



## A partial revision of the *Ameerega hahneli* complex (Anura: Dendrobatidae) and a new cryptic species from the East-Andean versant of Central Peru

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### Abstract

We describe a new species of poison frog from central Peru which has been referred to as *Ameerega picta* and *A. hahneli* for the past thirty years. To our knowledge the new species is endemic to Peru and occurs throughout the east-Andean versant between roughly 6 and 10 degrees south latitude. Recent phylogenies using molecular data show that the new species and *A. hahneli* are not closely related despite being similar in pattern, color, and morphology. Our data suggest that the new species is a sister taxon to *A. rubriventris*, which is readily distinguishable from the new species by its reddish venter. The new species can be distinguished furthermore from other *Ameerega* species by possessing white (rather than yellow or cream) dorsolateral stripes, and from the similar *A. hahneli* by differences in advertisement calls and larval morphology.

**Key words:** *Ameerega altamazonica* sp. nov., Dendrobatid frogs, *A. hahneli*, new species, Peru, poison frogs, taxonomy

### Resumen

Se describe una especie nueva de rana venenosa del centro del Perú la cual había sido erróneamente asignada a *A. picta* y *A. hahneli* durante los últimos treinta años. Según nuestros conocimientos, la especie nueva es endémica al Perú y se distribuye a través de la vertiente oriental de los Andes entre aproximadamente 6 y 10 grados de latitud sur. Recientes filogenias utilizando datos moleculares muestran que la nueva especie y *A. hahneli* no están cercanamente emparentadas, a pesar de ser similar en patrones, color, y morfología. Nuestros datos sugiere que la nueva especie es una especie hermana a *A. rubriventris*, que puede distinguirse de la nueva especie por su vientre rojizo. Además se puede distinguirse de la mayoría de otras especies de *Ameerega* por presentar rayas dorsolaterales blancas (en lugar de amarillo o crema), y se diferencia de *A. hahneli* por diferencias en los cantos y morfología larval.

### Introduction

Species richness of dendrobatid frogs in the upper Peruvian Amazon is unparalleled, particularly in the genus *Ameerega* (Roberts *et al.* 2006, Lötters *et al.* 2007). Of the ca. 25 recognized species in this genus, 11 are endemic to the east-Andean versant and surrounding lowlands of Peru. Recent, intensified sampling in this region combined with molecular phylogenetic analysis is revealing that there may be many more species of dendrobatids in this area than previously suspected. As a result, several new species of poison frogs are currently being described from this area, most of which dwell in the Cordillera Oriental in central Peru.

One of these species, the subject of this paper, has been known for quite some time but by an incorrect name, having first been referred to as a population of *Phyllobates pictus* (= *Ameerega picta*), and later referred to as a population of *A. hahneli* (e.g. Silverstone 1976, Lötters *et al.* 1997). The type locality of *A. hahneli*

(Boulenger 1883) is Yurimaguas, a small town on the lower Río Huallaga in Peru. The validity of this name was questioned by some authors (e.g. Lutz 1952, Silverstone 1976) who considered *A. hahneli* to be a variant of *A. picta*. This arrangement was rejected in later studies (Martins and Sazima 1989, Haddad and Martins 1994), which concluded that *A. picta* sensu Silverstone (1976) represented at least four distinct species (*A. braccata*, *A. flavopicta*, *A. hahneli*, *A. picta* sensu stricto), and furthermore raised the possibility that *A. hahneli* may represent two or more species based differences in advertisement calls between Brazilian and Peruvian populations. In the past decade or so, specimens from many other localities in Peru, Brazil, and Bolivia have been referred to as *A. hahneli*, all bearing a similar pattern of a black or brown dorsum with white dorso-lateral stripes (e.g. Lötters *et al.* 1997, 2005, 2007, Schulte 1999, Roberts *et al.* 2006, 2007). A recent study using molecular genetics (Roberts *et al.* 2006) revealed a polyphyletic *A. hahneli*, with one Amazonian clade sister to a larger group containing several other species of *Ameerega*, and a second (primarily montane) clade sister to *A. macero*.

Around the same time the polyphyly of *A. hahneli* became known to us, we began to notice during our field investigations that different populations of putative *A. hahneli* made two distinctly different advertisement calls, an observation which had been previously made by Lötters *et al.* (1997). One group of frogs, including individuals from near the *A. hahneli* type locality, has an advertisement call consisting of a long, trill-like train of notes which can last three minutes or longer. The area around Yurimaguas is almost completely deforested, making the acquisition of type material difficult. However, we have sequenced *A. hahneli* from a site 45 km to the southwest (Convento), recorded them from a site 31.5 km southeast (Shucusyacu), and recorded and sequenced them from a site 360 km to the northeast (Iquitos) (Roberts *et al.* 2006, present study). Based on field observations and molecular genetics, it is evident that these frogs all have a trill call and form a monophyletic clade, and agree well with photos of *A. hahneli* lectotypes. We here refer to it as *A. hahneli* sensu stricto. Yurimaguas is geographically positioned within this region, which is a continuous stretch of lowland forest between 140 and 180 m elevation. Frogs with similar calls were later found along the east bank of Río Ucayali near Contamana and in the Río Pachitea drainage near Puerto Inca in central Peru.

Members of the second clade of putative *A. hahneli*, particularly those associated with premontane habitats of the east-Andean versant, have an advertisement call consisting of a single ‘peep’ rather than a train of notes. No individuals with this call type have ever been found in the lowlands near Yurimaguas, despite frequent field surveys in this region since 2004. Eventually it became clear that the call differences coincided with the phylogenetic divide in this group – frogs of the nominal Amazonian clade consistently have trill calls, while frogs from the montane clade invariably have peep calls. This character finally provides a basis for easy diagnosis between two species that are not particularly closely related but are nearly indistinguishable morphologically.

Though several recent studies have recognized that the name *A. hahneli* sensu Haddad and Martins (1994) refers to at least two distinct species, no formal taxonomic revisions have been made. The goals of this paper are to (1) describe a new species in order to restrict the usage of *A. hahneli* so that it refers to a monophyletic taxon, and (2) to provide a basic taxonomic and systematic framework for future assessment of specific diversity in both the *A. hahneli* sensu stricto clade and the clade containing the new species described herein.

## Material and methods

The type series of the new species is deposited in 70% ethanol in the Museo de Historia Natural San Marcos, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM), with the exception of two paratypes and three tadpoles which are deposited in the East Carolina University field collection (ECU-F). The following measurements were made with mechanical calipers and a micrometer to the nearest 0.01 mm, following Myers (1982) and Brown *et al.* (2006): snout-vent length (SVL), femur length from vent to lateral edge of

knee (FL), tibia length from medial edge of heel to lateral edge of knee (TL), knee-knee distance with both legs extended straight (KK), foot length from proximal edge of metatarsal tubercle to tip of toe IV (FoL), hand length from proximal edge of metacarpal tubercle to tip of longest finger (HaL), head length from most exposed corner of occiputum to tip of snout (HL), head width between tympana (HW), body width under axillae (BW), upper eyelid width (UEW), interorbital distance (IOD), internarial distance (IND), horizontal tympanum diameter (TD), horizontal eye diameter (ED), distance from outer corner of eye to tympanum (DET), length of finger I from proximal edge of median palmar tubercle to tip of finger disc (L1F), length of finger II from proximal edge of median palmar tubercle to tip of finger disc (L2F), width of disc of finger III (W3D), and width of finger III just below disc (W3F). Sex was determined by checking for the presence of vocal slits; additionally, several males were observed calling prior to collection. We compared type material for the new species to photos of *A. hahneli* sensu stricto from Iquitos and to photos of *A. hahneli* lectotypes from Yurimaguas.

Two calling males of the new species were recorded in the type locality with a Sony DCR-JC42 camera and Sony ECM-HGZ1 gun microphone. Calls were analyzed in Raven 1.2 (Charif 2004) and compared to vocalizations of *A. hahneli* sensu stricto from near Yurimaguas and Iquitos, Peru.

