one sub-adult female (MUJ 6606), all collected with the holotype.

Additional referred material. A batch of four tadpoles (MUJ 6610) bred in captivity.

Etymology. The species is dedicated to Chief Panché Supatá (or Chupatá), who lived during the time of the Spanish Conquest (first half of the 16th Century) in the Gualivá Province, where the municipality of Supatá is located. He is believed to have died defending his people in the battle of Tocarema, when the Spanish and their Chibcha allies defeated the Panché in 1537. We also dedicate this species to the modern inhabitants of Supatá for embracing the Supatá Golden Frog as a conservation icon and incorporating it into their culture and festivities.

Vernacular name. Supatá Golden Poison Frog (Rana Dorada de Supatá).

Definition. *Andinobates supata* **sp nov.** is a small-sized dendrobatid frog assigned to the *A. bombetes* group based on the following combination of traits: (1) SVL less than 20 mm (SVL 16.0–18.4 mm; Table 1). (2) Dorsum bicolored, lacking markings; head uniformly ocher or golden; dorsal coloration fades from a brightly colored head to sepia (dark reddish-brown) in the lower dorsum. A cephalic hood covers the sides of the head and a large part of the tympanum (Figures 3 & 4). (3) Conspicuous dorsolateral stripes absent; abdominal flanks sepia with large, round bluish-white spots (Figures 3 & 4). (4) Ventral coloration with distinct, bluish-white spots (Fig. 4). (5) Dorsal skin mostly smooth, becoming slightly granular on the sacral region and thighs. (6) Ventral skin slightly granular. (7) Advertisement calls are “short buzz” type (Brown & Twomey *et al.* 2011; Fig. 5), note length approximately 1.3 s, with 141–243 pulses per note and a mean dominant frequency of 4.7 kHz. (8) First finger shorter than second; thenar tubercle present. (9) Five toes on foot. (10) Distinct limb reticulation absent. (11) Hands and feet lack webbing. (12) Oral discs of the larvae are normal and non-umbelliform.

Comparisons with other species. *Andinobates supata* **sp. nov.** is a close relative of *A. opisthomelas*, *A. virolinensis*, *A. dorisswansonae*, *A. tolimensis*, *A. cassidyhornae*, and *A. bombetes*, all of which occur within roughly 100 km of the type locality of the new species. Of these, only *A. tolimensis* has yellow dorsal coloration, and therefore is the species most easily confused with *Andinobates supata* **sp. nov.** The remainder of these species all have red dorsal coloration (versus yellow in *A. supata* **sp. nov.**), including *A. virolinensis*, which is the only other *Andinobates* species occurring in the same Eastern Cordillera as *Andinobates supata* **sp. nov.** *Andinobates tolimensis* has dark bluish spots on the venter (versus pale bluish ventral spots in *A. supata* **sp. nov.**) and has golden dorsal/cephalic coloration that does not cover the tympanum, leaving the impression of a black stripe running back from the eye (versus golden head coloration complete in *A. supata* **sp. nov.**) (Figures 3 & 4). SVL between both species are similar and overlapping although *A. tolimensis* may be slightly larger (17.7–18.9 mm; n=6) than *Andinobates supata* **sp. nov.** (16.0–18.4 mm).

