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A new species of *Dendrobates* (Anura: Dendrobatidae) from the Amazonian lowlands in Perú

JASON L. BROWN[1], RAINER SCHULTE[2], KYLE SUMMERS[1]

[1]*East Carolina University, Department of Biology, Greenville NC, 27858. E-mail: jlb0627d2@mail.ecu.edu*
[2]*INIBICO, Tarapoto, San Martín, Perú*

Abstract

We describe a new species of poison frog from Amazonian Peru. *Dendrobates uakarii*, **sp. nov.** is distinguished by the presence of paired parallel dorsolateral lines: one yellow oblique lateral and one red dorsolateral (on each flank), with one vertebral line, similar in color to the dorsolateral lines. Phylogenetic analysis show that *D. uakarii*, **sp. nov.** and closely related taxa (*D. ventrimaculatus* sp. aff. Shreve from Porto Walter, Brazil and another from Amazonas, Brazil) form the sister group to *D. fantasticus* Boulenger. This new species can be distinguished from its sister taxa on the basis of 19 unique mitochondrial gene nucleotide site substitutions. Comparisons between closely related species show a slight difference in call repetition rate and mean frequency.

Key words: *Dendrobates*, *duellmani*, *uakarii*, Amazonia, Peru, new species, taxonomy

Introduction

Amphibian species richness and endemism in the upper Amazon basin of Peru are extraordinarily high (Duellman and Mendelson 1995), as exemplified by the dendrobatid frogs inhabiting this area (e.g., Silverstone 1976; Schulte 1999; Vences *et al.* 2000). Over 40 species are currently known from Amazonian Peru (Morales 1995; Schulte 1999; Vences *et al.* 2000), which make up about 20% of the total number of dendrobatids desrcibed (cf. Glaw and Kohler 1998).

The members of the genus *Dendrobates* have long been considered to be comprised of at least three species groups that represent valid evolutionary entities: *tinctorius* group (Silverstone 1975 as modified by Myers and Daly 1979), *histrionicus* group (Myers *et al.* 1984) and *quinquevittatus* group (Caldwell and Myers 1990). In recent years there have been numerous phylogenetic investigations studying the evolutionary histories of these groups (Clough and Summers, 2000; Symula *et al.*, 2003; Vences *et al.* 2003; Roberts *et al.* 2006; Noonan and Wray 2006). These analysis revealed that many members of the *quinquevittatus* group are complexes of species displaying a high level of sequence

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divergence between members, i.e *Dendrobates ventrimaculatus* (Roberts *et al.* 2006; Noonan and Wray 2006).

The Tamshiacu-Tahuayo Reserve in the upper Amazon basin of Peru is surrounded by Rios Amazonas, Ucayali, and Javari. Due to this geographic isolation, geneflow to and from this region is reduced. Although collections of amphibians from this area are limited (Schulte 1999; Rodriguez and Duellman 1994), few species are known to co-occur on both sides of Rio Amazonas. In 1999, a new species, *Dendrobates flavovittatus* Schulte, was reported from this region. Schulte (1999) also described *D. duellmani* from northern Peru near San Jacinto, near the Ecuadorian border. Jungfer and Lötters (2002) criticized Schulte's description, however regarded *D. duellmani* a valid species because of its unique color pattern compared to all other species. Here we provide phylogenetic, biogeographical, acoustical, and morphological support for the designation of a new species previously assumed to be part of *D. duellmani.*

Material and methods

Specimens were collected by Mario Callegari on 20 June 2004 in Tamshiyacu-Tahuayo Reserve along a small tributary of Quebrada Blanco (4º 11'21.88" S, 73º6'15.66" W). Adults were preserved in 70% ethanol. Coloration of species was determined from living specimens and color photographs. Specimens of the new species were compared to published descriptions of all other Amazonian *Dendrobates*. Definitions of characters and a diagnosis follow Myers (1982). Diagnosis of the new species is based on adult specimens only. Measurements were taken with digital calipers to the nearest 0.01 mm. Sex identification was determined by calling and courting activity, however because we are not positive on all sex identification, especially females, sex differences were included, but not used in this analysis. To facilitate comparisons with similar species, the type series description follows the scheme of Grant and Rodriguez (2001).

Measurements taken: SVL, snout-vent length; FL, femur length; TL, tibia length; KK, knee-knee distance, when extended straight; FoL, foot length, from proximal edge of metatarsal tubercle to tip of Toe IV; HaL: hand length, from proximal edge of metacarpal tubercle to tip of longest finger; HL, head length, from the most exposed corner of the occipitum to the tip of snout; HW, head width, between tympana; BW, body width taken just under axillae; UEW, upper eyelid width; IOD, inter-orbital distance; TD, horizontal tympanum diameter; ED, horizontal eye diameter; L1F, length of Finger I, from inner edge of inner metacarpal tubercle to tip of finger disc; L2F, length of Finger II, from junction between Fingers I and III to tip of finger disc; DET, distance from outer-corner of eye to tympanum.