Three free-living tadpoles (ECU-F 102-104) were preserved in 70% ethanol for description, and staged according to Gosner (1960). Mouthpart formulas follow McDiarmid and Altig (1999). Tadpoles were not preserved in formalin so that species identification could be made using molecular genetics. Larvae of the new species were compared to three larvae of a similar stage from *A. hahneli* sensu stricto from Iquitos (ECU-F 105, 106).

The potential geographic ranges of the new species and *A. hahneli* sensu stricto were estimated using the ecological niche-modeling program Maxent 3.0 Beta (Phillips *et al.* 2006). The niche model for the new species was built using 22 presence points; the *A. hahneli* model used 29 presence points. Occurrence data were obtained through personal observations and from published records (Silverstone 1976, Haddad and Martins 1994, Roberts *et al.* 2006). Climatic data were obtained from the WORLDCLIM website (<http://www.worldclim.org/>); we used the 1 km resolution BIOCLIM data (variables 1–18) for current climatic conditions (ca. 1950–2000). Maxent was run with the following parameters: random test percentage = 50%, regularization multiplier = 1.0, maximum iterations = 500, convergence threshold = 0.00001, number of background points = 10,000. Environmental variables were jackknifed to determine the contribution of each BIOCLIM variable to the model. We estimated the actual distribution of *A. altamazonica* in ArcGIS 9.1 by drawing a minimum convex polygon around known localities and subtracting from that polygon areas with an elevation lower than 180 m (floodplain) and higher than 900 m using the WORLDCLIM digital elevation model.

Genetic data used for the phylogenetic analysis were adopted primarily from Grant *et al.* (2006) and Roberts *et al.* (2006), with the exception of two topotypic *A. rubriventris*, four *A. altamazonica* individuals from two localities, one topotypic *A. smaragdina*, one *A. macero* (representing a large range extension), and one *A. hahneli* individual from Puerto Inca. We sequenced 12s, 16s, and CytB, totaling 1756 bp. Tissue collection, DNA extraction, amplification, sequence alignment, and sequence analysis of new samples followed the methods of Roberts *et al.* (2006). Phylogenetic analysis was done using Maximum Likelihood with a GTR model of nucleotide substitution with gamma distributed rate heterogeneity and a proportion of invariant sites (as suggested by Modeltest 3.7; Posada and Crandall 1998) in GARLI 0.951 (Zwickl 2006). The final data set included 72 individuals. The topology of the generated phylogeny is consistent with that of Roberts *et al.* (2006), and the phylogenetic affinity of the additional samples (mentioned above) are consistent with another study in which they were included (Grant *et al.* 2006).

***Ameerega altamazonica* sp. nov.**

Figures 1, 2, 4

*Phyllobates pictus* (non Bibron in Tschudi): Silverstone 1976 p. 40–41, pattern 4 (partim).*Dendrobates pictus* (non Bibron in Tschudi): Myers, Daly, and Malkin 1978 p. 332 (by implication).*Epipedobates hahneli* (non Boulenger): Lötters *et al.* 1997 p. 33–34, sketch 2 (partim); Schulte 1999: p. 227–237 (partim).*Ameerega hahneli* (non Boulenger): Grant *et al.* 2006 (by implication); Lötters *et al.* 2007: p. 336–342 (partim).

**Holotype.** MUSM 26937, an adult male that was observed calling, collected by J. Brown, K. Fieselman, and E. Twomey in Departamento San Martín, Perú, 3.5 km N of Tarapoto, Río Shilcayo drainage, 401 m elevation, 6° 27' 44" S, 76° 21' 6" W, 9 June 2007.

**Paratopotypes.** MUSM 26936, 26938, 26939 collected same date and location as holotype.

**Paratypes.** All from Peru. **San Martín:** 20 km SW of Tocache, upper Río Tocache drainage, 865 m elevation, 8°18'32" S, 76°40'33" W (MUSM 24939–24944), collected 11–13 July 2006 by M. Pepper, E. Twomey, and W. Olthof); 7 km NW of Saposoa, Río Shima drainage, 408 m elevation, 6°53'47" S, 76°49'41" W (MUSM 26974), collected 24 June 2007 by J. Brown and E. Twomey); Chazuta, Río Tunumtunumba drainage, 244 m elevation, 6°33'36" S, 76°7'19" W (MUSM 26934, 26935), collected 11–12 June 2007 by E. Twomey); 7 km SW of Huicungo, Río Huayabamba drainage, 352 m elevation, 7°22'3" S, 76°48'48" W (MUSM 26977), collected 25 June 2007 by J. Brown and E. Twomey); 6.5 km N Campanilla, 313 m elevation, 7°25'39" S, 76°39'53" W (MUSM 26981, 26982), collected 25 June 2007 by J. Brown and E. Twomey).

**Loreto:** Pampa Hermosa, west bank of Río Ucayali, 153 m elevation, 7°12'27" S, 75°19'25" W (ECU-F 100, 101), collected 21 July 2006 by M. Pepper and E. Twomey).

**Etymology.** The specific epithet is composed of the Latin adjective ‘*altus*’, meaning ‘high’, and the Spanish adjective ‘*Amazónica*’, meaning ‘pertaining to the Amazon’. Combined to signify ‘upper-Amazonian’, referring to the species’ distribution, being known from the upper Río Huallaga and Ucayali drainages, both major headwaters of Río Amazonas.

**Definition and diagnosis.** A small species of *Ameerega* with an adult SVL of approximately 18–25 mm. Dorsal skin granular, black or brown, usually with white dorsolateral stripes extending from loreal region to groin. Yellow or orange spots present above groin, under axillae, and on shanks. White labial stripe present starting behind nares and ending at forelimb. Tadpole dark brown with large white spots lateral to mouth.

The combination of white dorsolateral stripes and a blue venter with black marbling distinguish *A. altamazonica* from the multitude of *Ameerega* species possessing one but not both of these characteristics. *Ameerega yungicola* and *A. hahneli* sensu stricto are the only other species of *Ameerega* possessing both these characters. *Ameerega yungicola* has maxillary teeth (teeth absent in *A. altamazonica*), red (versus orange or yellow in *A. altamazonica*) flash marks, and an advertisement call consisting of 4.5–5.0 notes per second with a dominant frequency of 3590–3719 Hz (versus 2–3 notes per second with a dominant frequency of 4300–5140 Hz in *A. altamazonica*). *Ameerega hahneli* sensu stricto is morphologically most similar to the new species but has an advertisement call consisting of 6–10 notes per second for several minutes. Its tadpole has enlarged and pointed (versus reduced and rounded in *A. altamazonica*) marginal papillae on the posterior labium. Other species similar in appearance to *A. altamazonica* include *A. boliviana*, *A. picta* sensu stricto, *A. petersi*, *A. pulchripectus*, (all of which have yellowish or green dorsolateral stripes), and *A. rubriventris* (which has a reddish-orange venter instead of a blue venter in *A. altamazonica*). The last mentioned species is the sister taxon to *A. altamazonica*, genetically distinct on the basis of 24 unambiguous nucleotide substitutions.

**Measurements (in mm).** The male holotype (Figs. 1 & 2) has SVL 21.4; FL 10.4; FL 10.9; KK 20.0; FoL 10.2; HaL 10.7; HL 6.8; HW 6.1; BW 6.5; UEW 1.6; IOW 3.0; IND 2.9; TD 1.4; ED 1.6; DET 1.8; L1F 3.2; L2F 2.9; W3D 0.6; W3F 0.3. For paratypes from Tarapoto and Chazuta regions see Table 1.

