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Further complicated histories: a revision of the *Ameerega bassleri* species group (Anura: Dendrobatidae) and a new species from the Cordillera Escalera of Peru

BREANN GERALDS[1], EVAN TWOMEY[2], MICHAEL S. DEUTSCH[3], GERMÁN CHÁVEZ[4] & JASON L. BROWN[1,*]
[1.] *School of Biological Sciences, Southern Illinois University, Carbondale, IL, USA*
bregeralds@siu.edu; https://orcid.org/0009-0002-8703-2824
[2.] *Faculty of Biological Sciences, Goethe University, Frankfurt am Main, Germany*
twomey@em.uni-frankfurt.de; https://orcid.org/0000-0002-8001-4343
[3.] *University of Washington, Seattle, WA, USA*
mikiedeutsch@gmail.com; https://orcid.org/0000-0003-4933-790X
[4.] *División de Herpetología – CORBIDI, Lima, Perú*
vampflack@yahoo.com; https://orcid.org/0000-0002-9291-156X
[*]*Corresponding Author: jasonleebrown@gmail.com; https://orcid.org/0009-0007-2639-5302*

Abstract

We describe a new species of poison frog from north-central Peru that was previously considered a morph of *Ameerega bassleri*. Our phylogenetic results indicate that *A. bassleri* as currently defined is polyphyletic, with the nominal clade (*A. bassleri* sensu stricto) sister to *A. pepperi,* and a second, as yet unnamed clade, sister to *A. yoshina*. This latter clade contains the well-known yellow morph occurring in the mountains near Tarapoto, which for the last ca. 20 years was erroneously thought to represent the nominal form of *A. bassleri.* Observations of color-pattern and analyses of male advertisement call traits (note-rate and dominant frequencies) reveal consistent differences between *A. pepperi*, *A. yoshina*, and the two lineages of *A. bassleri* (treated as separate groups), supporting the hypothesis that these four clades are independent evolutionary lineages. Based on these results, we restrict *A. bassleri* to the clade containing the Chrome-green and Black morphs and describe the Yellow morph as a new species.

Key words: dendrobatid frogs, poison frogs, ultraconserved elements, UCE, *Ameerega kuriinti* sp. nov.

Introduction

Detailed investigations of Peruvian poison frogs have often revealed cases where a single, widespread 'species' actually represents multiple cryptic species (Myers 1982, Schulte 1986, Morales 1992, Myers *et al*. 1998, Schulte 1999, Brown *et al*. 2006, Twomey & Brown 2008, Brown 2019). While certain taxonomic groups have undergone substantial revisions and restrictions (e.g. *Dendrobates quinquevittatu*s sensu Silverstone 1975), others have persisted as 'taxonomic dustbins' (e.g. *Allobates femoralis,* Simoes *et al.* 2010). One taxonomic group that was recently uncovered to be a complex of species is the *Ameerega bassleri* species group (ABSG), a group of three species (*A. pepperi*, *A. yoshina*, and *A. bassleri*) of large aposematic frogs restricted to montane habitats and riverine valleys throughout the departments of San Martin and northern Loreto, Peru.

In 2009, Brown and Twomey described *A. pepperi* and *A. yoshina.* They based their taxonomic descriptions on the species' unique advertisement calls and distinct coloration (discussed below), and despite extensive paraphyly in a mtDNA phylogeny, where *A. bassleri* and *A. yoshina* were both rendered polyphyletic by multiple lineages. In 2020, Guillory *et al.* reevaluated the evolutionary relationships of the ABSG based on eleven samples (*A. bassleri* n = 3, *A. pepperi* n = 4, *A. yoshina* n = 4), which were sequenced using the Tetrapods-UCE-5Kv1 probe set (ultraconserved.org) that targets 5060 ultraconserved elements (UCE), producing hundreds of thousands of base-pairs sampled across the nuclear genome. Guillory *et al.* (2020) concluded that this group was a well-supported monophyletic group comprised of three morphologically variable species, each reciprocally monophyletic (*A. bassleri*, *A. pepperi*,

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and *A. yoshina*). In the tree topology of Guillory *et al.* (2020), all *A. bassleri* samples represented a single morph - the Yellow morph, which was sister to *A. yoshina,* together forming a clade sister to *A. pepperi* (Guillory *et al.* 2020). In contrast to the mtDNA phylogenetic results by Brown and Twomey (2009), the nuclear UCE loci fully recovered the monophyly of each species (sensu Brown and Twomey 2009).

The three species of the ABSG can be distinguished by the combination of their advertisement calls and coloration. *Ameerega yoshina* has the most distinctive call, with notes emitted at a much higher rate than other species in the group. This species has a black ground coloration with bright red, brick red, or orange stippling that fades out near the sacral region on the dorsum. It occurs in the small ridge east of Contamana, with additional populations west of Rio Ucayali in the Cordillera Azul (Brown & Twomey 2009, this study). *Ameerega pepperi,* which in a few regions (i.e. Nuevo San Martín) overlaps with *A. yoshina* in terms of coloration, and has a slower call than both *A. yoshina* and *A. bassleri.* It occurs in the upper Huallaga River valley, south of the confluence of Rio Huallaga and Rio Abiseo. This species displays clinal variation across its range and has conspicuous dorsolateral stripes with red and orange in the southern parts of its range and yellow coloration on the dorsum in the north. *Ameerega bassleri* is variable, with three known color morphs under its current definition: (1) The Chrome-green morph, which is metallic greenish-blue with black marbling or irregular large spotting patterns on the dorsum occurring north of the Rio Huallaga between Rio Mayo and Rio Huayabamba (Myers 1982; Brown & Twomey 2009), 2) the Black Morph, characterized by regular yellowish-green spotting on a black dorsum and yellow-green longitudinal dorsolateral stripes start at the groin and continue around the snout and found exclusively in the Cordilleras West of Rio Saposoa, and 3) the Yellow Morph, a brightly colored yellow or orange on the dorsum that occurs in northern regions of San Martin throughout the Cordillera Escalera (See Fig. 1).