Call comparisons were done in Raven 1.2 (Charif *et al.* 2004). Calls were recorded with a Sony TCM 5000 EV tape recorder and a Sennheiser ME 66-K6 microphone. Sonograms and mean frequency were compared among similar species.

All holotype and paratype specimens are deposited at the Museo de Historia Natural San Marcos, Universidad Nacional Mayor de San Marcos, Lima, Peru (MHNSM)

Phylogenetic Analysis

Sample Collection, Sequence and Phylogenetic Analysis. The sequences used in this study are all derived from previous studies (Clough and Summers 2000; Summers, Weight et al. 1999; Symula *et al.* 2001; Symula *et al.* 2003; Roberts *et al.* 2006; Darst and Cannatella 2004; Noonan and Wray 2006; Graham *et al.* 2004; Santos 2004). 16S rRNA, 12S rRNA, cytochrome oxidase I, and cytochrome *b* gene regions were used in this analysis. All phylogenetic methods used are described in Roberts, *et al.* 2006. Character state reconstruction used to diagnose linages was performed in PAUP* using ACCTRAN optimization (Bond 2004, Swofford 2002). All unambiguous character changes were mapped for the node of interest in MacClade (Maddison and Maddison 2001).

Dendrobates uakarii, sp. nov.

Holotype. MHNSM 23246, (Field number MC0140), an adult female collected on 20 June 2004 by Mario Callegari upstream Quebrada Blanco in Tamshiyacu-Tahuayo Reserve, Departamento Loreto, Peru (4º 11’21.88” S, 73º6’15.66” W), Elevation: 140 m.

Paratypes. MHNSM 23247-23250, (Field numbers MC0141-MC0144), adults collected on 20 June 2004 by Mario Callegari upstream Quebrada Blanco in Tamshiyacu-Tahuayo Reserve, Departamento Loreto, Peru (4º 11’21.88” S, 73º6’15.66” W), Elevation: 140 m.

Diagnosis

A species of *Dendrobates* as characterized by the first finger, which is shorter than the second, the lack of webbing between the toes, absence of premaxillary and maxillary teeth (Myers 1982). *Dendrobates uakarii,* **sp. nov.** is a species of small size (16.16 mm SVL in female holotype); with smooth skin; paired-parallel dorsolateral lines: one yellow oblique lateral and one red dorsolateral (on each flank), with one vertebral line, which is the same color of the dorsolateral lines; black coloration between the dorsolateral lines and the vertebral line generally creates a “U” around the snout. This species can be distinguished from its sister taxa on the basis of 19 unique mitochondrial gene nucleotide site substitutions (Fig. 4).

The new species can be distinguished from all known species of *Dendrobates* occurring in the Amazonian lowlands by the presence of differently colored parallel dorsolateral lines (as described above). The new species is similar in appearance to *D. duellmani* and *D. ventrimaculatus*. *Dendrobates uakarii,* **sp. nov.** is distinguished from *D.*

ventrimaculatus sensu strico and *D. ventrimaculatu* sensu lato (Fig. 2) by: complete parallel dorsolateral stripes; red to orange red in life (vs. yellow to orange-red "Y" to single incomplete vertebral stripe on dorsum), presence of a single broad oblique lateral stripe (vs. often connecting, or fine single oblique lateral stripe) and presence of black "U", which is formed from the vertebral and dorsolateral lines. *Dendrobates uakarii*, **sp. nov.** is distinguished from *D. duellmani* by: dorsolateral stripe red in life (vs. reddish pink), and broad yellow oblique lateral stripe present (vs. fine blue oblique stripe, matching the color of reticulation on limbs, Fig. 2).

Description of Holotype

Size small, SVL 16.16 mm (Table 1). Widest part of head between eyelids. Body slightly wider than head. Greatest head-width 30.6% of SVL. Eyes very protuberant. Tongue small, oval. Teeth absent.