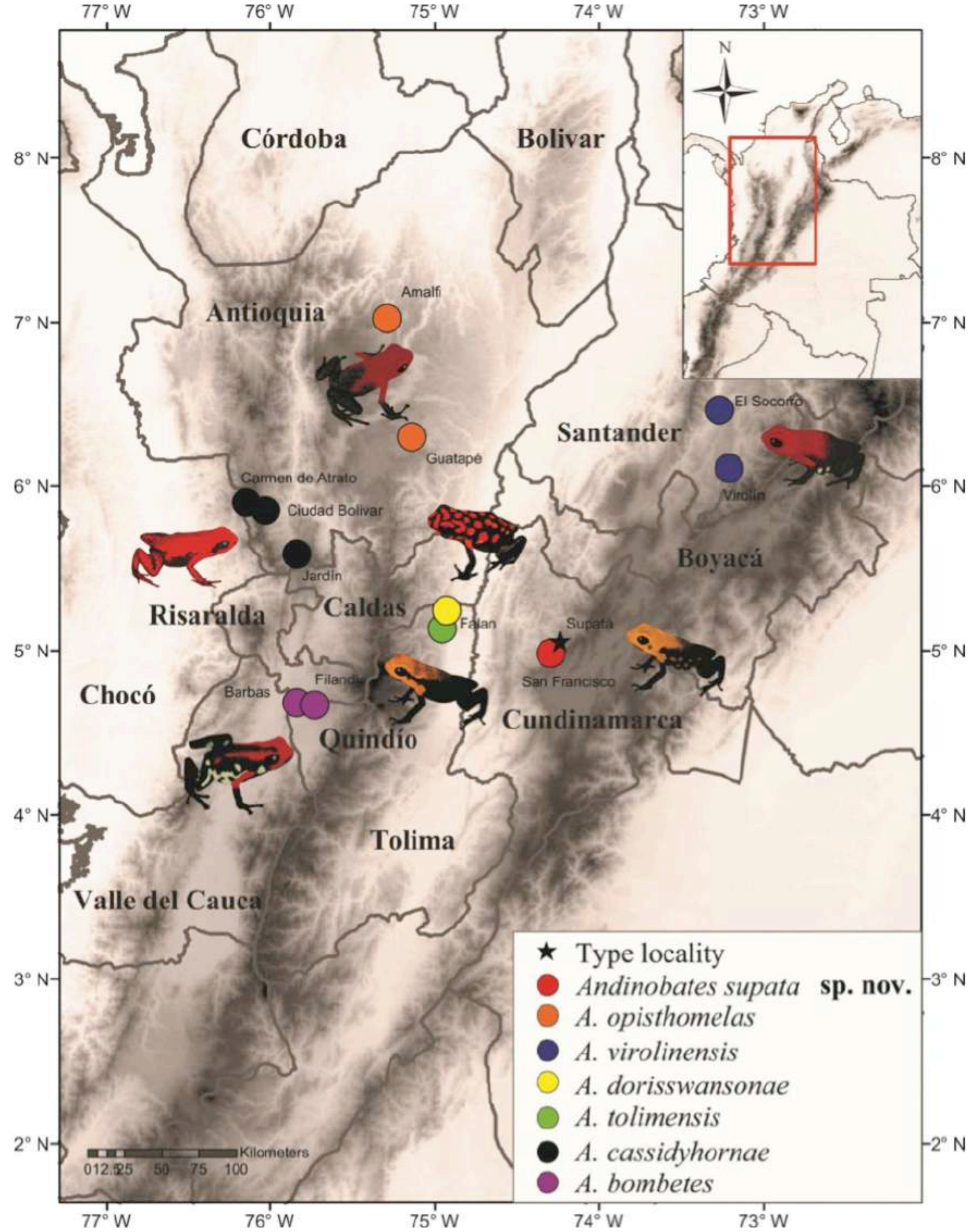

FIGURE 1. Localities of *Andinobates supata* **sp. nov.** and six species of *Andinobates* used in the phylogenetic analysis (*A. cassidyhornae, A. opisthomelas, A. bombetes, A. tolimensis, A. virolinensis* and *A. dorisswansonae*).