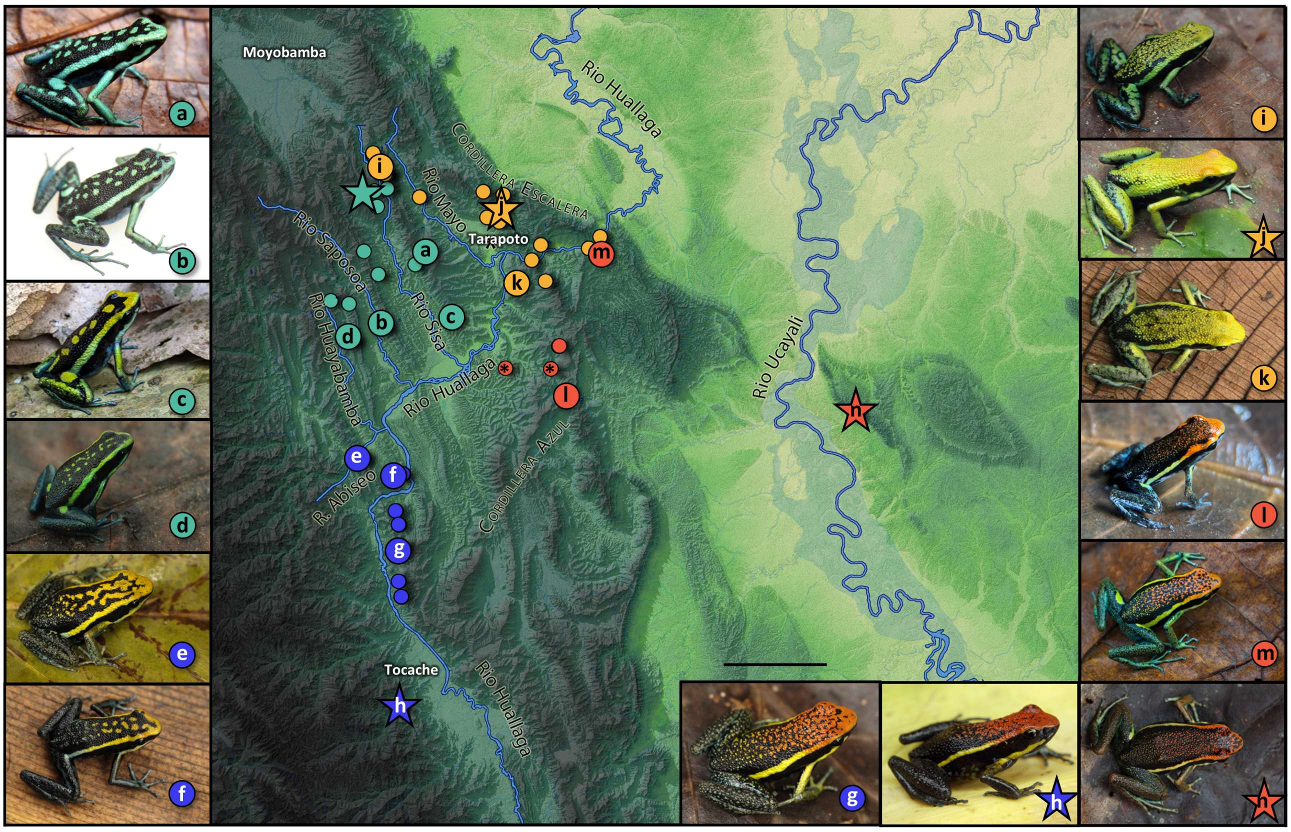

FIGURE 1. Geographic distribution of species within the *Ameerega bassleri* species group and their morphological variation. (a–d) *Ameerega bassleri sensu stricto* from (a) near San Jose de Sisa, (b) Nuevo San Andreas, (c) Ojos de Agua Pucacaca, and (d) Shima; (e–h) *A. pepperi* from (e) Río Abiseo near Huicungo, (f) Campanilla, (g) Nuevo San Martín, and (h San Francisco; (i–k) *A. kuriinti* **sp. nov.** from (i) nearby Roque, (j) Cainarachi Valley, and (k) Sauce; *A. yoshina* from (l) Shamboyacu, (m) Callanayacu, and (n) Contamana, Loreto, Peru. Asterisk depicts sites where *A. yoshina* is presumed to occur based on previous studies, however, we have not observed it during field surveys. Black bar = 40 km. Unless stated, all localities are from San Martín, Peru. Stars depict type localities for each species.

Here we reevaluated the systematics and taxonomy of the *Ameerega bassleri* species group by analyzing the most comprehensive sampling of this group and genomic-wide sequencing of the nuclear genome. We also provide an extensive reanalysis of male advertisement calls, adding several dozen additional calls (total = 88), and include call data from four new populations. Our phylogenetic results demonstrate that *A. bassleri*, as currently defined, is polyphyletic, with one clade that is sister to *A. pepperi* and a second clade that is sister to *A. yoshina*. Based on our inspection of the type material of *A. bassleri* and new samples obtained from the type locality, we conclude that the clade sister to *A. pepperi* represents the nominal clade for this species, while the clade that is sister to *A. yoshina*, represents a new and undescribed species.

Materials and Methods

Type specimens (KU 211979, KU 209399, KU209400, KU 209401, and KU 211978) of the new species are housed in the University of Kansas Biodiversity Institute (KU). 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 surface of knee (FL), tibia length from heel to lateral surface 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 tip of snout to angle of jaw (HL), head width between tympanum (HW), body width under axillae (BW), upper eyelid width (UEW), interorbital distance (IOD), 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 3 just below disc (W3F). Data used in this paper are provided for download (https://doi.org/10.5281/zenodo.17981806).

Acoustic Analyses. Calling males were recorded with a Zoom H1n Handy Recorder (stored as wav files with a sampling rate 48Khz) and a Sennheiser ME 66-K6 shotgun microphone. Dominant frequency, average note length, notes per second, and average space between notes are consistent within individuals and rarely change with environmental conditions such as temperature in *Ameerega* (French *et al.* 2019). Therefore, these variables are considered bioacoustic standards as means for species delimitation of anurans (Köhler *et al.* 2017). Initial isolation of the vocalization from background noise outside the call's frequency range was conducted in Audacity 2.1.3 (https://audacityteam.org/), using the Noise Reduction tool. The reduction filter was set to 40 dB, 6.00 sensitivity, and 3 bands for smoothing. After processing, eight consecutive notes from the center of each recording were then trimmed and exported as a .wav file. Measurements for each note exported were done in Raven Pro 1.5 (Bioacoustics Research Program 2022), measuring dominant frequency (kHz), note length (seconds), and silence between notes (seconds), and the mean note interval (seconds) which was the measurement from the beginning of one note to the beginning of the next note and represents the sum of silence between notes and note length based on the spectrogram (vs. waveform as done by Brown & Twomey 2009). For these measurements we used the following settings: window type = Hann; window size = 1024 samples; 3 dB filter bandwidth = 67.4 Hz; brightness = 50%; contrast = 50%; overlap (locked) = 85%; hop size (temporal resolution = 3.21 ms); DFT size (locked) = 1024 samples (spectral resolution = 46.9 Hz). The mean was then calculated for each variable. We calculated notes per second by dividing the mean note interval by one. Our final dataset consisted of a total of 88 call recordings collected from the extensive field surveys that occurred from 2004–2021 (Brown *et al.* 2009; unpublished data) (Table 2): 24 calls of the new species described here from 4 localities, 27 *A. bassleri* from 4 localities, 15 *A. pepperi* calls from 3 localities, and 31 *A. yoshina* calls from 2 localities). Analyses were performed in RStudio (v4.1.0; R Core Team 2024) using one-way Analysis of Variance (ANOVA). As sample sizes between species were unbalanced, Tukey's post-hoc tests were used for pairwise comparisons.

Elevational Distribution. During all field surveys conducted from 2004 to 2021, GPS points were recorded for all individuals collected. Our final dataset included 91 samples (*A. bassleri* n = 27; *A. pepperi* n = 23; *A. yoshina* n = 18; and the new species n = 23). In ArcGIS (ESRI 2022) we transformed our points to a shapefile and extracted elevation values using a 90 m STRM elevation layer (downloaded from Worldclim 2.0) (Hijmans *et al.* 2005). Analyses were performed in RStudio (v4.1.0; R Core Team 2024) using one-way ANOVAs. As sample sizes between species were unbalanced, Tukey's post-hoc tests were used for pairwise comparisons.

TABLE 1. Relationships of call structures of *A. kuriinti* **sp. nov.**, *A. bassleri*, *A. pepperi*, and *A. yoshina*. Mean ± standard deviation (min, max, pairwise significance).

Species	Note length (sec)	Dominant frequency (Hz)	Silence between notes (sec)	Mean note interval (sec)	Notes per second	*N*
A. kuriinti	0.30 ± 0.05 (0.20-0.42, a)	2660.74 ± 163.25 (2433.25-3000.00, b)	0.22 ± 0.06 (0.13-0.34, b)	0.52 ± 0.05 (0.44-0.61, c)	1.92 ± 0.19 (2.25-1.64, c)	24 indiv., 4 local.
A. bassleri	0.22 ± 0.05 (0.16-0.32, c)	2950.47 ± 159.98 (2670.12-3187.50, a)	0.59 ± 0.19 (0.21-0.95, a)	0.81 ± 0.17 (0.54-1.14, b)	1.23 ± 0.26 (1.86-0.88, b)	27 indiv., 4 local.
A. pepperi	0.28 ± 0.06 (0.21-0.44, ab)	3011.48 ± 133.35 (2806.00-3234.38, a)	0.69 ± 0.21 (0.40-1.03, a)	0.98 ± 0.20 (0.63-1.31, a)	0.98 ± 0.20 (1.59-0.76, a)	15 indiv., 3 local.
A. yoshina	0.26 ± 0.03 (0.20-0.33, b)	3046.01 ± 173.88 (2625.00-3380.73, a)	0.07 ± 0.05 (0.01-0.15, c)	0.33 ± 0.06 (0.24-0.49, d)	3.03 ± 0.57 (4.11-2.05, d)	31 indiv., 2 local.
ANOVA	$F_{3,93}$ 12.8 $p < 0.001$	$F_{3,93}$28.7 $p < 0.001$	$F_{3,93}$ 113.1 $p < 0.001$	$F_{3,93}$ 120.2 $p < 0.001$	$F_{3,93}$ 169.3 $p < 0.001$	

TABLE 2. Summary table of individuals used in acoustic analysis to include the years of observation and localities of collected acoustics.