TABLE 1. Measurements of *D.uakarii.*

	MHNSM 23246	MHNSM 23247	MHNSM 23248	MHNSM 23249	MHNSM 23250	MHNSM** 23251	Average ± StDev***
SVL	16.16	15.47	14.79	15.70	14.82	13.04	15.39 ± 0.59
FL	6.46	6.32	6.24	6.44	6.27	5.36	6.35 ±0.10
TL	7.10	7.11	7.02	7.05	6.71	5.82	7.00 ±0.17
KK	12.70	13.19	12.87	13.62	12.80	11.35	13.04 ±0.37
FoL	6.08	6.13	5.96	6.01	5.77	4.75	5.99 ±0.14
HaL	4.11	3.82	3.63	3.83	3.61	3.08	3.80 ±0.20
HL	5.49	5.43	5.24	4.94	4.89	4.40	5.20 ±0.27
±HW	4.95	5.27	5.08	5.17	4.92	4.52	5.08 ±0.15
BW	5.88	5.52	5.04	5.84	4.88	4.61	5.43 ±0.46
TD*	0.58	0.49	0.62	0.62	0.53	0.44	0.57 ±0.06
ED*	1.47	1.60	1.64	1.51	1.60	1.42	1.56 ±0.07
IOD*	2.27	2.27	2.22	2.35	2.13	1.96	2.25 ±0.08
L1F*	1.20	1.07	1.24	1.24	1.02	0.89	1.15 ±0.10
L2F*	1.69	1.47	1.64	1.69	1.47	0.93	1.59 ±0.11
DET*	0.58	0.58	0.58	0.62	0.53	0.49	0.58 ±0.03
UEW*	1.38	1.29	1.33	1.24	1.38	0.98	1.32 ±0.06
SEX	♀	♂	♂	♀	♂	–	

* Measurements taken with dissecting microscope
**sub-adult, not used in description
*** MHNSM 23251 not included

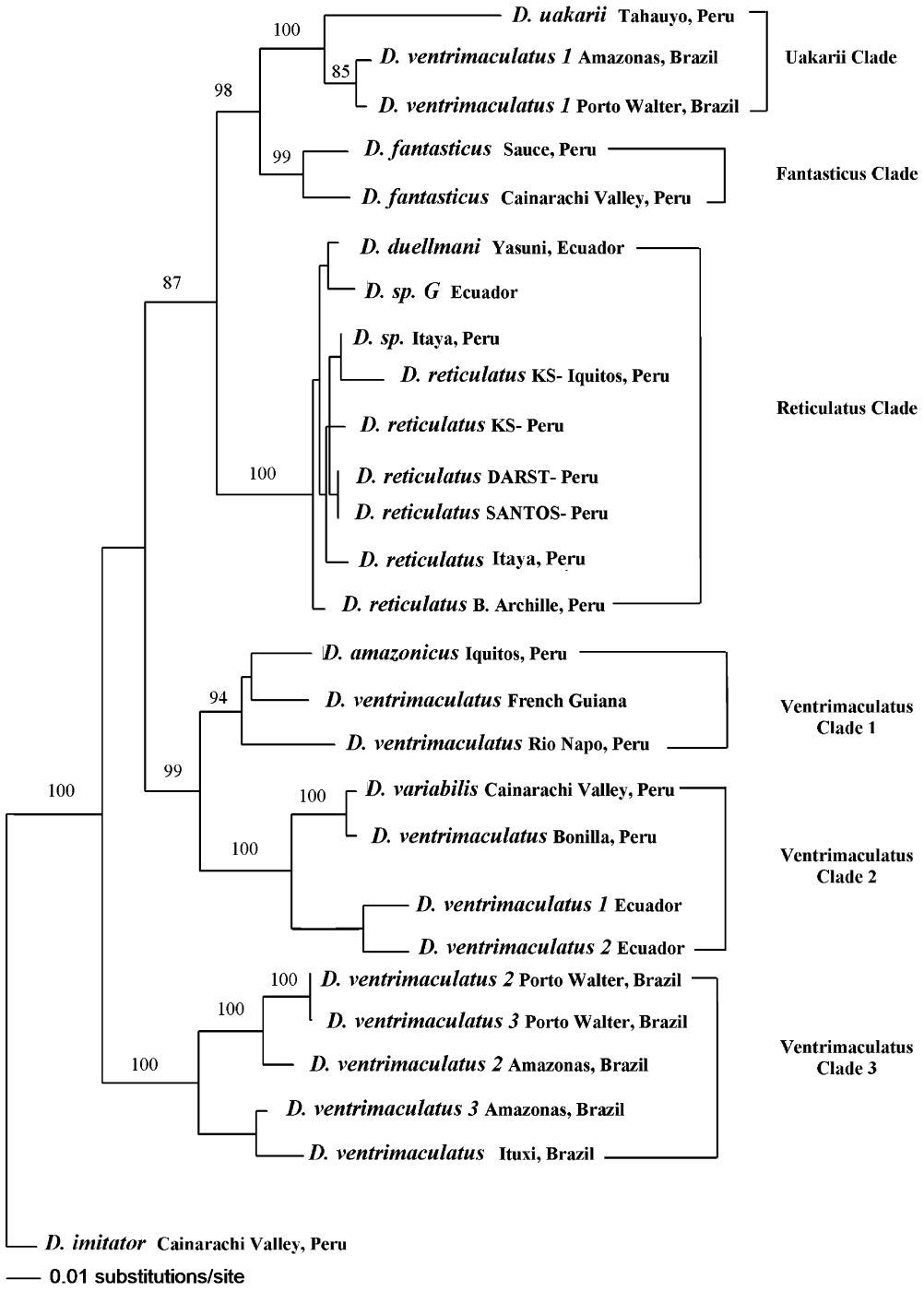

FIGURE 1. Maximum likelihood phylogram derived from a Bayesian backbone constraint consensus tree constructed using only taxa for which 12S, 16S, cytochrome *b* and cytochrome oxidase I sequence data were available. Numbers indicate posterior probabilities from the Bayesian analysis. Species of the Ventrimaculatus group are denoted with s.s. (sensu stricto), s.l. (sensu lato) and sp. aff (species affinis).