**Description of type series.** A small species of *Ameerega*, adults 17.4–24.5 mm, males slightly larger than females: 15 adult males 17.4–22.9 mm (mean 20.5 mm), six adult females 18.0–24.5 mm (mean 22.1 mm). Sexual dimorphism is exhibited only by males being slightly smaller and possessing vocal slits and a subgular vocal sac. Maxillary teeth absent; tongue gray, ovoid, attaching anteriorly on front one-quarter; choanae circular. Skin granular, especially on the dorsum and the dorsal surfaces of hindlimbs. Dorsal surfaces of forelimbs slightly granular, flanks and venter non-granular. In life, dorsal coloration of the head, back, and limbs ranges from black (as in holotype and topotypes) to copper-brown, thin white dorsolateral stripe usually present including holotype (one population lacks dorsolateral stripes, see below). Flanks black, some individuals have light blue spotting (spots absent in holotype). Venter smooth, dark to light blue with black marbling, yellow (as in holotype) or orange spots present under axillae and on medial face of tibia. Limbs light to dark brown on dorsal surfaces, ventral surfaces of forelimbs are light blue distally, yellow proximally. Underside of head pigmented as the venter but often darker (i.e. more black marbling), more evident in males. Iris dark brown with golden ring around pupil. All light and flash colors fade to white or gray in preservative.

**TABLE 1.** Measurements (in mm) of *Ameerega altamazonica* from type locality and Chazuta. Averages (with standard deviation) were calculated from the type series plus 6 additional undeposited specimens from Tocache (MUSM 24939–24944).

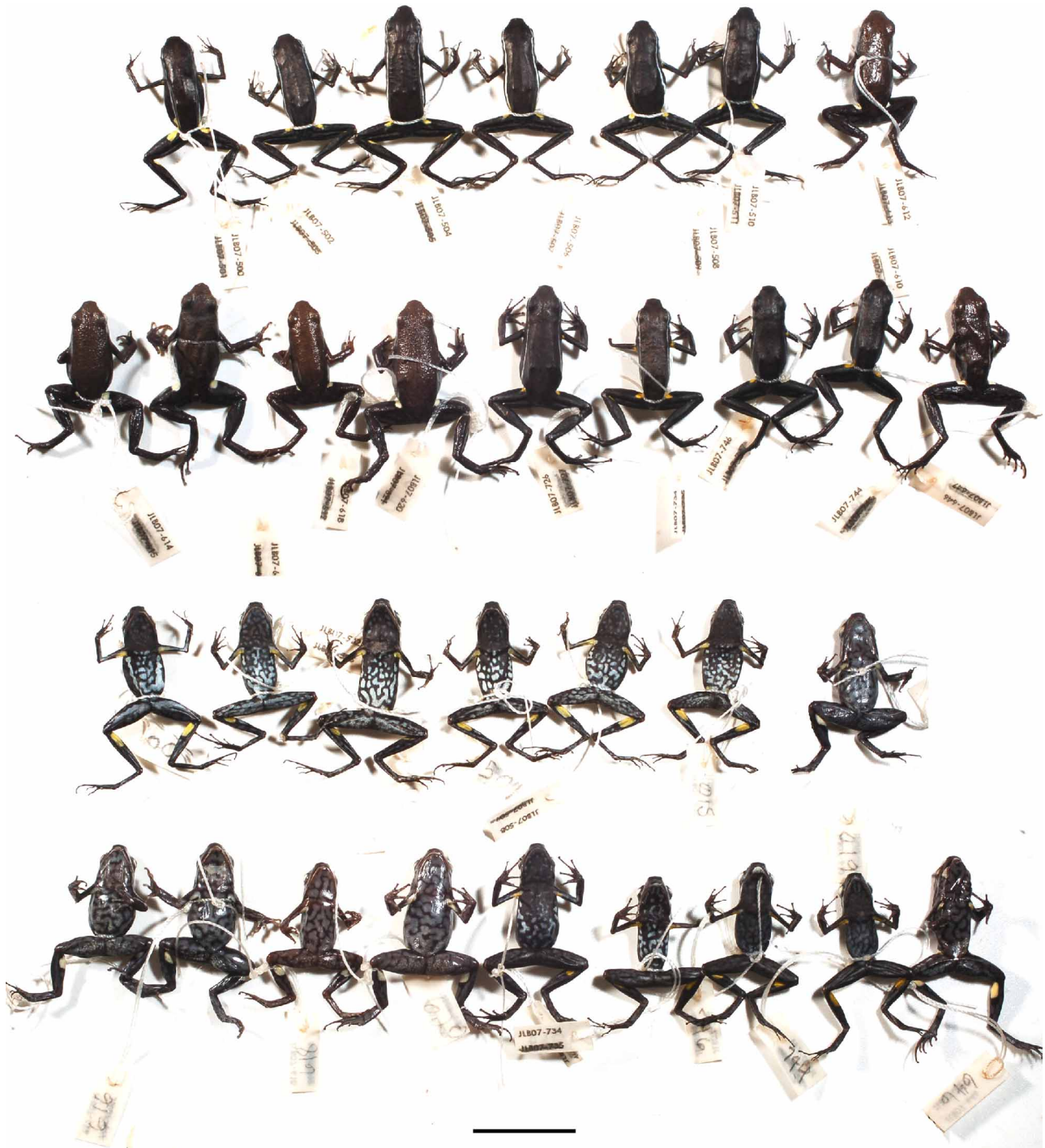
Character	MUSM 26934	MUSM 26935	MUSM 26936	MUSM 26937	MUSM 26938	MUSM 26939	Average (N = 23)
SVL	20.3	20.9	24.5	21.4	20.2	21.0	20.5 ± 2.3
FL	10.5	9.9	11.1	10.4	9.5	9.9	9.2 ± 1.1
TL	11.4	10.9	11.7	10.9	10.6	10.2	10.0 ± 1.0
KK	20.5	20.0	21.6	20.0	19.8	9.3	18.2 ± 2.8
FoL	9.1	10.0	20.8	10.2	9.8	9.2	9.4 ± 2.8
HaL	6.1	5.9	6.5	5.7	5.9	5.5	5.4 ± 0.7
HL	6.2	7.1	7.9	6.8	7.8	6.4	6.5 ± 0.8
HW	5.9	6.3	6.9	6.1	6.3	6.2	6.0 ± 0.6
BW	6.6	6.4	6.9	6.5	7.3	7.0	6.2 ± 0.9
UEW	1.6	1.6	2.1	1.6	1.7	1.7	2.8 ± 0.5
IOW	3.2	3.3	3.2	3.0	2.7	2.9	2.6 ± 0.4
IND	2.9	2.9	3.2	2.9	3.0	2.9	2.8 ± 0.2
TD	1.3	1.3	1.4	1.4	1.4	1.1	1.0 ± 0.2
ED	1.9	1.6	1.7	1.6	1.4	1.6	2.4 ± 0.4
DET	0.6	1.1	1.2	0.8	0.9	1.0	0.7 ± 0.2
L1F	3.5	3.5	3.6	3.2	3.5	3.5	3.3 ± 0.3
L2F	4.0	3.2	3.2	2.9	3.2	3.2	3.1 ± 0.3
W3D	0.6	0.5	0.6	0.6	0.5	0.5	0.5 ± 0.1
W3F	0.3	0.3	0.3	0.3	0.3	0.3	0.3 ± 0.1
SEX	M	M	F	M	M	M	

Head widest at jaw articulations, slightly narrower than body in most individuals (head width at tympanum 95% of body width at axillae); head width 26–31% of SVL. Snout sloping laterally; bluntly rounded dorsally; truncate ventrally. Nares situated and directed posterolaterally to the tip of snout; nares visible from front and below, not so from above. Canthus rostralis sloped, slightly rounded; loreal region slightly concave (nearly vertical). Interorbital distance nearly same width of superior upper eyelid. Eye large and prominent,



with a maximum diameter of 9.9% of the snout vent length; pupil rounded and horizontally elliptical. Tympanum circular, partially concealed posterodorsally, lacking tympanic annulus; tympanum width 41.5% of eye diameter. Supratympanic fold absent.