Species	Locality	Call ID	Year Collected
A. kuriinti	Alto Shilcayo	0472; 0474; 0476; 0477a; 0477b	2021
A. kuriinti	Chazuta	0200; 0164; 0165; 0166; 0167; 0169; 0233; 0235	2007; 2008; 2011
A. kuriinti	Lejia	0099	2007
A. kuriinti	Tunnel	0209; 0210; 2011; 0213a; 0213b; 0421; 0422; 0426; 0427; 0428	2008; 2019
A. bassleri	Pucacaca	0478; 0480a; 0480b; 0481; 0483; 0484	2021
A. bassleri	Saposoa	0214; 0105; 0106; 0107; 0368; 0369; 0371; 0374; 0380; 0381; 0382; 0383; 0386; 0392	2007; 2008; 2018
A. bassleri	Puente Shucshuyacu	0458; 0449; 0460; 0465; 0467; 0468a; 0468b	2019
A. pepperi	Abiseo	0085; 0445a; 0445b; 0446; 0447a; 0447b; 0449; 0450; 0452	2007; 2019
A. pepperi	Balsayacu Campanilla	0202; 0204	2008
A. pepperi	Pizana	0203	2008
A. yoshina	Callanayacu	0100; 0101; 0102; 0344a; 0344b; 0345; 0347a; 0347b; 0347c; 0349; 0353; 0355; 0359; 0360; 0361; 0362; 0364	2007; 2018
A. yoshina	Shamboyacu	0431; 0432; 0435; 0441a; 0441b; 0444; 0470a; 0470b	2019; 2021

Molecular Analyses

Sequence acquisition

We acquired genetic samples from fieldwork, museums, and collaborators, sampling areas of the known distribution for this group. Here, 91 tissue samples were used from this collection that represent all localities where the ABSG (Table 3) was encountered and an additional 12 samples serve as the outgroups (representing *Ameerega cainarachi, Ameerega ignipedis, Ameerega parvula, Ameerega pongoensis, Ameerega silverstonei*, and *Ameerega trivittata*). For each sample, we extracted genomic DNA with the Qiagen DNeasy Blood and Tissue Kit (Valencia, CA) and quantified yield with a Qubit 3 fluorometer (ThermoFisher Scientific). We sent extracted DNA to RAPiD Genomics (Gainesville, FL, USA), who performed sequence capture and Illumina sequencing of UCEs in the manner of Faircloth *et al*. (2012). The samples were enriched with the Tetrapods-UCE-5Kv1 set of 5,472 probes, targeting 5,060 UCE loci. This study was conducted in accordance with the Institutional Animal Care and Use Committee of Southern Illinois University (Protocol number: 18-009, Animal Assurance number: D16-00044).

TABLE 3. Summary table of individuals used in phylogenetic analysis to include the location of collected individuals. Unless otherwise indicated, all individuals were collected from the San Martín region of Peru.

Species	Latitude	Longitude	Locality	Sequence ID
A. kuriinti	-6.450353	-76.289984	Cainarachi Valley	0184
A. kuriinti	-6.450353	-76.289984	Tunnel	0578; 0938; 0939, 0940; 1057; 1058; 1059
A. kuriinti	-6.617751	-76.178720	Chumia	0182; 0190; 0941; 0945; 1061
A. kuriinti	-6.30899	-76.69567	Ponazapa	0959; 0960; 0961; 1033; 1051; 1052
A. kuriinti	-6.346818	-76.727389	Roque (6km NE of town)	0183; 0189
A. kuriinti	-6.378141	-76.604444	Lamas	0511
A. kuriinti	-6.726631	-76.222691	Sauce	0187
A. yoshina	-6.588031	-75.922544	Callanayacu	0230; 0231; 0800; 0801; 0803; 0804
A. yoshina	-7.259	-74.995	Contamana, Loreto PE	0229; 0447; 0466
A. yoshina	-6.9422	-76.07806	Picota	0587
A. yoshina	-7.03653	-76.09114	Shamboyacu	0998; 0999; 1000; 1001; 1002; 1003; 1072; 1073
A. bassleri	-6.897	-76.829	Altoshima	0185
A. bassleri	-6.355817	-76.77518	Pueblo Nuevo (6km S. of Roque township)	0432; 0433
A. bassleri	-6.83874	-76.46478	Pucacaca	1004; 1005; 1006; 1007; 1009
A. bassleri	-6.865057	-76.73501	Nuevo San Andreas	0818
A. bassleri	-6.897	-76.829	Shima	0191; 0806; 0808; 0811; 0812; 0813; 0822; 0823; 0824; 0825; 1076
A. bassleri	-6.62106	-76.62466	Puente Shucshuyacu	0946; 0947; 0948; 1064
A. bassleri	-6.58299	-76.50974	Sisa	0186; 0593; 0791
A. pepperi	-7.367468	-76.811893	Abiseo	0211; 0295
A. pepperi	-7.427395	-76.664801	Campanilla	0296; 0449; 0952; 0953; 0954; 0955; 1065; 1066
A. pepperi	-7.568823	-76.692877	Chumanza	0192; 0193
A. pepperi	-7.367468	-76.811893	Huicungo	0956; 0957; 0958; 1069
A. pepperi	-7.647355	-76.665631	Nuevo Jaen	0949; 0950; 0951
A. pepperi	-8.308876	-76.675924	Nuevo San Martin	0208; 0210
A. pepperi	-8.308417	-76.677111	Tocache	0207; 0209
A. cainarachi	-6.617751	-76.178720	Chumia	0005
A. cainarachi	-6.543194	-76.110974	Curiyacu	0006
A. ignipedis	-7.259	-74.995	Contamana	0198; 0289
A. parvula	-4.412067	-77.644731	Cordillera Campanquiz, Amazonas, PE	0204; 0205
A. pongoensis	-6.571697	-75.96403	Huallaga Canyon	0214
A. pongoensis	-6.032094	-75.856995	Shucushuyacu, Loreto PE	0215
A. trivittata	-6.29592	-76.23327	Pongo de Cainarachi	0226
A. trivittata	-10.30289	-74.95894	Puerto Bermudez, Pasco PE	0225
A. silverstonei	-9.16116	-75.8035	Divisora, Huánuco PE	0031; 0032

Read quality trimming, sequence assembly, and alignment

Most of the bioinformatic processing of our UCE dataset was conducted using the PHYLUCE v1.7.1 software package (Faircloth 2016), with some modifications. In brief, raw reads were quality-trimmed using Illumiprocessor v2.0.6 (Faircloth 2013), a Python wrapper for Trimmomatic v0.36 (Bolger *et al*. 2014). Trimmed reads were then assembled with SPAdes v3.15.3 (Prjibelski *et al*. 2020). The UCE data was phased into haplotypes following the approach outlined by Anderman *et al*. (2018). Phasing involves identifying variable positions within loci and sorting them into two allele sequences at the same locus on the same chromosome. Edge-trimmed exploded alignments were used as reference contigs, and raw reads were aligned to these contigs to phase the UCE data. Phased contigs were mapped to successfully sequenced UCE loci using PHYLUCE, and only loci present in at least one sample were retained. From this step we retained 3,003 UCE loci. Per-locus alignments were then conducted with MUSCLE v3.8.31 (Edgar 2004). Matrix incompleteness was filtered by only retaining loci present in 75 percent or more of the samples. The filtering step reduced our dataset to 1,142 loci. This helped minimize inaccurate results in downstream coalescent-based analyses by excluding loci with lower representation.

Phylogenetic inference

A maximum likelihood (ML) analysis was conducted on the concatenated UCE dataset using the program IQ-TREE v1.6.5 (Nguyen *et al*. 2015). The loci were concatenated into a single alignment and the matrix was partitioned. We used the ModelFinder Plus option (-m MFP) to select the best nucleotide substitution model for the data (Kalyaanamoorthy *et al*. 2017) and support was assessed using 10,000 ultrafast bootstrap replicates (Minh *et al*. 2013). A species tree of the UCE dataset was inferred on the basis of coalescent theory using ASTRAL-III v.5.6.1 (Zhang *et al*. 2018) that summarizes per-locus gene trees that have been previously made in IQ-TREE using the appropriate substitution model with 1,000 ultrafast bootstrap replicates. To reduce gene tree and further downstream biases, short branch lengths were contracted into polytomies using the *-czb* option recommended by Persons *et al*. (2016).