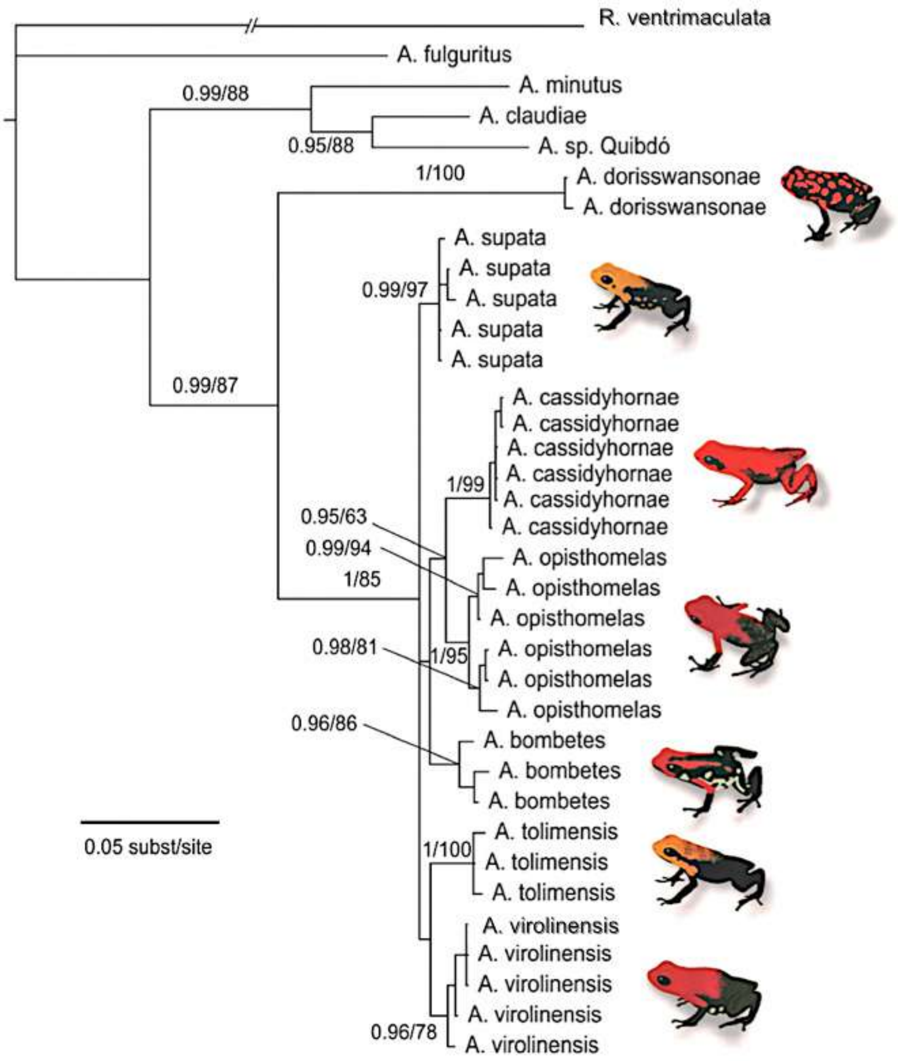

FIGURE 2. Bayesian mtDNA phylogeny of 11 *Andinobates* species, based on 16S and Cytb genes, with *Ranitomeya ventrimaculata* used as outgroup. Nodal support is represented on internodes as Bayesian posterior probability/ML bootstrap. Values for nodes with support below 0.9/0.7 are not shown. Support values for some intraspecific nodes are also not shown to improve visualization.

Description of the holotype. Adult female, 18.4 mm SVL. Dorsal skin smooth on head and anterior part of the body, slightly granular through sacral region and dorsal surface of hindlimbs. Skin on the belly and flanks weakly granular. Head slightly wider than long, relatively short and rounded snout in lateral and dorsal views. Eyes large, diameter more than 40% of head length. *Canthus rostralis* not very prominent; flat, vertical loreal region. Small rounded nares situated near the tip of the snout, separated from the orbits by a distance equal or slightly shorter than the diameter of the eye. Pupil nearly rounded; horizontal diameter barely exceeding vertical diameter. Tympanum vertically oval and slightly angled in anteroposterior position, separated from the eye by a distance shorter than its own diameter. Tympanic ring prominent, only visible in the anterior and ventral sides. Premaxillary and maxillary teeth absent. Choanae small and rounded, separated from each other, covered by the maxillary palatal arch when seen from above. Tongue spatulate, fixed to the floor of the mouth and free in most of its extension. Medial lingual process absent.

Relative length of adpressed fingers is: III >IV>II>I; finger I reaches below the disc of II; finger II reaches the distal subarticular tubercle of finger III; tip of digit IV barely exceeds its base. Finger and toe discs smooth, truncated, more expanded on fingers than toes; width is proportional to length. Basal subarticular tubercles large, rounded, slightly elevated, as wide as the digit. Distal subarticular tubercle of fingers half the size of basal ones, rounded, slightly protuberant; supernumerary tubercles absent; palmar tubercles large and rounded; thenar tubercle oval, almost three times smaller than palmar tubercle. Fingers lack webbing. Digits rounded without skin on the edge.

Hind limbs exhibit five well-developed, externally visible toes. Relative length of adpressed toes is: IV >III>II>V>I. Disc of toe I as wide as digit. Subarticular tubercles of toes are elongated, barely prominent. Basal tubercles larger than distal ones; sole of foot smooth with supernumerary tubercles absent; inner metatarsal tubercle elongated and slightly raised, almost two and half times larger than outer one; outer metatarsal tubercle rounded and conical. A small tubercle (about half the size of the external metatarsal tubercle) located in the inner and medial edge of the tarsus. Toes lack webbing. When the hind limbs are close to the sides of the body and stretched forward the heel barely reaches the anterior edge of tympanum. Fingers and toes with paired dermal pads on dorsal surfaces of discs.