Hands relatively small, length 26% of SVL. Relative length of appressed fingers: III > IV ≈ II > I. Discs moderately expanded, disc on finger III 1.6 times width of finger below disc. A large, circular outer metacarpal tubercle is present on the median base of the palm; a smaller inner metacarpal tubercle present on base of finger I; one well developed and prominent subarticular tubercle on fingers I and II, two on fingers III and IV.



**FIGURE 1.** *Ameerega altamazonica*, dorsal and ventral views of same specimens. Top row, left to right: MUSM 26934, 26935 (Chazuta); MUSM 26936–26939 (near Tarapoto); ECU-F 107 (Tocache, non-paratype); second row, left to right: ECU-F 108-111 (Tocache, non-paratypes); MUSM 26974 (Saposoa); MUSM 26977 (Huicungo); MUSM 26981, 26982 (Campanilla); 646 (Tocache); ventral photos are in the same order. Bar in bottom center represents 10 mm.

Hind limbs relatively small, femur 44% of SVL, tibia 48% of SVL. Relative lengths of appressed toes IV > III > V > II > I; first toe short, barely reaching bottom of subarticular tubercle on base of second toe, with unexpanded disc; toes II and III with barely expanded discs (much smaller than finger discs), and toe IV and V with discs expanded (disc 1.5 times broader than adjacent phalanx). Inner and a smaller outer metatarsal tubercle present, somewhat protuberant with rounded surfaces. One slightly protuberant subarticular tubercle present on toes I and II, two on toes III, IV, and V. Hands and feet lacking supernumerary tubercles, lateral fringes, and webbing. No basal webbing or toe fringes.

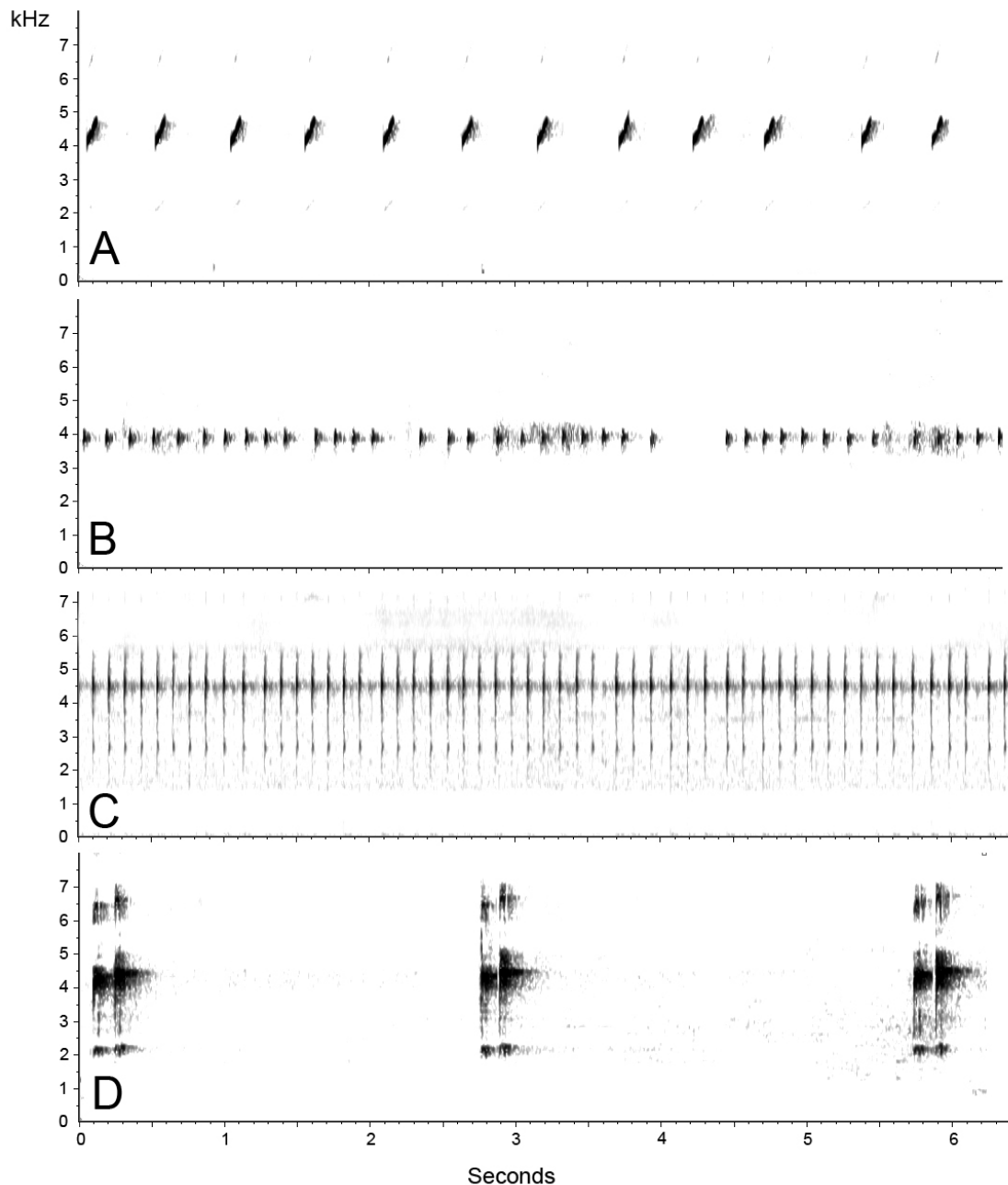
**Remarks on geographic variation.** Individuals from near Chazuta closely resemble the individuals from the type locality in both colors and pattern. The Pampa Hermosa population from the west bank of the Ucayali has larger groin spots that are bicolored (orange and yellow). There seems to be a north-south transition in the Huallaga valley from northern frogs having a black dorsum with well-defined dorsolateral stripes to southern populations having a copper-brown dorsum with reduced (and in some cases absent) dorsolateral stripes. The population from near Tocache best demonstrates this shift; this population is described as follows: dorsal skin more granular (compared to conspecific populations to the north), color metallic copper- or rust-brown, dorsolateral stripes absent, pale blue-white labial stripes extending from the corner of the mouth to axillae. Some individuals possess faint tan stripes outlining the snout, though these stripes do not extend posterior past the eyes. In some individuals a faint dorsolateral ridge can be noted separating the dorsum from the flanks. Venter and flank coloration is identical: sky-blue with black reticulation. Bright-orange spots present ventrally under axillae, dorsally over groin, and on medial surface of shanks (Fig. 2, middle right and bottom right)



**FIGURE 2.** Interpopulation variation in *Ameerega altamazonica*. Individuals in the top row are from near Tarapoto (holotype), Chazuta, and Saposoa (left to right); individuals in the middle row are from Río Abiseo, Campanilla, and Tocache (left to right). In the Huallaga valley there is a cline from a black dorsum with well-defined dorsolateral stripes in the northern populations (e.g. Tarapoto) to a brown dorsum with dorsolateral stripes faint or absent in southern populations (e.g. Tocache). Bottom row showing ventral pattern in adults from Tarapoto, Río Abiseo, and Tocache (left to right).



**Vocalizations.** The advertisement call for *A. altamazonica* (Fig. 3) is a ‘retarded trill’ (following the definitions by Lötters *et al.* 2003). Notes are repeated at a rate of 1.3–2 notes per second, duration of individual notes ranges from 60–80 ms. Dominant frequency is modulated; notes start at 4100–4300 Hz and end at 4600–4680 Hz. This single-note advertisement call is given most frequently in the evening as males chorus. We also noted a second call type in *A. altamazonica* consisting of two notes in quick succession (within 10 ms of each other), repeated once every 3–5 seconds. Unlike in the advertisement call, these notes are not frequency-modulated, though the first note is typically lower in frequency than the second by 100–150 Hz. This two-note call appears to function as an aggressive or territorial call and is most frequently heard in the early morning.