Results

Phylogenetic results. Our ASTRAL and ML phylogenetic analyses show that populations previously referred to as *A. bassleri* are polyphyletic, with one clade sister to *A. yoshina* and another sister to *A. pepperi.* (Fig. 2). Our results are consistent with those of another study that analyzed phylogenomic UCE data from all *Ameerega* species (Guillory *et al*. 2020) and found the same relationships between three of the species mentioned above (note that *A. bassleri* sensu stricto in this study is absent from Guillory *et al*. (2020), and the new species was referred to as *A. bassleri* in that study). Guillory *et al*. (2020) recovered the same relationships with much broader outgroup taxon sampling, alleviating any concerns that adding taxa to our dataset would alter the topology.

Acoustic Analysis. We performed comparisons between the four lineages of the ABSG. We found that the four putative species differ in all acoustic parameters analyzed (note length: $F = 12.8$, $p < 0.001$; dominant frequency: $F = 28.7$, $p < 0.001$; silence between notes: $F = 113.1$, $p < 0.001$; mean note interval: $F = 120.2$, $p < 0.001$; notes per second: $F = 169.3$, $p < 0.001$) (Figs. 3-4; Table 1).

Elevational Distribution. We found that the four putative species differ in their elevational distribution ($F = 16.59$; $p < 0.001$) and post-hoc results indicate statistical significance in elevation between *A. yoshina* and *A. bassleri* ($p < 0.001$), *A. yoshina* and the new species ($p < 0.001$), and *A. pepperi* and the new species ($p < 0.001$) (Fig. 5; Supplemental Data).

Taxonomic accounts

Ameerega bassleri species group (Guillory *et al.* 2020)

A monophyletic assemblage of four species: *Ameerega bassleri* (Melin 1941), *A. pepperi* Brown and Twomey 2009, *A. yoshina* Brown and Twomey 2009, and a new species (this paper; see Fig. 6). Frogs in the *Ameerega bassleri* species group are large brightly colored species that are restricted to montane habitats and riverine valleys throughout San Martin and northern Loreto, Peru, and possess a unique ‘retarded trill’ male advertisement call (Lötters et al. 2003).

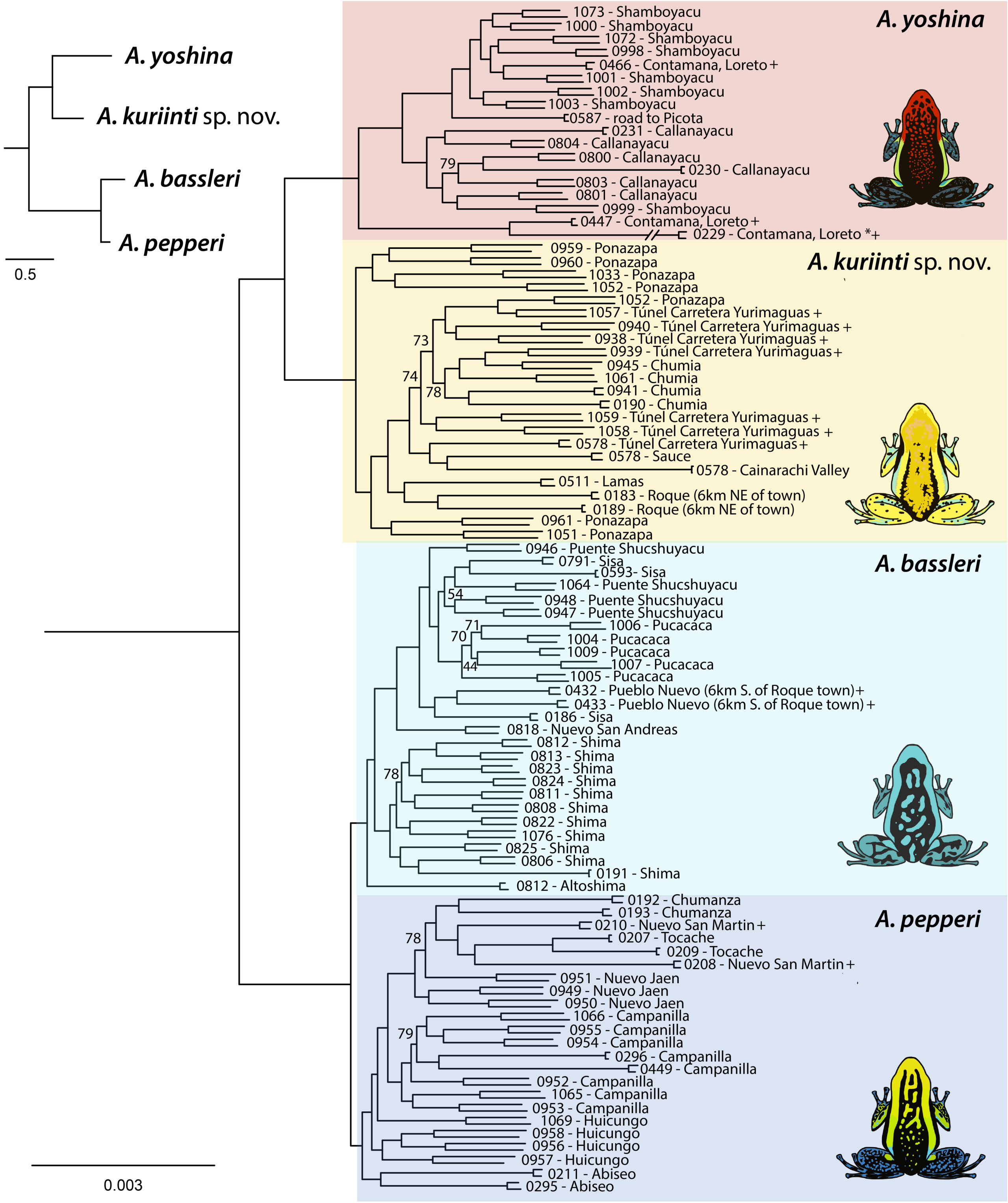

FIGURE 2. (upper left) A species tree of the UCE dataset was inferred on the basis of coalescent theory using ASTRAL-III v.5.6.1 summarizing per-locus gene trees made in IQ-TREE where short branch lengths were contracted. (right) A Maximum likelihood phylogenetic tree constructed from nuclear genomic data (phased ultra-conserved elements; UCEs) run in IQ-TREE. These results depict strong genomic structure between species, with each species being reciprocally monophyletic. Bootstrap values below the threshold of ≤ 85 are displayed for each corresponding branch. Outgroups were used in the analyses, but were manually removed for visual clarity. Each terminal label is centered on two branches, because sequences for each individual were phased. Asterisk indicates manually shortened branch to increase visual clarity; branch length = 0.0059. + indicates populations closest to the type localities of each species. Frog drawings by Wilson X. Guillory.