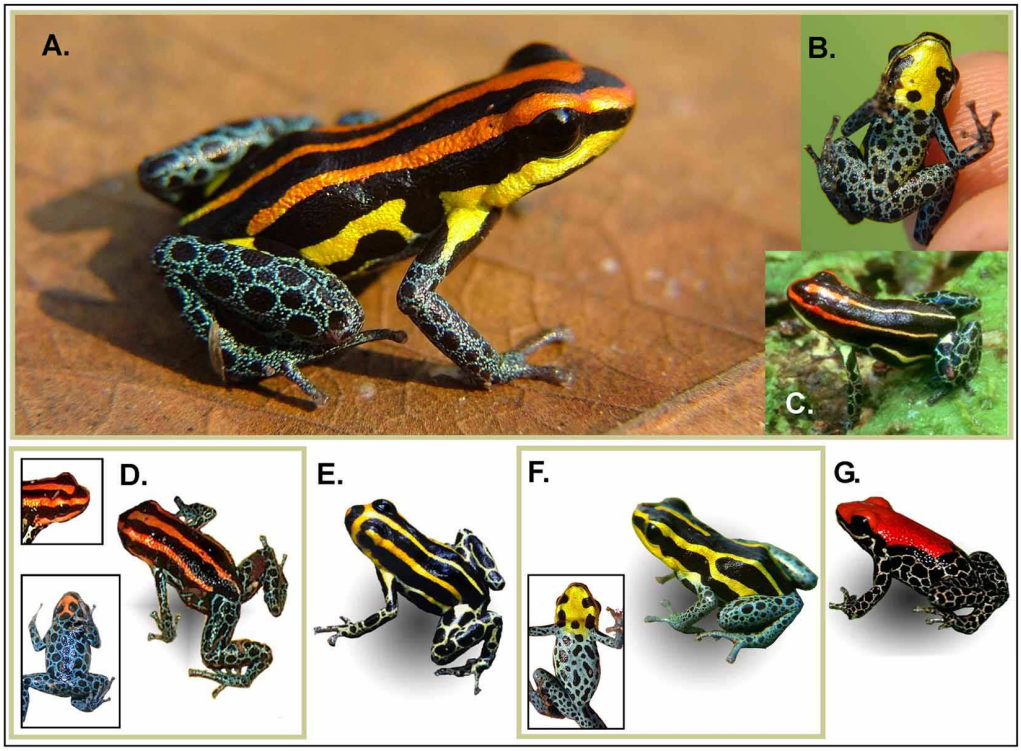

FIGURE 2. A photographic illustration comparing *D. uakarii,* **sp. nov.** to similar species. *D. uakarii,* **sp. nov.** (holotype) from Tamashiyacu-Tahauyo Communal Reserve (**A.** Dorsum **B.** Venter). Near Rio Yarapa, south of Rio Tahuayo, populations have thinner dorsolateral and vertebral lines with brighter red stripes (**C.** photo: Devon Graham). **D.** *D. duellmani,* Yasuni, Ecuador (photo: Petra Bartelds). **E.** *D. ventrimaculatus* sp. aff. Solimoes, Amazonas, Brazil (photo: Janalee P. Caldwell). **F.** *D. ventrimaculatus* sensu lato, Tamashiyacu-Tahauyo Communal Reserve, Peru. **G.** *D. reticulatus,* Iquitos, Peru (photo: Evan Twomey).

Skin in preservative completely smooth on all surfaces of body. Snout sloping laterally; bluntly rounded dorsally; truncate ventrally. Nares situated and directed laterally to the tip of snout; both nares barely visible from front, well from below but not from above. Canthus rostralis rounded; loreal region sloping and flat or slightly concave. Interorbital distance 1.7 times wider than upper eyelid. Tympanum circular, half concealed posterodorsally (7 o'clock to 2 o'clock, when center of snout is at 3 o'clock), without tympanic annulus, its area less than 50% of ED.

Hands relatively small, length being 25.4% of SVL. Relative length of appressed fingers 1<2<4<3; finger I slightly shorter than finger II. Discs conspicuously expanded on all fingers but finger I. In adults disc on finger III is 2 times wider than distal end of adjacent phalanx. A large, circular outer metacarpal tubercle on median base of palm; a smaller inner metacarpal tubercle on base of finger I; one prominent subarticular tubercle on fingers I, II, and IV, two on finger III.