**FIGURE 3.** (A) Advertisement call of *Ameerega altamazonica*, recorded at type locality 9 June 2007 at 23° C. (B) Advertisement call of *A. hahneli sensu stricto*, recording of captive male from 56 km S Iquitos, Peru, at 24° C. (C) Advertisement call of *A. hahneli sensu stricto*, individual from Bolivia (recording made available by S. Lötters). (D) Aggressive call of *A. altamazonica*, recorded at type locality 9 June 2007 at 23° C.



Schlüter (1980) published spectrographs of *A. altamazonica* advertisement calls (as *Phyllobates pictus*) from the Panguana region of central Peru, which had notes repeated at a rate of twice per second and were frequency modulated. Morales (1992) published a spectrograph of a call from a frog he referred to as *Dendrobates* sp. 2, which was from Tingo Maria, and has many similarities with the *A. altamazonica* advertisement call (i.e. 2–3 notes per second, note duration 42 ms). Since he made no mention of ventral coloration of this species, we assume the venter was ‘unremarkable’ (i.e. blue), and since the call did not have notes of alternating frequency (as in *A. rubriventris*), we suppose that Morales’ *Dendrobates* sp. 2 can be referred to *A. altamazonica*. Lötters *et al.* (1997) presented advertisement call data for *A. hahneli* sensu lato from Tarapoto (= *A. altamazonica*), noting the similarity to those of *A. rubriventris*, although the latter species has a call with notes of alternating frequency.

The advertisement call of *A. altamazonica* is easily distinguished from that of *A. hahneli* sensu stricto, which consists of a train of notes repeated at a rate of 5–9 notes per second, each note with a duration of 11–18 ms (Schlüter 1980, Morales 1992, Haddad and Martins 1994, De La Riva *et al.* 1996, Köhler and Lötters 1999). Dominant frequency ranges from 2700–7000 Hz and is not frequency-modulated. *Ameerega yungicola*, has an advertisement call resembling that of *A. hahneli* but differs in that it has a lower dominant frequency (3590–3719 Hz), slower repetition rate (4.5–5 notes/second), and longer note duration (31–34 ms) (Lötters *et al.* 2005). The call of *A. altamazonica* is similar to the call of *A. rubriventris*, except the latter species has notes of alternating frequency whereas the former does not.

**Tadpole (measurements in mm).** A stage 30 tadpole (ECU-F 102) was chosen for the description (Fig. 4). It was free-living but species identity was confirmed by sequencing the 16S and cytochrome b gene regions. Total length 19.6, body length 7.2, maximum width 3.3, depth 2.8. Snout rounded when viewed from above; body ovoid and elongate in dorsal view. Eyes black, dorsal but angled laterally, pupils white in preservative. Nares not forming tube, situated half-way between eye and tip of snout, directed dorsally. Spiracle sinistral; vent dextral. Ventral tail fin begins at tail base, dorsal tail fin begins just posterior to plane of vent opening, deepest depth 1.4 measured 1/3 towards distal end. Caudal musculature deepest at tail base, musculature depth 0.77.



**FIGURE 4.** Lateral view (right) and oral disc (left) of tadpole of *Ameerega altamazonica* from Chazuta, San Martín, Peru. Bar under tadpole represents 10 mm and under oral disc 1 mm.

The mouth is directed anteroventrally. Oral disc emarginate, anterior and posterior labia forming flaps free from body wall. Marginal papillae absent on anterior labium, present in one complete row on posterior labium. Papillae white, rounded; submarginal papillae absent. Jaw sheaths medium in longitudinal width, finely serrate. Anterior jaw sheath has a medial indentation with reduced serration, posterior jaw sheath V-shaped and has serration throughout. Lateral processes long, extending well past lower jaw. Labial tooth row formula is 2(2)/3. A-1 complete, A-2 with medial gap, same width as A-1. P-1, P-2, and P-3 complete; P-1 and P-2 equal width, P-3 shorter. In preservative, the head appears dark gray due to subdermal pigmentation. Dermal pigmentation on dorsum is uniform translucent white with small black melanophores. Ventral coloration is translucent gray; under a dissecting microscope the ventral skin appears white with large black melanophores concentrated around anterior half of body and over intestinal coils. Tail musculature white, fins white, melanophores are present in small, irregular clusters along length of tail. Life color was dark gray or black with two distinct white spots lateral to the mouth. While these spots are also present in other species (such as

the sympatric *A. bassleri*), in *A. altamazonica* the spots extend back almost to the eye; in other species the spots extend back only to the level of the nares. Two additional stage 30 *A. altamazonica* tadpoles (ECU-F 103, 104) were examined and agree with this description.

Our examinations of *A. hahneli* tadpoles note the following differences from *A. altamazonica*: (1) dorsal and ventral skin (in preservative) uniform black with white marbling on rump and snout (versus translucent skin with black melanophores in *A. altamazonica*), (2) lateral edges of anterior labium not forming free-flap (versus flap distinctly free from body wall in *A. altamazonica*), (3) marginal papillae on posterior labium conspicuously large and somewhat pointed (versus reduced and rounded posterior marginal papillae in *A. altamazonica*), (4) keratin on all three posterior labial tooth rows reduced or absent (versus present in *A. altamazonica*), and (5) tail heavily mottled (versus white with irregular melanophore clusters in *A. altamazonica*). Our examination of two *A. hahneli* tadpoles from Iquitos (ECU-F 105, 106) agrees well with the description by Haddad and Martins (1994) of an individual from Presidente Figueiredo, Brazil. The tadpole of *A. altamazonica* appears to be similar to that of *A. rubriventris* based on the sketches and description by Lötters *et al.* (1997). Mouthpart formulas are identical in the two species, but the tadpole shape is slightly different in that *A. rubriventris* larvae are more elongate and have a slightly upturned tail near the tip.

**Distribution and natural history.** *Ameerega altamazonica* is distributed throughout the east-Andean versant and surrounding lowlands of central Peru at elevations of 150–865 m. This species is distributed widely throughout Departamento San Martín, and known from scattered localities in the east-Andean versant of Departamentos Huánuco and Loreto (Fig. 5). Jackknife tests of BIOCLIM variable contributions in Maxent indicate precipitation seasonality (coefficient of variation of precipitation) contained the most information (i.e. resulted in the highest gain increase when used alone) used to generate the niche model of *A. altamazonica*. In *A. hahneli*, jackknife tests of BIOCLIM variables show that temperature seasonality contained the most information used in generating the niche model.