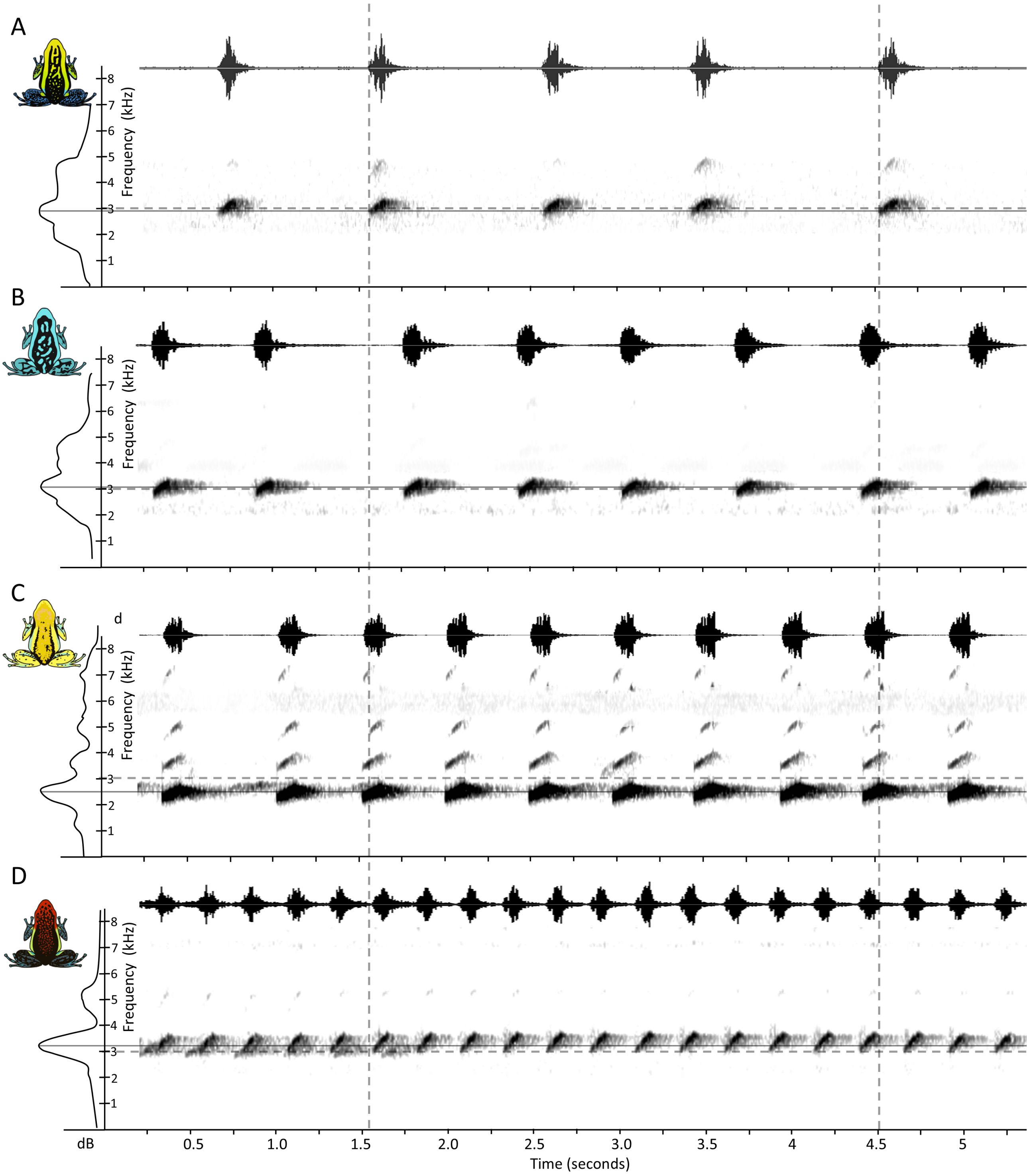

FIGURE 3. Advertisement calls of the species in the *Ameerega bassleri* species group. (A) *A. pepperi* from near Huicungo on Rio Abiseo, Peru, 23.1°C on 9 July 2019 (B) *A. bassleri* from Puente Shucshuyacu, near San Jose de Sisa, Peru, 23.2°C on 26 July 2019 (C) *A. kuriinti* **sp. nov.** from the Túnel Carretera Yurimaguas (Cordillera Escalera, km 20, on road from Tarapoto to Yurimaguas, Peru), 22.2°C on 3 July 2019 (D) *A. yoshina* from Callanayacu, Quebrada Pacuyacu, Peru, temperature 24.4°C on 26 June 2018. Horizontal dotted lines indicate 3kHz on each plot (as a reference line). Solid horizontal lines depict mean frequency (Hz) for each species and vertical dotted lines indicate the time required for a 3 note call series of *A. pepperi*. Frog drawings by Wilson X. Guillory.

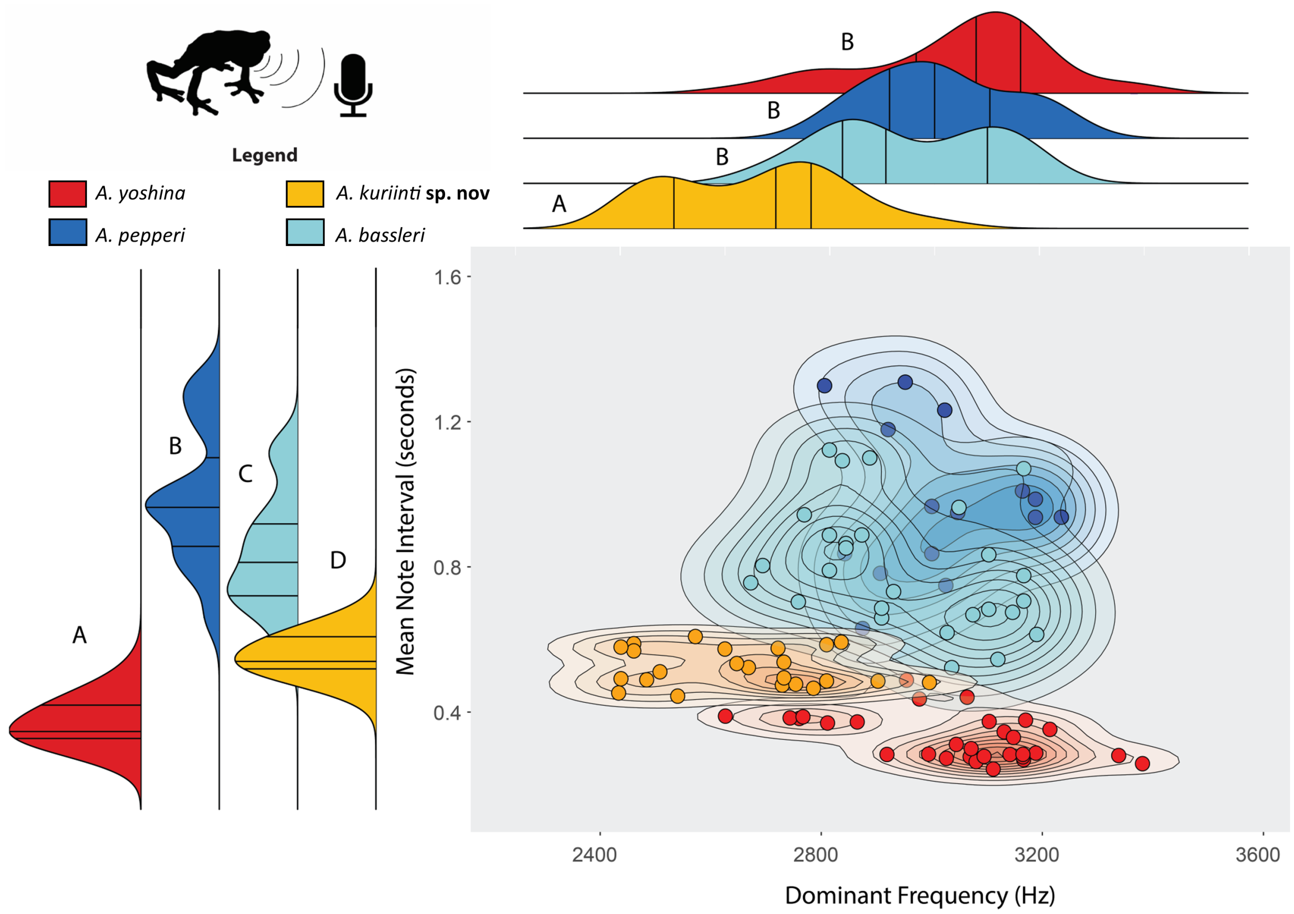

FIGURE 4. Acoustic advertisement call variation within the *Ameerega bassleri* species group. The plot in the center depicts the 2D call space occupied by each species with the x-axis representing advertisement call dominant frequency and y-axis representing mean note interval (in seconds). Density plots extend from each axis and depict the relative frequency of each species' values. Letters depict significant differences among taxa (ANOVA: dominant frequency, df=3, F= 2.26e6 , $p<0.001$; mean note interval, df=3, F= 5.77, $p<0.001$). Black lines in density plots on each axis depict median, upper-, and lower-quartiles for each species. The isopleths in center plot depict a 2D kernel density estimation of each species' call space.