FIGURE 3. Body coloration of the two yellow species of *Andinobates* described to date. Note the postocular dark band in *A. tolimensis* (above) as opposed to the complete cephalic hood in *A. supata* **sp. nov.** (below). Photos by Manuel H. Bernal and Jennifer Del Río, respectively.

Measurements (in mm) and mass of the holotype. SVL 18.4; TL 7.9; GBW 9.5; HW 6.2; IOD 2.2; HL 5.8; TSCN 0.6; NED 1.6; IND 2.3; ED 2.3; HDT 1.0; MET 0.9; HaL 4.6; W3FD 0.8; W3F 0.5; W3TD 0.7; W3T 0.5; W4TD 0.6; W4T 0.4; body mass 0.4 g.

Color in life. Iris black; cephalic hood gold, transitioning to dark brown to sepia near vent and suprascapular region. The remaining body surfaces are sepia. Abdominal flanks, hidden surfaces of the limbs, and belly are predominantly black with large bluish-white spots. Cephalic hood completely covers the back and sides of the head with exception of the black nares and black anterior region of the tympanum.

Color in preservative (ethanol 70%). Head, anterior surface of the trunk, and posterior part of the arm are metallic bluish gray. Posterior surface of the body gray to bronze, gradually fading into sepia. Arms and dorsal surface of the thighs, legs, and foot are sepia or blackish. Lateral surface and belly are sepia or black with large and rounded white to light blue spots. Thighs and hidden surfaces of the forelimbs and hind limbs all black with little bluish to white spots.

Vocalization. Advertisement calls are of the 'buzz' type (Brown & Twomey et al. 2011; Myers & Daly 1976), in which a single trunk muscle contraction produces what humans perceive as a single 'buzz'. Therefore, the recommended behavioral unit of analysis is one 'buzz' (Erdtmann & Amézquita 2009). In the corresponding oscillogram and sonogram, the buzz consists of a long series of pulses with amplitude but not frequency modulation (Fig. 5), approximately 1.3 s in length. Calls contain 141–243 pulses per call (201.8 ±39.7) and the peak frequency ranges between 4.67–4.84 kHz (4.7 ±0.07 kHz).

Sexual dimorphism and inter-individual variability. Adult females are slightly larger in SVL (both females 18.4 mm in females vs. 16.0–17.1 mm in males) and slightly heavier than males (0.4 g in females vs. 0.3–0.4 g in males). Dorsal skin is more granular in males than females, however there is considerable variation among individuals. Lastly, on some specimens the yellow coloration of the arm is reduced to a patch on its base (Figures 3 & 4). Measurements of additional specimens are presented in Table 3.

TABLE 3. Body measurements (mm) of the type series of *Andinobates supata* **sp. nov**. See methods section for explanation of abbreviations.

Character	MUJ 6604	MUJ 6605	MUJ 6606	MUJ 6607	MUJ 6608	MUJ 6609	Median	SD
SVL	18.4	17.0	18.1	16.0	17.1	18.4	17.63	0.97
TL	7.9	8.0	7.8	7.5	7.8	8.1	7.85	0.18
GBW	9.5	7.3	6.2	7.1	7.6	8.4	7.42	1.15
HW	6.3	5.6	5.4	5.2	5.6	5.8	5.63	0.37
IOD	2.2	2.2	2.2	2.2	2.1	2.5	2.20	0.12
HL	5.8	5.9	5.8	5.4	5.6	6.1	5.83	0.23
TSCN	0.6	0.7	0.5	0.8	0.6	0.8	0.61	0.11
NED	1.6	1.7	1.7	1.5	1.7	1.6	1.65	0.07
IND	2.3	2.3	2.2	2.1	2.3	2.4	2.28	0.08
ED	2.3	2.3	2.2	2.2	2.3	2.4	2.28	0.07
HDT	1.0	1.0	1.3	1.0	1.0	1.2	1.02	0.11
MTD	0.9	0.9	0.8	0.7	0.7	0.8	0.84	0.10
HaL	4.6	4.7	4.5	4.3	4.5	5.1	4.56	0.25
W3FD	0.8	0.9	0.7	0.8	0.9	0.9	0.84	0.08
W3F	0.5	0.4	0.4	0.4	0.5	0.5	0.44	0.06
W3TD	0.8	0.7	0.7	0.8	0.7	0.8	0.74	0.05
W3T	0.5	0.4	0.4	0.4	0.4	0.5	0.43	0.04
W4TD	0.7	0.7	0.6	0.7	0.7	0.7	0.69	0.04
W4T	0.4	0.3	0.3	0.2	0.3	0.4	0.30	0.07
Body mass (g)	0.4	0.3	0.3	0.3	0.4	0.4	0.35	0.05