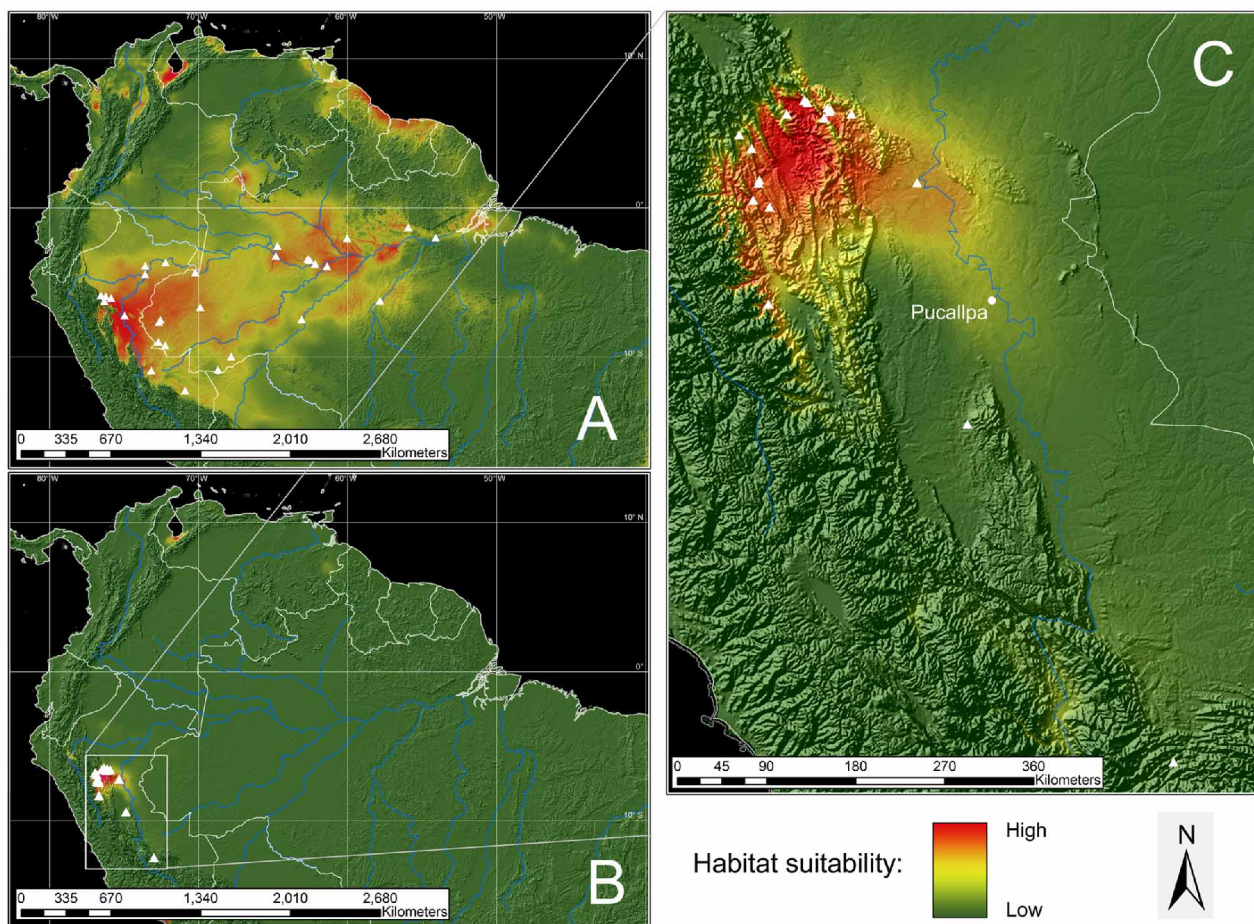
*Ameerega altamazonica* is currently not known from the east-Andean versant of Pasco and Junín, though this is probably attributable to sampling deficit and not their distributional limit, as dendrobatid sampling has been poor in central Junín and Pasco. Toothless specimens referred to as *Phyllobates pictus* by Silverstone (1976) from Chanchamayo (Departamento Junín) and Luisiana (Departamento Cusco), Peru, likely represent *A. altamazonica*, being from the highlands of the east-Andean versant. A single individual included in our phylogeny from Ivochote, Cusco (labeled *A. sp. aff. 'hahneli'*), likely represents a new species, being both genetically and geographically distant from the clade containing *A. rubriventris* and *A. altamazonica*. *Ameerega altamazonica* appears to be a species associated with mountains, and although it does occur in lowland habitats, these localities are relatively close to the east-Andean versant (< 35 km). This is in contrast to *A. hahneli* sensu stricto, which occupies a more Amazonian distribution, occurring throughout Amazonian Peru, Bolivia, Colombia, and east into Brazil and French Guiana (Haddad and Martins 1994, Lescure 2000, Lötters *et al.* 2005, 2007, Grant *et al.* 2006). We are unaware of any populations of *A. hahneli* sensu stricto that occur in montane habitats.

*Ameerega altamazonica* is most common in disturbed habitats, especially near small creeks or along roads. This species is less common in secondary forest and rare in primary forest. The activity patterns appear to be distinctly crepuscular, being most easily found in the early morning (6–8 h) or evening (16–18 h), when males are calling vigorously. Males typically call from the leaf litter, but some individuals were also found calling from clearly exposed positions in leaves approximately 0.5 m above ground level. Clutches of eggs have not been found in the field, but in captivity this species deposits eggs in leaf litter or on plant leaves near the ground. Clutches typically contain 14–22 eggs but can contain up to 26 (Mark Pepper pers. comm.). One uncollected male was observed transporting twelve tadpoles on 11 March 2006 in the type locality. Nearby water sources were limited to a small creek which for most of the year is not flowing and consists of a series of small lentic pools. We have found free-living *A. altamazonica* tadpoles in roadside ditches along the Tarapoto-Chazuta road, co-occurring with tadpoles of *A. bassleri*, *A. trivittata*, and *Phyllomedusa tomopterna*.

*Ameerega altamazonica* may serve as a (Batesian?) mimetic model for two species of *Allobates* with which it occurs sympatrically. Though we have no toxin information data on *A. altamazonica*, we suspect that it is 'mildly toxic' like other species of semi-aposematic *Ameerega* (see Summers and Clough 2001). In some areas of northern San Martín, *A. altamazonica* is sympatric with *Allobates femoralis* sensu lato, a complex of weakly- or non-toxic species which (here) share a similar pattern of a black dorsum and white dorsolateral stripes. In the central Huallaga valley, *A. altamazonica* is sympatric with an undescribed species in the *Allobates femoralis* complex (identifiable by a distinct advertisement call), which has a copper-brown dorsum and



closely resembles the local *A. altamazonica*. *Ameerega altamazonica* may at the same time be a Müllerian mimic with the sympatric *A. hahneli* sensu stricto. Also, the possibility exists that a black dorsum with white dorsolateral stripes is an ancestral state in *Ameerega* and does not have any mimetic function in these two species.



**FIGURE 5.** Niche prediction models of *Ameerega altamazonica* and *A. hahneli* generated with Maxent. Warmer colors shows more suitable habitat than colder ones. White triangles represent presence points used in generating niche models. (A) Predicted niche of *A. hahneli*, (B) Predicted niche of *A. altamazonica* with magnified inset of central Peru (C). Test AUC values for *A. altamazonica* and *A. hahneli* were 0.999 and 0.891, respectively, suggesting high accuracy of models.

**Conservation status.** Following the IUCN Red List criteria (IUCN 2001), we suggest *A. altamazonica* be listed as Least Concern (LC) under the following criteria: (1) we estimate its area of occupancy at 48,300 km<sup>2</sup>, and part of this range lies within two National Parks (Río Abiseo and Cordillera Azul), (2) it occurs extensively throughout suitable habitat and thrives even in disturbed areas, (3) population sizes are assumed to be large since it is common in several habitat types, (4) populations do not appear to be declining, and (5) demand for the pet trade is presumed to be low.

## Discussion

Early authors using only museum specimens failed to recognize *A. altamazonica* as a distinct species, a fact which is not surprising given that *A. altamazonica* is nearly indistinguishable from *A. hahneli* based on morphology alone. Though Silverstone (1976) was perhaps too ‘conservative’ in his arrangement of *A. picta* by lumping several distinct species (*A. altamazonica*, *A. braccata*, *A. flavopicta*, *A. hahneli*, *A. picta*, *A. picta guayanensis*), he did recognize several distinct patterns which in certain cases are reflective of current species boundaries. However, his ‘Pattern 4’ appears to have included individuals from both the nominal *hahneli* clade (e.g. individuals from Iquitos) and the *altamazonica* clade (e.g. individuals from Tocache). Specimens

Silverstone (1976) assigned to 'Pattern 5', which occur near Satipo and Río Pachitea in central Peru possess teeth, dorsal spots, and a calf spot which extends onto the thigh. As Silverstone (1976) pointed out, presence of teeth is variable within some populations, so this character alone may not be informative. We have seen photos of frogs from the Panguana region<sup>1</sup> (exact localities unknown) with faint olive-brown dorsal spots. We suspect Silverstone's (1976) 'Pattern 5' was referring these, but without detailed call data corresponding to these photos we cannot determine whether these represent populations of *A. altamazonica*, *A. hahneli*, or an undescribed species.