Ameerega bassleri (Melin 1941)

Pleasing poison frog

Dendrobates bassleri: **Melin 1941** p. 65-66
Phyllobates bassleri: **Silverstone 1975** (by implication) p. 1-55; **Silverstone 1976** (partim) p. 1-53 (Figure 2: (F) NMG 511)
Epipedobates bassleri: **Myers 1987** (by implication) p. 301-306; **Schulte 1999** (partim) p. 180-188 (Figures: DB-041, DB-042); **Roberts *et al*. 2006** (partim) p. 149-164 (Table 1: DQ523153, DQ523012, DQ523083, DQ523140, DQ522999, DQ523070, DQ523143, DQ523002, DQ523073, DQ523155, DQ523014, DQ523085, DQ523158, DQ523017, DQ523088; Table 2: P1, P2, P8, P9); **Roberts *et al*. 2007** (partim) p. 417-426 (DQ339049, DQ339058, DQ339059, DQ339060, DQ339062)
Ameerega bassleri: **Lötters *et al*. 2007** (partim) p. 371-376 (Figures: 461-463); **Brown & Twomey 2009** (partim) p. 1-38 (Figure 3: 7-9; Figure 6: 9-16, 19-22; Figure 12: e-o; Table 6: 9-16, 19-22); **Kahn *et al.* 2016** (partim) p. 121-126; **Neves *et al.* 2017** (partim) p. 485-493 (supplementary table 1: DQ523070, DQ523073, DQ523083, DQ523085, DQ523088, FJ752266, FJ752267, FJ752268, FJ752269, FJ752270, FJ752271,); **Guillory & Brown 2021** (partim) p. 1033-1045 (supplemental)
Other authors mention *Ameerega bassleri or Epipedobates bassleri* (**Riechers *et al.* 1998; Spande *et al.* 1999; Jeckel *et al.* 2021**) but we cannot confirm true identity of samples used referenced in both the text or in supplemental materials
Ameerega pepperi: **Guillory *et al.* 2020** (partim) p. 1-8 (supplemental table 1: 0432)

Holotype. NHMG 511 collected 1925 by Melin in Roque, Peru.

Background information. The exact identity of the 'true' *A. bassleri* requires clarification. In the past, authors of this paper (ET and JLB) created confusion regarding the identity of the type specimen of *A. bassleri*. In mid-June 2007, E. Twomey and J. Brown surveyed the areas immediately around Roque, San Martin, the type locality of *A. bassleri*. After hiking 5.7 kilometers NE of Roque, they collected two calling male frogs. These frogs had a yellow dorsum and were phenotypically very similar to the Yellow morph known from the mountains near Tarapoto (here described as a new species). Brown and Twomey published this information in their 2009 paper and thus implied that the Yellow morph represented the morph of the holotype of *A. bassleri*, a sensible (yet erroneous) conclusion given the proximity to the type locality.

In early July 2019, J. Brown returned to Roque to further investigate this group. During this time he encountered a population of *A. bassleri* of the Chrome-green morph ca. 6.7 km SE from Roque. Thus, based solely on locality, both lineages could be ascribed to the type locality. This led us to reevaluate Melin's description of *A. bassleri* (then called "*Dendrobates bassleri*").

Melin (1941 pg. 65) states: *"Colour almost entirely black with light green designs: medial row of large dots from the eye; dorso-lateral bands round the tip of the nose, above the eyes, and along the body, and possibly also some transversal spots on the upper side of thighs."*

A color painting of the holotype of *Ameerega bassleri* (Fig 7a, Göteborgs Naturhistoriska Museum) shows a frog with all the characteristics of the Chrome-green morph, rather than the Yellow morph (here described as a new species). Given this clear distinction, we unequivocally conclude that the holotype belongs to the Chrome-green morph of *A. bassleri*.

Definition and diagnosis. A large species of *Ameerega*, adults range from 35.0–45.0 mm SVL with females being a bit larger. The dorsal skin is moderately granular and is pigmented in various colors and patterns (see descriptions below). The flanks are black extending from the groin to the nostrils. The venter is generally blue with diffuse black markings. Blue marbling extends to all ventral surfaces of forearms and hind limbs. Tympanum not well defined. The first finger is longer than the second. Finger discs moderately expanded, 1.5 times the width of finger. Vocal slits present in males. Two primary morphs are currently known; Chrome-green morph (sensu Brown and Twomey 2016a, p. 121–126) and the Black morph (sensu Brown & Twomey 2016a, p. 121–126): **1**) The Chrome-green morph is characterized by irregular metallic blue, turquoise, or yellow-green spotting or blotched-reticulation on a black dorsum. Forearms lack granulation and are colored as the dorsal pattern, coloration extends up the upper forearm surface, anteriorly around the lower jaw. Hind limbs are lightly granular and marbled or flecked on a black ground color. The Chrome-green morph is found in the central cordilleras of San Martin and the core of its range in the mountains between Río Mayo and Río Huayabamba north of Río Huallaga. **2**) The Black morph is characterized by regular yellowish-green spotting on a black dorsum. Yellow-green longitudinal dorsolateral stripes start at the groin and continue around the snout. Forearms lack granulation and are either olive green, grey, or slate blue, at the elbows; yellow coloration extends onto the upper arm surfaces and anteriorly around the jaw. Hind limbs are lightly granular, finely flecked in olive to blue spots, and have bright yellow femoral spots. The Black morph is known from the forests around Shima (ca. 6 km west of Saposoa town) between Río Saposoa and Rio Huayabamba.

Description of larvae. Tadpoles are small (≥25 mm TL) with an ovoid body. In life, the dorsal surface is grey-brown, tail translucent with brown mottling, tail musculature grey-brown, belly brown. Cream spots are present between corners of the upper lip and nostrils. Eyes are dorsally oriented; fin is dorsally arched; not extending onto body, the tail musculature is broad. The LTRF is 2(2)/3; A-2 gap well defined, P3 slightly shorter than P2. The oral apparatus is oriented anteroventrally. The oral disk is emarginated. Anterior and posterior labium contains a single row of marginal papillae (Brown & Twomey 2016a). Larvae feed on detritus and, when available, dead tadpoles. They complete metamorphosis in about 2 months, gaining adult coloration months after completing metamorphosis. The overall external morphology of tadpoles in the ABSG is highly conserved, but *A. bassleri* typically co-occur with other distinguishable congeneric species *Ameerega trivittata* and *Ameerega altamazonica.*

Similar Species. No species occurring within the range of *A. bassleri* could be confused with this species. The most similar species is *A. pepperi*, and populations near Río Abiseo are similar in appearance to the Black Morph of *A. bassleri.*

Natural history. *Ameerega bassleri* is predominantly found in montane regions, most frequently occurring at elevations between 480–1089 m. This species has an average elevational distribution of 697 m, which is statistically distinct from that of *A. yoshina* in the ABSG (See Fig. 5; Supplemental data).