Tadpole description. We describe one specimen from lot MUJ 6610, in stage 36 *sensu* Gosner (1960). The description was complemented with the remaining three larvae, between stages 32–36. All specimens were obtained from individuals bred and maintained in captivity.

Body elongated, depressed, ventrally flat. Head rounded when viewed from above and from the side. Eyes dorsal, small, not prominent, spaced by about 1.5 times their own diameter. Nares small, located in the anterior dorsal region, spaced from each other and the eyes by a distance roughly equal to the orbital diameter. Operculum located in the latero-ventral margin of the left side of the body. Anal tube dextral and short.

Oral disc emarginated, transversally elliptic, located in the ventral and anterior extreme of the head; surrounded by a row of small, digitiform papillae on the sides and bottom. Submarginal papillae absent; upper labium is smooth and lacks papillae on most of its anterior margin. Labial tooth row formula is 2/3. Outer tooth rows well developed compared to the inner rows. Second tooth row of the upper labium is discontinuous towards the sides of the mouth. Beak has tiny serrations on the edges.

Tail long and laterally compressed with the tip slightly rounded and the caudal musculature well developed. Musculature at mid-tail greatly exceeds musculature of the fins. Upper fin barely visible in the anterior third of the tail, reaching maximal width halfway through the tail.

In preservative larvae are dark gray; the tail is lighter than the body. Abdominal surfaces are opaque, with internal organs hardly visible.

Measurements: ToL 26.9 mm; HBL 8.9 mm; BW 6.3 mm; BH 3.2 mm; TaL 18.0 mm; TH 3.7 mm; TMW 2.0 mm; TMH 2.4 mm; MTMW 2.5 mm.

Distribution. *Andinobates supata* **sp. nov.** occurs in a few small forest fragments at the type locality, and near the municipality of San Francisco (Cundinamarca, Colombia). Despite numerous expeditions undertaken by our colleagues and us over the last decade in the western versant of the Andes in Cundinamarca, with the specific objective of finding populations of this and other endangered amphibian species (e.g. *Atelopus* spp. *Bolitoglossa* spp.), we are not aware of any other locality where this species occurs. Citizen science-based efforts and publicity campaigns attempting to crowdsource new reports of this species have also been unsuccessful.