There appears to be two cryptic species occurring in sympatry in the Pachitea drainage, something which has been suspected for several years. Schlüter (1980) and Morales (1992) presented call data for several species of poison frogs from the Panguana region of central Peru, which led Haddad and Martins (1994) and De la Riva *et al.* (1996) to suspect the existence of two cryptic species in this region resembling *A. picta*. During an expedition to the Panguana in 2007 we were able to confirm this, as we recorded what seemed to be two distinct species, some with 'peep' calls and others with 'trill' calls. One of these species can be allocated to *A. altamazonica* due to similarities in the spectrographs of their advertisement calls. The species with the 'trill' call can now be assigned to *A. hahneli* due to the phylogenetic position of an individual from the Cordillera El Sira in the nominal *hahneli* clade and call similarity. These two species are therefore sympatric in the Pachitea drainage in central Peru.

Our phylogeny supports the taxonomic status of *A. rubriventris*, which forms a monophyletic clade, characterized by 15 unique unambiguous site substitutions, sister to *A. altamazonica* (Fig. 6). Grant *et al.* (2006) included in their study an *Ameerega* sample from Porto Walter, Brazil ('PortoWalter1'), which, following their topology, would represent a third, yet undescribed species in the *A. altamazonica-rubriventris* clade. Our topology, which includes *A. altamazonica* and additional *A. rubriventris* and *A. macero*, places 'PortoWalter1' sister to *A. macero*, a species whose range is considerably larger than previously thought. In our phylogeny we included a single *A. macero* from near La Merced (Departamento Junín, Peru), a locality 311 km northwest from next nearest sample (Ivochote, Cusco, Peru). This sample was found at an elevation of 1767 m, which is the highest known locality for this species by nearly 1000 meters. Additional populations of *A. macero* have been observed on the eastern slopes of the Cordillera El Sira in central Peru (M. Pepper pers. comm.), and to our knowledge this is the northernmost extent of this species' distribution. This suggests that *A. macero* is distributed throughout the drainages of the Ene, Perené, Tambo, and Chanchamayo rivers in eastern Junín. Both the Sira and La Merced populations resemble typical lowland populations of *A. macero* in pattern and color. Without further data, we cannot address whether 'PortoWalter1' represents a distinct species or another outlying population of *A. macero*.

Lötters *et al.* (2005) described *A. yungicola* from Bolivia which resembles both *A. hahneli* and *A. altamazonica* in appearance but differs in advertisement call, presence of teeth, and nucleotide sequences. Despite its similar morphology, *A. yungicola* is not a close relative of either *A. altamazonica* or *A. hahneli* but rather *A. picta*, and is sister to a Guyana population of the latter species (Fig. 6).

The clade here referred to as *A. hahneli* sensu stricto is widely distributed throughout Brazil, northern Bolivia, French Guiana, Amazonian Peru, Colombia, and Ecuador (Haddad and Martins 1994, Lescure 2000, Lötters *et al.* 2005), and still may represent a complex of cryptic species. For the purposes of this paper we consider this genetically diverse clade as one species, since they form a monophyletic clade and are united by a similar advertisement call. Currently, there are not enough data available to address whether this clade represents one or several species, and therefore we do not attempt to formally redefine *A. hahneli* sensu stricto in this paper. However, Grant *et al.* (2006) presented a phylogeny including several *A. hahneli* belonging to this clade and found large phylogenetic break between individuals from Leticia, Colombia and other localities, suggesting the possibility of a species complex. Our phylogeny suggests the possible existence of two cryptic sister species, one of which is distributed throughout the Ucayali drainage north to Iquitos and into Ecuador, and another which is distributed throughout extreme southeastern Peru and adjacent Bolivia, across the Brazilian Amazon basin into French Guiana. Increased taxon sampling, sampled throughout a clade's entire range, and detailed analyses of inter- and intrapopulation variation of calls, morphology, and molecular genetics will be necessary to determine the extent of specific diversity in these diverse and cryptic groups.

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1. Panguana is a site located at the confluence of Río Llullapichis and Río Pachitea. The terms 'Pachitea drainage' and 'Panguana region' are often used interchangeably.





FIGURE 6. Phylogenetic tree showing the Maximum Likelihood topology of genus *Ameerega* using mtDNA (12s rRNA, 16s rRNA and cytochrome b).

**TABLE 2.** List of localities and GenBank accession numbers for individuals included in the phylogeny.

Species	Locality	12S	16S	CytB	Reference
<i>altamazonica</i> 1	Saposa, San Martin, PE	DQ523015	DQ523086	DQ523156	Roberts <i>et al.</i> 2006
<i>altamazonica</i> 2	Chazuta, San Martin, PE	DQ522980	DQ523051	DQ523121	Roberts <i>et al.</i> 2006
<i>altamazonica</i> 3	Tarapoto, San Martin, PE	DQ522951	DQ523022	DQ523092	Roberts <i>et al.</i> 2006
<i>altamazonica</i> 4	Tarapoto, San Martin, PE	DQ522978	DQ523049	DQ523119	Roberts <i>et al.</i> 2006
<i>altamazonica</i> 5	Tarapoto, San Martin, PE	DQ522955	DQ523026	DQ523096	Roberts <i>et al.</i> 2006
<i>altamazonica</i> 6	San Jose de Sisa, San Martin, PE	DQ523008	DQ523079	DQ523149	Roberts <i>et al.</i> 2006
<i>altamazonica</i> 7	Tarapoto, San Martin, PE	DQ523007	DQ523078	DQ523148	Roberts <i>et al.</i> 2006
<i>altamazonica</i> 8	Chazuta, San Martin, PE	DQ522966	DQ523037	DQ523107	Roberts <i>et al.</i> 2006
<i>altamazonica</i> 9	Tocache, San Martin, PE	EU517662	EU517665	EU517671	this study
<i>altamazonica</i> 10	Tocache, San Martin, PE	EU517661	EU517663	N/A	this study
<i>altamazonica</i> 11	Pampa Hermosa, Loreto, PE	EU517660	EU517664	EU517672	this study
<i>altamazonica</i> 12	Pampa Hermosa, Loreto, PE	EU517659	EU517666	EU517677	this study
<i>bassleri</i>	near Chazuta, San Martin, PE	DQ522986	DQ523057	DQ523127	Roberts <i>et al.</i> 2006
<i>bilinguis</i> 1	Primavera, Napo, EC	DQ523003	DQ523074	DQ523144	Roberts <i>et al.</i> 2006
<i>bilinguis</i> 2	Cuyabeno, Sucumbios, EC	DQ502095	DQ502095	DQ502527	Grant <i>et al.</i> 2006
<i>bilinguis</i> 3	Cuyabeno, Sucumbios, EC	DQ502073	DQ502073	DQ502504	Grant <i>et al.</i> 2006
<i>bracatta</i>	Manso, Matto Grosso, BR	DQ502125	DQ502125	DQ502556	Grant <i>et al.</i> 2006
<i>cainarachi</i> 1	Cainarachi valley, San Martin, PE	DQ522953	DQ523024	DQ523094	Roberts <i>et al.</i> 2006
<i>cainarachi</i> 2	Cainarachi valley, San Martin, PE	DQ522982	DQ523053	DQ523123	Roberts <i>et al.</i> 2006
<i>flavopicta</i>	Rio Tocantins, Parana, BR	DQ502124	DQ502124	DQ502555	Grant <i>et al.</i> 2006
<i>hahneli</i> 1	Puerto Inca, Huanuco, PE	N/A	EU517669	EU517676	this study
<i>hahneli</i> 2	Panguana, Huanuco, PE	N/A	AF282248	N/A	Lotter & Vences 2000
<i>hahneli</i> 3	Puente Itaya, Loreto, PE	DQ522990	DQ523061	DQ523131	Roberts <i>et al.</i> 2006
<i>hahneli</i> 4	Leticia, Amazonas, CO	DQ502270	DQ502270	DQ502701	Grant <i>et al.</i> 2006
<i>hahneli</i> 5	Convento, San Martin, PE	DQ522961	DQ523032	DQ523102	Roberts <i>et al.</i> 2006
<i>hahneli</i> 6	Puente Itaya, Loreto, PE	DQ522962	DQ523033	DQ523103	Roberts <i>et al.</i> 2006
<i>hahneli</i> 7	Yasuni, Orellana, EC	AY364573	AY364573	N/A	Santos <i>et al.</i> 2003
<i>hahneli</i> 8	Rio Manati, Loreto, PE	DQ523004	DQ523075	DQ523145	Roberts <i>et al.</i> 2006
<i>hahneli</i> 9	Alto Purus, Ucayali, PE	DQ522970	DQ523041	DQ523111	Roberts <i>et al.</i> 2006
<i>hahneli</i> 10	Boca Manu, Cusco, PE	DQ522956	DQ523027	DQ523097	Roberts <i>et al.</i> 2006
<i>hahneli</i> 11	Rio los Amigos, Madre de Dios, PE	DQ522985	DQ523056	DQ523126	Roberts <i>et al.</i> 2006
<i>hahneli</i> 12	Alto Purus, Ucayali, PE	DQ522963	DQ523034	DQ523104	Roberts <i>et al.</i> 2006
<i>hahneli</i> 13	Cobija, Pando, BO	N/A	AF282246	N/A	Lotter & Vences 2000
<i>hahneli</i> 14	Alto Purus, Ucayali, PE	DQ523010	DQ523081	DQ523151	Roberts <i>et al.</i> 2006
<i>hahneli</i> 15	Madre de Dios, PE	DQ501997	DQ501997	DQ502422	Grant <i>et al.</i> 2006
<i>hahneli</i> 16	Madre de Dios, PE	DQ501996	DQ501996	DQ502421	Grant <i>et al.</i> 2006
<i>hahneli</i> 17	Amazonas, BR	DQ522992	DQ523063	DQ523133	Roberts <i>et al.</i> 2006