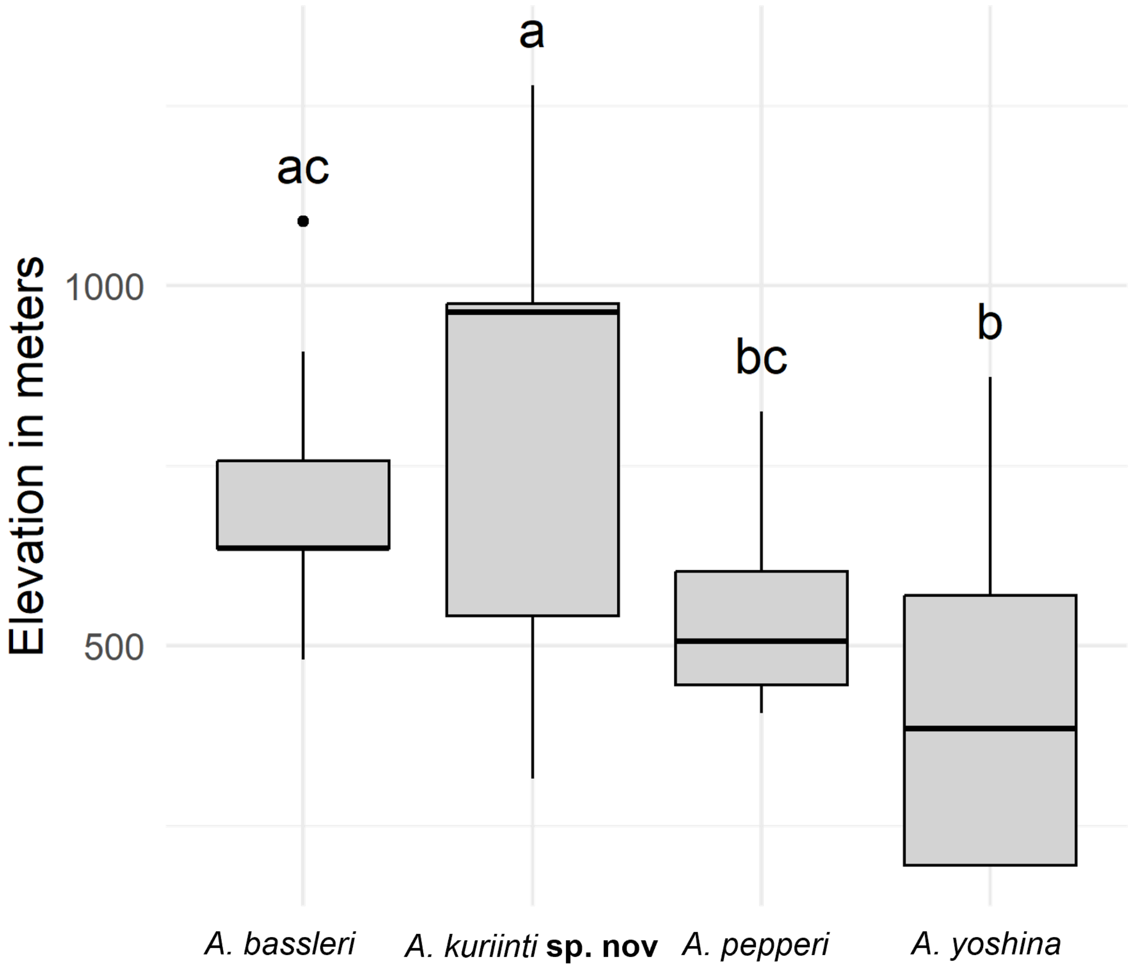

FIGURE 5. Boxplot of the elevational distribution of species of the *Ameerega bassleri* species group in meters. Letters depict significant differences among taxa (ANOVA: F = 16.59; p < 0.001).

Vocalizations. The advertisement call of *A. bassleri* (Fig. 4; Table 1) is categorized as a 'retarded trill' based on Lötters *et al*. (2003). The call comprises a sequence of musical notes that resemble brief 'whistles,' occurring at a note interval of 0.54–1.14 per sec. Each note lasts between 0.16–0.32 sec and is separated by intervals of 0.21–0.95 sec, with an overall average dominant frequency of 2950.47 Hz. The call of *A. bassleri* can be differentiated from the other species of the ABSG by an intermediate call rate; being the second slowest call rate in the group (Figs. 3-4; Table 1).

Distribution. Endemic to Peru, *A. bassleri* occurs throughout the central cordilleras north of the Rio Huallaga between Rio Mayo and Rio Huayabamba at elevations ranging from 481-1089 meters (See Fig. 1). In late July 2021, B. Geralds and J. Brown surveyed the forests around Pucacaca, San Martín. Upon speaking with the locals from the area, we were made aware of a potential population of *A. bassleri* in a small relict of locally preserved forest about 15 km north of Pucacaca in the Asociación Bosques del Futuro Ojos de Agua (or ABOFOA, commonly referred to as Ojos de Agua). Over 2 days, we observed more than 100 individuals, and most of the frogs were concentrated in a 0.5 km stretch of a mostly dried-up river bed. This population was the southernmost population in the easternmost range in the central cordilleras in San Martin, extending our knowledge of this species by ca. 35 km to the south. This population is similar to the Chrome-green morph except that this population has a dorsal coloration with yellow overtones rather than greenish-blue.

Conservation status. Following the IUCN Red List criteria 3.1 (IUCN 2012), we suggest *Ameerega bassleri* be listed as Vulnerable (VU) under the following criteria: (1) we estimate its extent of occurrence at 1,883 km^2 (Fig. 1), with only a small part of it range within a small regional protected forest (Asociación Bosques del Futuro Ojos de Agua, ABOFOA, 24 km^2), and most areas between known populations are seriously fragmented and deforested; (2) it occurs in undisturbed habitat and moderately disturbed habitats; (3) population sizes are unknown, but assumed to be moderately sized, with some populations exceeding hundreds of individuals (4) populations do not appear to be declining; and (5) demand for the pet trade is presumed to be moderate. Under the international CITES agreement it is listed under Appendix II, limiting international trade. Not until 2006 and 2010 had the Black and Chrome-green morphs been legally exported, respectively.

Ameerega kuriinti sp. nov.

Inti poison frog

"If so, Sherbrooke's orange specimens from Chazuta (USNM 166903A-C) probably belong to an undescribed species."

Silverstone (1976) regarding a specimen of *A. kuriinti* **sp. nov.**

Phyllobates bassleri (non Melin)*:* **Silverstone 1976** (partim) p. 1-53 (Figure A-D)

Phobobates bassleri (non Melin)*:* **Zimmerman & Zimmerman 1988** (by implication) p. 125-160 (likely *A. kuriinti* **sp. nov.** based on the availability of species in the hobby in the 1980s and early 2000s)

Epipedobates bassleri (non Melin): **Schulte 1999** (partim) p. 180-188 (Figures: DB-013, DB-042, DB-021); **Clough & Summers 2000** (by implication) p. 515-540 (Table 1); **Hagman *et al.* 2005** (partim) p. 69-73 (Table 1); **Grant *et al.* 2006** (partim) p. 1-262 (appendix 4); **Roberts *et al.* 2006** (partim) p. 149-164 (Table 1: DQ523115, DQ522974, DQ523045, DQ523150, DQ523009, DQ523080, DQ523113, DQ522972, DQ523043, DQ523157, DQ523016, DQ523087, DQ523130, DQ522989, DQ523060, DQ523127, DQ522986, DQ523057; Table 2: P3, P4, P5, P6, P7, P10, P11) **Roberts *et al.* 2007** (partim) p. 417-426 (DQ339050, DQ339052, DQ339054, DQ339055, DQ339057, DQ339061); **Santos *et al.* 2009** (by implication) p. 305-337 (supplemental table 3)

Ameerega bassleri: **Grant *et al.* 2006** (partim) p. 1-262 (appendix 6: AMNH 42313, AMNH 42867, AMNH 42944); **Lötters *et al.* 2007** (partim) p. 371-376 (Figures: 234; 457-460); **Twomey *et al.* 2008a** (by implication) p. 121-126; **Twomey *et al.* 2008b** (by implication) p. 1175-1184; **Twomey & Brown 2008** (by implication) p. 49-65 (Table 1: DQ522986, DQ523057, DQ523127); **Santos *et al.* 2009** (by implication) p. 305-337 (supplemental table 13); **Brown & Twomey 2009** (partim) p. 1-38 (Figure 1d; Figure 3: 1-6; Figure 6: 1-8, 17, 18; Figure 13; Table 6: 1-9, 17, 18) **Kahn *et al.* 2016** (partim) p. 121-126; **Grant *et al.* 2017** (by implication) p. 1-90 (appendix s2: MHNSM22600); **Serrano-Rojas *et al.* 2017** (by implication) p. 71-94 (appendix 2: DQ523080, FJ752272, FJ752273, DQ523057); **Neves *et al.* 2017** (partim) p. 485-493 (supplementary table 1: AF128563, DQ523043, DQ523045, DQ523060, DQ523080, DQ523087, EU342609, EU342610, FJ752272, FJ752273, FJ752290); **Santos Dias *et al.* 2019** (by implication) p. 323-328 (MUSM 22595, MUSM 22795, MUSM 6283); **Guillory *et al.* 2019** (by implication) p. 1-14 (supplemental); **Claessens *et al.* 2020** (partim) p. 158-162 (supplemental); **Guillory *et al.* 2020** (partim) p. 1-8 (supplemental table 1: 0511, 0183, 0184); **Guillory & Brown 2021** (partim) p. 1033-1045 (supplemental); **Mayer *et al.* 2023** (by implication) p. 63-77; **Medeiros *et al.* 2024** (by implication) p. 1-35

Holotype. KU 211979, an adult male collected by Rainer Schulte and William E. Duellman (field number: WED58488) on 18 February 1989 at km 21.8 on road from Tarapoto to Yurimaguas (ca. 11 km east-northeast of Tarapoto, ca. 2 km past the Túnel Carretera Yurimaguas) in the Cainarachi River valley, 970 m elevation on 15 February 1989, 6° 25' 55" S, 76° 18' 30" W (Fig. 8).