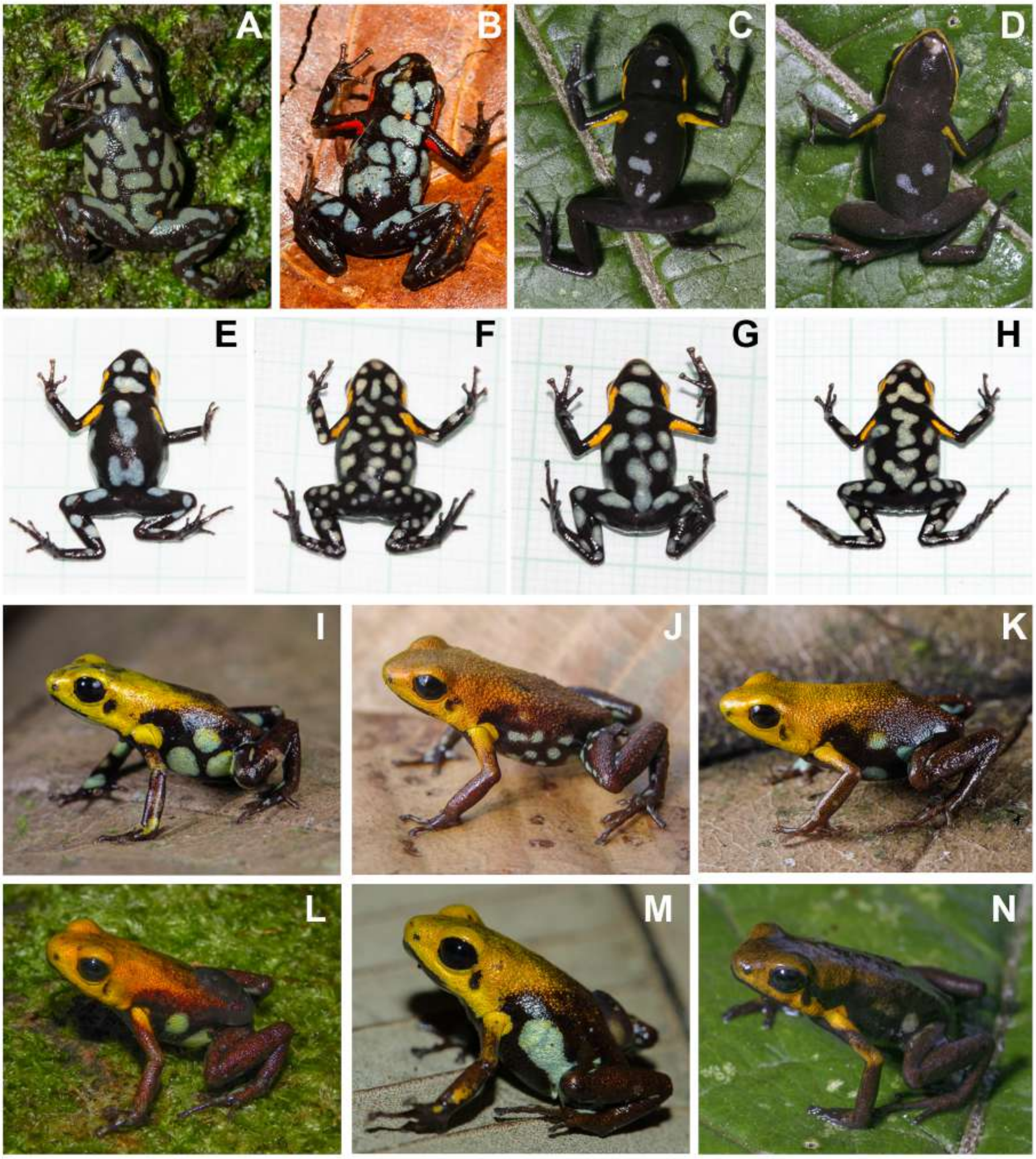

FIGURE 4. Ventral coloration of *Andinobates supata* **sp. nov.** compared to the geographically and genetically closest species of *Andinobates*. *A. bombetes* (A), *A. virolinensis* (B), *A. tolimensis* (C–D), and *A. supata* **sp. nov.** (E–H). Dorsolateral coloration of *Andinobates supata* **sp. nov.** (I–M) compared to *A. tolimensis* (N). Photos in B by Gert Benaets, A, E to M by Giovanni Chaves-Portilla, and C, D and N by Taran Grant.

Natural history and ecology. Like other dendrobatid frogs, *Andinobates supata* **sp. nov**. is a diurnal species with a bimodal calling activity pattern, peaking in early in the morning (6:00 to 9:00 am) and in the mid-afternoon (15:00 to 17:00). However, during several nocturnal surveys, males have been observed to be active and calling from the forest floor. Male density appears to be very high. In a single day we observed 39 individual males (individually identified by their ventral color pattern) within a ~0.6 hectare plot that included both forested and open areas. *Andinobates supata* **sp. nov.** is commonly found in the forest floor, among the leaf litter, or occupying small cavities in the ground, under fallen trunks, within tree roots, and even in cavities formed by grass tufts in open areas adjacent to the forest, sometimes up to 75 m away from the forest edge. Males attract females by emitting advertisement calls and actively repel other males by increasing call rate or by direct fighting. During courtship, the female will follow the male into a cave (usually under fallen logs or under the roots of trees), where mating and egg laying presumably occur. Once larvae hatch, males carry up to three tadpoles on their back (Fig. 6). In some instances, we observed males carrying tadpoles of noticeably different sizes, which lead us to suspect that they may be at different developmental stages. Males climb up tree trunks and presumably deposit the larvae in phytotelmata, where they develop until metamorphosis. Actively calling males are more common at sites where the density of bromeliads of the *Guzmania* genus is higher (Salazar E.N., Gil. J.D., Amézquita. A., unpublished data). Calling individuals are active throughout the year, but males carrying larvae are more often found during the rainy season. Some individuals have been observed feeding on small invertebrates such as Collembola, Protura and Diplura.