Hind limbs relatively short, with heel of appressed limb reaching the tympanum. Tibia 43.9% of SVL. Relative lengths of appressed toes 1<2<5<3<4; first toe short (but conspicuously present), barely reaching bottom of subarticular tubercle on base of second toe, with unexpanded disc; and toes II, III, and IV barely expanded (much smaller than finger discs), and toe IV expanded (disc 1.5 broader than adjacent phalanx). Moderate-sized inner and small outer metatarsal tubercles, somewhat protuberant with rounded surfaces. One slightly protuberant subarticular tubercle on toes I, II and V, two on toe III, and three on toe IV. Hands and feet lacking supernumerary tubercles, lateral fringes and webbing.

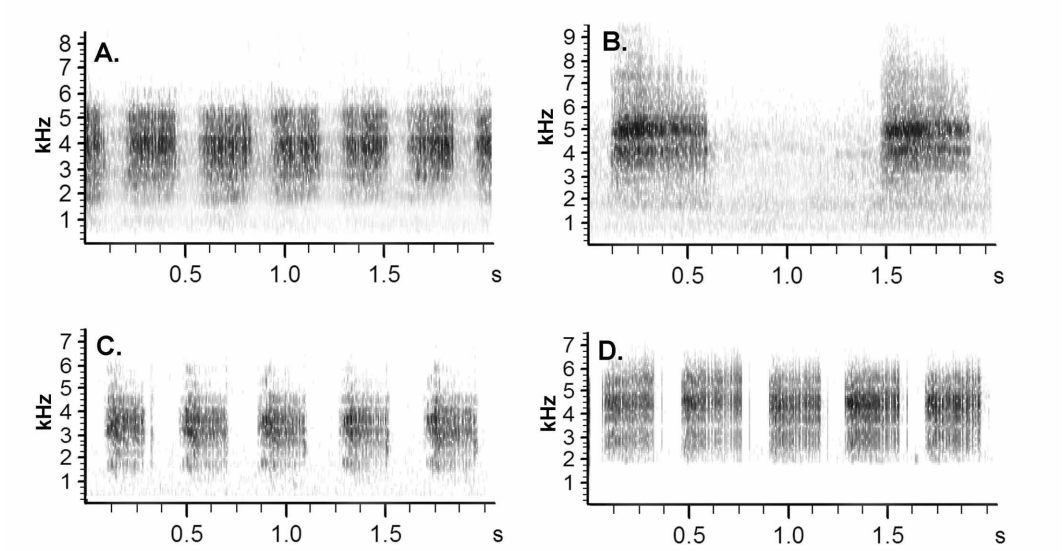

FIGURE 3. Call comparisons of closely related species. The data is listed as following: species (ambient temperature, location of individual, mean frequency). **A.** *D. uakarii* (26°C, Tahauyo, 3780 hz). **B.** *D. ventrimaculatus* sensu lato (24°C, Iquitos, 4900 hz) **C.** *D. fantasticus* (24°C, Iquitos, 3350 hz). **D.** *D. reticulatus* (29°C, Iquitos, 4130 hz).

Color in life (based on photographs of a living specimen, Fig. 2): dorsum and upper flanks black, with paired dorsolateral lines: one yellow oblique lateral and one red dorsolateral (on each flank); and one vertebral line, similar in color to the dorsolateral lines. The paired dorsolateral stripes are bright reddish-orange, which continue on the exterior edges of the eyelids, the canthus rostralis, and the superior part of the snout. The vertebral line spans from the preorbital to the sacral region. The paired oblique lateral lines extend from the groin to the upper forelimbs around the upper lip. Limbs, hands, feet, and belly blue with a fine reticulum of black dots and larger spots. Throat yellow, with paired black spots below the mandible, and large black gular spot. Iris black.

In 70% alcohol the color is almost identical to the living animal described above. The only differences are that the dorsolateral stripes and vertebral stripe changed to pinkish-yellow, and oblique lateral stripes and throat changed to silver-white.

TABLE 2. Species names, collection localities, and GenBank accession numbers (where applicable) for taxa included in the analysis.