<i>hahneli</i> 18	Amazonas, BR	DQ522996	DQ523067	DQ523137	Roberts <i>et al.</i> 2006
<i>hahneli</i> 19	near Manaus, Amazonas, BR	DQ502226	DQ502226	DQ502659	Grant <i>et al.</i> 2006
<i>hahneli</i> 20	near Manaus, Amazonas, BR	DQ502226	DQ502226	DQ502659	Grant <i>et al.</i> 2006
<i>hahneli</i> 21	Reserve Trinite, Saint-Élie, FG	N/A	AY263247	N/A	Vences <i>et al.</i> 2003
<i>hahneli</i> 22	Porto Walter, Acre, BR	DQ502084	DQ502084	DQ502515	Grant <i>et al.</i> 2006
<i>hahneli</i> 23	Porto Walter, Acre, BR	DQ502085	DQ502085	DQ502516	Grant <i>et al.</i> 2006
<i>hahneli</i> 24	Porto Walter, Acre, BR	DQ522993	DQ523064	DQ523134	Roberts <i>et al.</i> 2006
<i>macero</i> 1	near La Merced, Junin, PE	N/A	EU525852	EU525853	this study
<i>macero</i> 2	Manu, Madre de Dios, PE	DQ502155	DQ502155	DQ502591	Grant <i>et al.</i> 2006
<i>macero</i> 3	Ivohote, Cusco, PE	DQ522968	DQ523039	DQ523109	Roberts <i>et al.</i> 2006
<i>macero</i> 4	Alto Purus, Ucayali, PE	DQ523018	DQ523089	N/A	Roberts <i>et al.</i> 2006
<i>parvula</i>	Macas, EC	N/A	AY364574	N/A	Santos <i>et al.</i> 2003
<i>picta</i> 1	Kartabo Pt., Mazaruni-Potaro, GY	DQ502252	DQ502252	DQ502684	Grant <i>et al.</i> 2006
<i>picta</i> 2	Mataracu, BO	N/A	AF124126	N/A	Vences <i>et al.</i> 2000
<i>pongoensis</i>	Convento, San Martin, PE	DQ522973	DQ523044	DQ523114	Roberts <i>et al.</i> 2006
'PortoWalter1' 1	Porto Walter, Acre, BR	DQ502230	DQ502230	DQ502619	Grant <i>et al.</i> 2006
'PortoWalter1' 2	Porto Walter, Acre, BR	DQ502229	DQ502229	DQ502655	Grant <i>et al.</i> 2006
<i>pulchripectus</i>	Serra do Navio, Amapa, BR	DQ502033	DQ502033	DQ502464	Grant <i>et al.</i> 2006
<i>rubriventris</i> 1	near Aguaytia, Ucayali, PE	N/A	EU517667	EU517673	this study
<i>rubriventris</i> 2	near Aguaytia, Ucayali, PE	N/A	EU517668	EU517674	this study
<i>rubriventris</i> 3	near Aguaytia, Ucayali, PE	N/A	AF282247	N/A	Lotters & Vences 2000
<i>smaragdina</i>	Pan de Azucar, Pasco, PE	EU517658	EU517670	EU517675	this study
<i>silverstonei</i> 1	Tingo Maria, Huanuco PE	DQ523013	DQ523084	DQ523154	Roberts <i>et al.</i> 2006
<i>silverstonei</i> 2	captive bred, no data	N/A	N/A	DQ502582	Grant <i>et al.</i> 2006
<i>simulans</i> 1	Quincemil, Cusco, PE	DQ523020	DQ523090	DQ523160	Roberts <i>et al.</i> 2006
<i>simulans</i> 2	Mazuko, Madre de Dios, PE	DQ523019	N/A	DQ523159	Roberts <i>et al.</i> 2006
sp. aff. ' <i>hahneli</i> '	Ivohote, Cusco, PE	DQ522967	DQ523038	DQ523108	Roberts <i>et al.</i> 2006
<i>trivittata</i> 1	Alto Purus, Ucayali, PE	DQ522957	DQ523028	DQ523098	Roberts <i>et al.</i> 2006
<i>trivittata</i> 2	Tarapoto, San Martin, PE	DQ522950	DQ523021	DQ523091	Roberts <i>et al.</i> 2006
<i>yungicola</i>	Carnavi, La Paz, BO	N/A	AY263239	N/A	Vences <i>et al.</i> 2003
<i>Colostethus inguinalis</i>	San Roque, Caldas, CO	DQ502265	DQ502265	DQ502696	Grant <i>et al.</i> 2006
<i>C. fugax</i>	Morona-Santiago, EC	AY364547	AY364547	N/A	Santos <i>et al.</i> 2003
<i>C. panamensis</i>	Cana, Darien, PA	DQ502172	DQ502172	DQ502608	Grant <i>et al.</i> 2006
<i>C. cf. pratti</i>	Cana, Darien, PA	DQ502173	DQ502173	N/A	Grant <i>et al.</i> 2006
<i>Epipedobates anthonyi</i>	Ecuador	DQ502151	DQ502151	DQ502584	Grant <i>et al.</i> 2006
<i>E. boulengeri</i> 1	Ecuador	N/A	N/A	DQ502447	Grant <i>et al.</i> 2006
<i>E. boulengeri</i> 2	Ecuador	AF128555	AF128554	AF128556	Summers & Clough 2001
<i>E. spinosai</i>	Santo Domingo, Pichincha, EC	DQ502158	N/A	DQ502594	Grant <i>et al.</i> 2006
<i>E. tricolor</i>	Morasungo, Bolivar, EC	AY395961	N/A	N/A	Graham <i>et al.</i> 2004
<i>E. sp. QCAZ16589</i>	Mindo, Pichincha, EC	AY364575	N/A	N/A	Santos <i>et al.</i> 2003
<i>Silverstoneia flotator</i>	El Cope, Coclé, PA	DQ502164	DQ502164	DQ502599	Grant <i>et al.</i> 2006
<i>S. nubicola</i>	El Cope, Coclé, PA	DQ502165	DQ502165	DQ502600	Grant <i>et al.</i> 2006

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