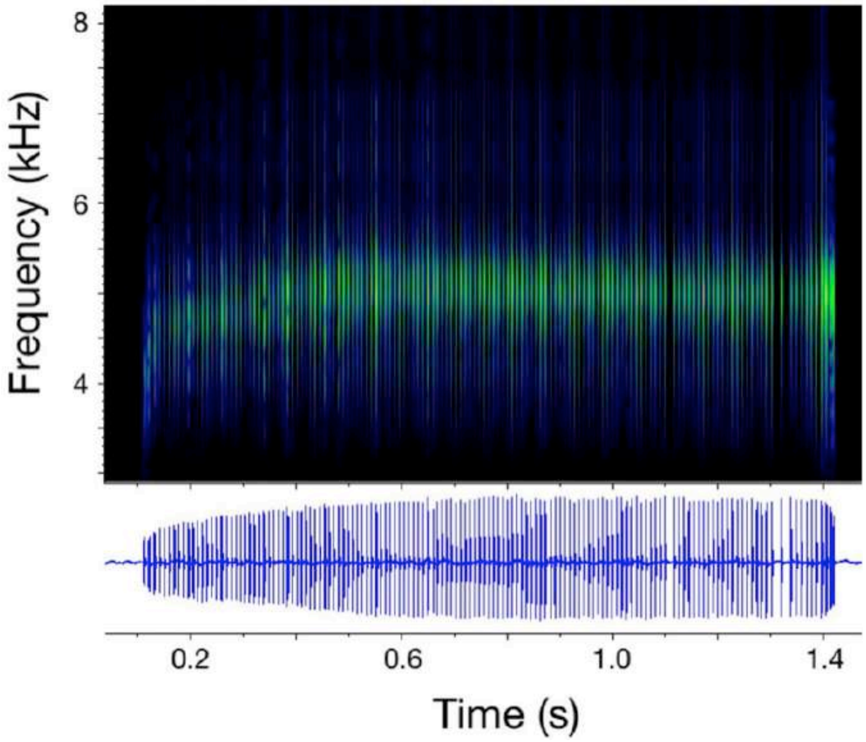

FIGURE 5. Oscillogram below and sonogram (above) of the advertisement call of *Andinobates supata* **sp. nov.** Male size (SVL) = 18.7 mm, body temperature = 18.4° C.