Species	Location	12S	16S	COI	CytB
D. amazonicus	Iquitos, Loreto, Peru	AF482770	AF482785	AF482815	AF482800
D. duellmani	Yasuni, Ecuador	AY364566	AY263246	NA	NA
D. fantasticus	N. Sauce, San Martin, Peru	AF412444	AF412472	AF412416	AF412500
D. fantasticus	Cainarachi, San Martin, Peru	AF412447	AF412475	AF412419	AF412503
D. imitator	Huallaga, San Martin, Peru	AF412448	AF412476	AF412420	AF412504
D. reticulatus	Punte Itaya, Loreto, Peru	AF482772	AF482787	AF482817	AF482802
D. reticulatus	B. Achille, Loreto, Peru	AF482771	AF482786	AF482816	AF482801
D. reticulatus DARST	Peru	AY326029	AY326029	NA	NA
D. reticulatus KS	Peru	NA	AF412467	AF412411	AF412495
D. reticulatus SANTOS	Peru	AY364567	AY364567	NA	NA
D. reticulatus KS	Peru	AF412439	AY263245	NA	NA
D. sp.	Puente Itaya, Peru	AF482777	AF482792	AF482821	AF482807
D. sp. G.	Ecuador	AY364568	AY364568	NA	NA
D. uakarii	Tahuayo, Loreto, Peru	DQ371305	DQ371316	DQ371325	DQ371335
D. variabilis	Cainarachi, San Martin, Peru	AF412463	AF412491	AF412435	AF412519
D. ventrimaculatus s.l.	N. Bonilla, San Martin, Peru	AF412466	AF412494	AF412438	AF412522
D. ventrimaculatus s.l.	Near Rio Napo, Loreto, Peru	AF482781	AF482796	AF482825	AF482811
D. ventrimaculatus s.l.	Ituxi, Acre, Brazil		Noonan and Wray 2006		
D. ventrimaculatus s.l.	French Guiana	DQ371302	DQ371313	DQ371325	DQ371332
D. ventrimaculatus sp. aff.	Solimoes, Amazonas, Brazil	DQ371307	DQ371318	DQ371327	DQ371337
D. ventrimaculatus s.l. 1	Solimoes, Amazonas, Brazil	DQ371308	DQ371319	DQ371328	DQ371338
D. ventrimaculatus s.l. 2	Solimoes, Amazonas, Brazil	DQ163089	DQ163079	DQ163063	DQ163074
D. ventrimaculatus sp. aff.	Porto Walter, Acre, Brazil	AF482782	AF482797	AF482826	AF482812
D. ventrimaculatus s.l. 1	Porto Walter, Acre, Brazil	DQ371301	DQ371312	DQ371322	DQ371331
D. ventrimaculatus s.l. 2	Porto Walter, Acre, Brazil	AF482783	AF482798	AF482827	AF482813
D. ventrimaculatus s.s. 1	Ecuador	AF482780	AF482795	AF482824	AF482810
D. ventrimaculatus s.s. *2*	Ecuador	AF128620	AF128619	AF097502	AF120013

Etymology

The red uakari Dendrobates. The specific epithet is a patronym for the red uakari (*Cacajao calvus ucayalii*), an endangered Amazonian primate. Both black (*C. melanocephalus*) and red uakari (*C. calvus*) are probably the primate species at greatest risk in South America (CITES). Because these monkeys are quite large and prefer flooded

forest habitats, they are easily hunted from boats. The epithet was chosen because both the red uakari and *D. uakarii,* **sp. nov.** shared similar historical distributions and have bright red dermal pigmentation.