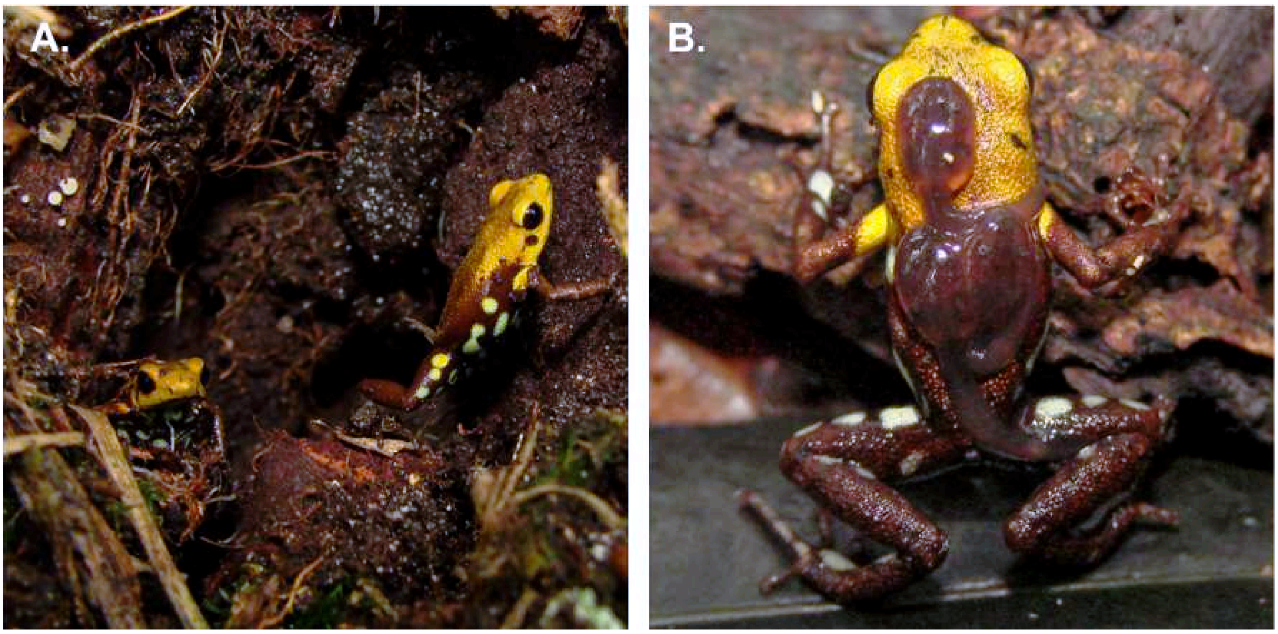

FIGURE 6. Male attracting female to his cave where mating and egg laying presumably occur (A). Male of *Andinobates supata* **sp. nov.** carrying three tadpoles presumably to a deposition site such as a bromeliad (B). Photos: Giovanni Chaves-Portilla.

FIGURE 7. View of the degraded habitat of *Andinobates supata* **sp. nov.** Photo: Giovanni Chaves-Portilla.

Comments about taxonomic and conservation status, and threats

Kahn *et al.* (2016) published a book on aposematic frogs of the Dendrobatidae family, in which a series of species accounts were compiled, including one for *Andinobates supata* **sp. nov.** under the name "*Andinobates supatae*". It is necessary to clarify that this does not constitute a taxonomic act, as a holotype is not specified in this book account, nor did the authors explicitly indicate the intention to describe a new taxon, which means that under Article 16 (names published after 1999) of the International Code of Zoological Nomenclature (ICZN 1999), this does not count as a description.

The conservation of the Supatá Golden Frog is a concern for both environmental authorities and NGOs in Colombia. It is endemic to tiny forest fragments, totaling about three hectares, that have been degraded by logging and grazing activities (Fig. 7). Although active individuals can be found in open areas around the forest edge, this species relies on the humidity and microhabitat complexity present within forested areas for egg survival and tadpole development. Therefore, the survival of this species is tied to the health of these forest fragments. Moreover, there is information from people who requested anonymity, about illegal traffic of this frog to Europe. Due to the extremely reduced distribution and the imminent risk of entire habitat loss, we suggest that the Supatá golden frog be classified as Critically Endangered (CR) under the A1c. B2a. B2b (i. ii. iv), B2c (i. ii. iii), IUCN criteria (IUCN 2012). Urgent research and conservation actions are needed for this new species, as well as for other threatened species reported in the small forest remnants of the Supatá-Gualivá region, such as the Black Inca (*Coeligena prunellei*), Cerulean Warbler (*Dendroica cerulea*), Gorgeted Wood Quail (*Odontophorus strophium*), Alban Salamander (*Bolitoglossa capitana*), Pandi Salamander (*Bolitoglossa pandi*), Inger's Robber Frog (*Strabomantis ingeri*) and the recently described species *Hyloxalus felixcoperari* (Acosta-Galvis & Vargas-Ramirez 2018).

Acknowledgements

We are grateful to the Supatá community for their commitment and active involvement in the conservation of this new species. We thank Jennifer Del Río, Taran Grant, Manuel H. Bernal and Gert Benaets for allowing us to use their photos for the figures, and Juan D. Fernández for the design of some of these. Financial support was generously provided by Conservation International Colombia, the Conservation Leadership Programme (CLP) and the Rufford Foundation. We also express our deep gratitude to all members of the Fundación Ecodiversidad Colombia, for their assistance and volunteer work throughout this process. Finally, we thank Jason L. Brown, M. Rivera-Correa and two anonymous reviewers, whose comments improved the quality of the manuscript. Biological collections for this study were authorized by permit No. 36 (Aug. 24th. 2012), granted by the Autoridad Nacional de Licencias Ambientales (ANLA). Access to genetic resources was authorized by the Ministerio de Ambiente y Desarrollo Sostenible (MADS) through Resolution No. 0103 (Feb. 8th, 2013).

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