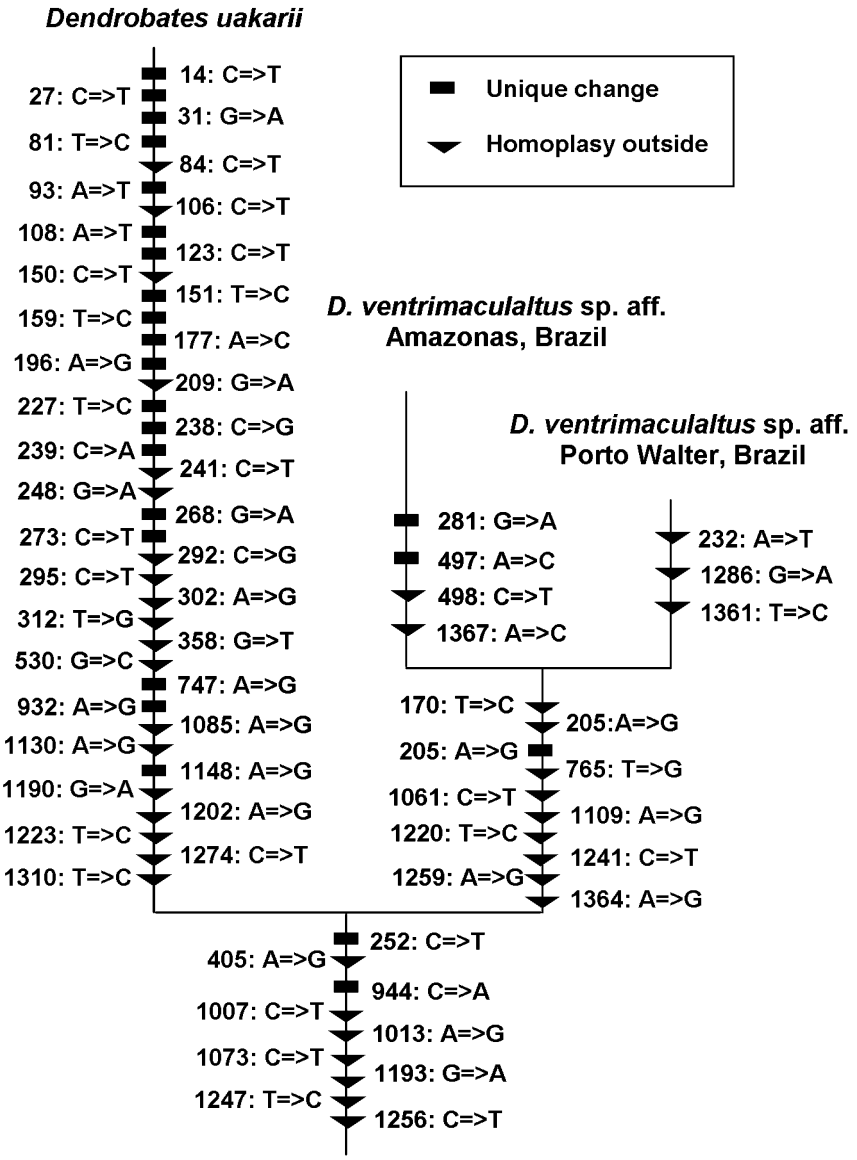

FIGURE 4. Character transformation for *Dendrobates uakarii,* **sp. nov.** diagnostic nucleotide site substitutions using ACCTRAN optimization. Alignment available online at http://www.dendrobates.org/permanent/duakarii.zip

Variation

Within populations the black between the dorsolateral lines and vertebral line may form a "U" around the snout (77%, n=13). Other individuals have a connected dorsolateral line and vertebral line near the canthus rostralis (23%, n=13). The black gular

spot is absent in some individuals (7%, n=13). Coloration and width of the dorsolateral and vertebral lines vary between populations. Near Rio Yarapa, south of Rio Tahuayo, populations have thinner dorsolateral and vertebral lines, are yellow near the sacrum (almost the same color as oblique lateral stripes), and change to brick-red near the occiput (Fig 2C). We amplified regions of the cytochrome *b* gene from two individuals from the Tamshiyacu-Tahuayo Reserve and uncovered only one haplotype; although the sample size is very small, this suggests that intrapopulation variation may be minimal.

Distribution and ecology

We found *Dendrobates uakarii,* **sp. nov.** throughout the Tamshiyacu-Tahuayo Community Reserve and further south to Pacaya Samiria Reserve, on the Rio Yarapa. Its distribution is likely between Rio Amazonas, Rio Javari, and Rio Ucayali (north of the Contamana-Sierra Divisor Arch) in western Brazil and eastern Peru. This putative distribution is supported by Christmann's (2004) book, which contains pictures of a similar looking species 200 km east of Iquitos, south of Rio Napo, and further east to the tributaries on the south side Amazon, near the Brazilian border. In Tahuayo, it occurs sympatrically with two other species of *Dendrobates: D. ventrimaculatus* sensu lato and *D. flavovittatus. D. uakarii*, **sp. nov.** occurs in primary forests. It spends a majority of its time on the forest floor, however it occasionally ventures a few meters into the canopy. The call is a long series of soft buzz-like notes, similar to *D. fantasticus*, but with shorter pauses between each note, making the call sound nearly continuous (Fig 3). Males have been observed to carry one to four tadpoles to large phytotelmata such as bromeliads.

Phylogeny and biogeography

The placement of the new species in the genus *Dendrobates* is supported by molecular phylogenetic data (Fig. 1), grouping with the Amazonian clade containing *D. fantasticus* and *D. reticulatus*. Phylogenetic analysis shows that *D. uakarii,* **sp. nov.** and closely related taxa (*D. ventrimaculatus* sp. aff.) form a sister group to *D. fantasticus* (Fig. 1).

Populations of *Dendrobates duellmani* from eastern Ecuador are most closely related to *D. reticulatus* Boulenger and species from Puente Itaya, Loreto, Peru and Ecuador. *Dendrobates uakarii,* **sp. nov.** is sister to specimens identified as *D. ventrimaculatus* sp. aff., which are phylogentically distinct from all other Ventrimaculatus clades (Fig 1). This incongruence may be the result of mimicry between the Uakarii clade and the Ventrimaculatus clades (both at Porto Walter and Amazonas, Fig 1), however this hypothesis has yet to be tested. The uncorrected pair-wise distance between *D. uakarii,* **sp. nov.** and its sister taxa was 5.09%, closer than the distance between the *D. duellmani* and *D. uakarii,* **sp. nov.** (5.41%). The high Jukes-Cantor genetic distances (> 5.0%) between *D. uakarii,* **sp. nov.** and all other individuals in this study suggest deep divergence between it and all other *Dendrobates* in the Western Amazonia (Fig 1).

The distribution pattern for *Dendrobates uakarii*, **sp. nov.** is consistent with phylogenetic affinity, with sister taxa occurring in southwestern Brazil. This supports the hypothesis of northward radiation by southern ancestors from southern Peru and central-western Brazil radiating into northern Peru, Ecuador, Colombia, northern Brazil and French Guiana (Roberts *et al.* 2006, Noonan and Wray 2006, Symula *et al.* 2003). The similarly restricted distribution of the sympatric *D. flavovittatus* suggests that the area inhabited by these species is effectively isolated from geneflow, and despite the recent criticisms of the Riverine-Barrier hypothesis (Patton *et al.*, 1994; Lougheed *et al.*, 1999; Gascon *et al.*, 2000), the Amazon River remains a well defined barrier and only a few species are known to occur on both sides.

Remarks

The polyphyly observed in *D. ventrimaculatus* suggests the need for further subdivision (Fig 1). At least four distinct clades have been resolved: two from western Brazil (Uakarii clade and Ventrimaculatus clade 3) and two clades containing all other South American species being called *D. ventrimaculatus* (Ventrimaculatus clade 1 and 2). Ventrimaculatus clades 1 and 2 are geographically isolated, creating an east Andes versant group (clade 2), containing *D. variabilis*, and an Amazonian lowland group (clade 1) containing *D. amazonicus* (Schulte 1999). The taxonomic validity of *D. variabilis* and *D. amazonicus* is currently an issue of contention (Caldwell and Myers 1990; Symula *et al.* 2001; Schulte 1999). However, the designation of both species has begun to draw attention to cryptic species currently being called *D. ventrimaculatus.* Lastly, we wanted to clarify our 2006 paper (Roberts *et al.* 2006) in which *D. uakarii*, **sp. nov.** was referred to as *D. duellmani* Tamshiyacu-Tahuayo.

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Appendix. List of comparative material examined

Repository abbreviation as follows: Museo de Historia Natural San Marcos, Universidad Nacional Mayor de San Marcos, Lima, Peru (MHNSM), East Carolina University, North Carolina, USA (ECU), Instituto de investigación de la Biología de Cordillera Oriental, Tarapoto, San Martin, Peru (INI), Museum of Natural History, University of Kansas, Lawrence, USA (KU), and personal collection Janalee P. Caldwell (JPC).

Dendrobates amazonicus Schulte, non-type (INI)
Dendrobates biolat Morales, holotype (MHNSM)*
Dendrobates biolat Morales, non-type (INI)
Dendrobates duellmani Schulte, holotype (KU)*
Dendrobates duellmani Schulte, non-type (INI)
Dendrobates fantasticus Boulenger, non-type from Sauce, PE (INI)
Dendrobates fantasticus Boulenger, non-type from Cainarcahi Valley, PE (ECU, INI)
Dendrobates fantasticus Boulenger, non-type from Varadero, PE (INI)
Dendrobates fantasticus Boulenger, non-type from Pongo de Cainarcahi, PE (INI)
Dendrobates fantasticus Boulenger, non-type from Sauce, PE (ECU, INI)
Dendrobates flavovittatus Schulte, non-type (INI)
Dendrobates imitator Schulte, non-type from Cainarachi Valley, PE (INI)
Dendrobates imitator Schulte, non-type from Sauce, PE (INI)
Dendrobates imitator Schulte, non-type from Huallaga, PE (INI)
Dendrobates imitator Schulte, non-type from Pongo de Cainarachi (INI)
Dendrobates imitator Schulte, non-type from Varadero, PE (INI)
Dendrobates lamasi Morales, holotype (MHNSM)*
Dendrobates reticulatus Boulenger, non-type (INI, ECU)
Dendrobates mysteriosus Myers, non-type (INI)
Dendrobates variabilis Zimmermann and Zimmermann, non-type Cainarachi Valley, PE (INI, ECU)
Dendrobates variabilis Zimmermann and Zimmermann, non-type Saposoa, PE (INI)
Dendrobates variabilis Zimmermann and Zimmermann, non-type Huallaga Canyon, PE (INI)
Dendrobates ventrimaculatus sensu stricto Shreve, non-type, EC (ECU)
Dendrobates ventrimaculatus sensu lato Shreve, non-type from Iquitos, PE (INI)
Dendrobates ventrimaculatus sensu lato Shreve, non-type from Tamshiyacu-Tahuayo, PE (INI)
Dendrobates ventrimaculatus sensu lato Shreve, non-type from Pongo de Cainarachi, PE (INI)
Dendrobates ventrimaculatus sensu lato Shreve, non-type from Huallaga Canyon, PE (INI)
Dendrobates ventrimaculatus sensu lato.Shreve, from Porto Walter, BZ (JPC)*
Dendrobates ventrimaculatus sp. aff. Shreve, from Solimoes, Amazonas, BZ (JPC)*

*Actual specimen was not examined; photographs, measurements, and field observations were used.