Paratypes. All from the region of San Martin, Peru (Fig. 7). KU 209399, KU209400, and KU 209401 were collected by R. Schulte, in Peru, San Martin region at km 20 on road from Tarapoto to Yurimaguas (ca. 10 km east-northeast of Tarapoto, ca. 1 km past the Túnel Carretera Yurimaguas) in the Cainarachi River valley, 1048 m elevation, 6° 27' 0" S, 76° 17' 35" W on unknown date (presumed early 1980s). KU 211978 (field number: WED 57330) was collected by M.E. Morrison at km 15 northeast of Tarapoto, ca. 800m elevation on 11 February 1989, 6° 27' 30" S,76° 17' 50" W (Fig. 8). In life, all frogs possessed yellow-orange limbs and dorsal coloration (Figs. 9 & 10).

Etymology. The specific epithet *kuriinti* (pronounced ***koo****·ree* ***een****-tee*) is derived from two Kichwa words: an adjective, 'kuri', which means 'golden' and a noun, 'inti', which means 'sun'. The specific epithet *kuriinti* is meant as an invariable noun in apposition to the generic name. Indigenous people throughout Peru, Ecuador, and Colombia widely speak the Kichwa language. Here we use the Kichwa language to honor the Kichwa-Lamista

Indigenous people (also known as the Llakwash-Runa people) from the Cordillera Escalera region of San Martin, Peru. The '*inti*' portion of the name references the species' crepuscular habits, calling intensely as the sun rises and sets throughout the valleys of Cordillera Escalera and '*kuri*' references the species' bright yellow dorsal coloration that often turns to bright orange at the rostrum.

Generic Placement. Assigned to the genus *Ameerega* due to the combination of the following characteristics: presence of maxillary and premaxillary teeth, first finger longer than the second (in one individual the first finger is equal length to second, however this is likely an artifact of poor preservation). Further assigned to the *A. bassleri* species group of *Ameerega* on the basis of molecular phylogenetic relationships (see below for further details and comparisons of calls).

Definition. A medium-large species of brightly colored *Ameerega*, characterized by the following combination of characters: (1) mean adult SVL of 31.9 mm (range 29.9-33.3 mm), (Table 1); (2) dorsal skin granular, especially on the back and the dorsal surfaces of the legs, dorsal surfaces of forelimbs lightly granular or non-granular, flanks and venter non-granular; (3) finger III swollen in adults; (4) absence of lateral fringes and basal webbing on fingers; (5) maxillary and premaxillary teeth present; (6) fingers and toes discs expanded, larger in toes II, III, and IV; (7) basal webbing between toes II–III and III–IV; (8) finger I longer than finger II, occasionally equal in some individuals; (9) toe III length reaches or surpasses the middle of the central sub-articular tubercle of toe IV; (10) metatarsal fold absent; (11) tympanum conspicuous and small; (12) in life, dorsal and limb coloration ranging from dull chartreuse yellow to brightly colored yellow or orange concentrated on mid-dorsum to dorsal-rostrum; in some individuals dorsal color transitions from yellow-orange on the mid-dosum to rostrum; (13) oblique lateral stripe absent; (14) usually with dorsolateral stripes extending from groin to mid-dorsum where they fuse with dorsal coloration; (15) labial stripe present in most (occasionally broken or absent in some individuals), starting behind nares and ending at forelimb; (16) flanks black, most individuals have bright bluish, occasionally light-teal, spotting or marbling extending from venter; (17) venter smooth, bright blue to light-teal, with black marbled undertones or black reticulations; (18) large yellow spots present posterodorsally at the insertions of the forelimbs and hindlimbs, and on medial face of tibia; (19) ventral surfaces of forelimbs are light blue; underside of head pigmented as the venter but often darker (i.e. more black marbling), especially in males. (20) iris dark brown with golden ring around pupil; (21) in preservative, all lighter pigments and flash colors fade to white or gray; (22) advertisement call is categorized as a 'retarded trill' according to Lötters *et al*. (2003) that is repeated 1.6–2.3 times per s for several min; each note is short (0.30 s, mean), with the dominant frequency from 2433 to 3000 Hz; (23) presence of exotrophic tadpoles carried to small terrestrial pools, where they are deposited in groups.

Diagnosis. *Ameerega kuriinti* **sp. nov.** can be distinguished from other species of *Ameerega* by its dorsal coloration pattern, with a yellow dorsum (uniformly black dorsum in *A. altamazonica*, *A. hahneli*, *A. pongoensis*, *A. ignipedis*; yellow-green coloration in *A. trivittata*; black ground coloration with red stippling in *A. yoshina* and *A. parvula*; and red dorsum with yellow dorsolateral stripes in *A. cainarachi*). Within the ABSG, it is most similar to *A. pepperi*, but this species has bluish to black limbs (vs. yellow in most *A. kuriinti* **sp. nov.**). The dorsal coloration of most *A. pepperi* populations have distinct spots with coloration concentrated on the head (vs. solid coloration and most for the dorsal surface and brightly colored in *A. kuriinti* **sp. nov.**), and the dorsolateral stripes are complete and distinct, mostly separate from dorsal coloration (vs. in *A. kuriinti* **sp. nov.**, dorsolateral strips are absent in many with individuals and they possess entirely solid dorsal coloration). When dorsum is not entirely colored in *A. kuriinti* **sp. nov.**, the dorsolateral stripes extend from groin to mid-dorsum where they fuse entirely with dorsal coloration (vs. distinct dorsolateral stripes present in *A. pepperi*). *Ameerega kuriinti* **sp. nov.**, *A. bassleri, A. yoshina* and *A. pepperi* have an advertisement call consisting of a series of regularly-spaced whistle-like notes given at a rate of 3.0 ± 0.6 notes per second in *A. yoshina,* 1.2 ± 0.3 notes per second in *A. bassleri*, 1.0 ± 0.2 notes per second in *A. pepperi* (vs. 1.9 ± 0.2 notes per second in *A. kuriinti* **sp. nov.**). Further, although the dominant frequencies of *A. bassleri, A. yoshina* and *A. pepperi* and *A. kuriinti* **sp. nov.** overlap, *A. bassleri, A. yoshina* and *A. pepperi* have a significantly higher-pitched calls (2950–3046 Hz vs. 2601 Hz in *A. kuriinti* **sp. nov.**, Fig. 4).

Measurements of holotype (in mm). SVL 33.8; FoL 17.3; TL 18.6; KK 33.1; FL 18.1; HaL 10.3; HL 13.3; HW 10.8; BW 10.2; UEW 3.4; IOD 4.6; IND 4.9; TD 2.1; ED 4.8; DET 1.0; L1F 8.4; L2F 7.8; W3D 1.2; W3F 0.8. For paratypes see Table 4.

TABLE 4. Measurements (in mm) of *Ameerega kuriinti* **sp. nov.** type series.

Character	**KU 209399**	**KU 209400**	**KU 209401**	**KU 211978**	**KU 211979**	**Mean (n=5)**
SVL	32.6	29.8	33.3	39.2	33.8	33.7 ± 3.4
FL	15.6	14.8	16.1	18.7	17.3	16.5 ± 1.5
TL	16.4	15.3	16.7	21.2	18.6	17.6 ± 2.3
KK	32.5	28.3	31.2	38.2	33.1	32.7 ± 3.6
FoL	13.0	13.5	16.3	17.8	18.1	15.7 ± 2.4
HaL	8.9	9.3	10.1	10.3	10.3	9.8 ± 0.6
HL	12.3	11.3	11.2	13.4	13.3	12.3 ± 1.1
HW	9.7	8.9	9.8	11.4	10.8	10.1 ± 1.0
BW	9.8	10.1	9.8	10.4	10.2	10.1 ± 0.3
UEW	1.9	2.3	2.7	3.2	3.4	2.7 ± 0.6
IOD	4.5	3.4	4.8	4.2	4.6	4.3 ± 0.5
IND	4.2	4.5	4.4	4.8	4.9	4.6 ± 0.3
TD	2.2	2.5	2.2	2.5	2.1	2.3 ± 0.2
ED	4.2	4.1	4.5	4.5	4.8	4.4 ± 0.3
DET	0.8	0.7	0.9	0.8	1.0	0.8 ± 0.1
L1F	7.1	7.1	7.8	8.3	8.4	7.7 ± 0.6
L2F	8.4	7.2	7.9	8.3	7.8	7.9 ± 0.5
W3D	1.1	1.2	1.0	0.9	1.2	1.1 ± 0.1
W3F	0.6	0.6	0.7	0.6	0.8	0.7 ± 0.1
SEX	M	M	M	M	M	

Description of holotype. The holotype is an adult male, 33.8 mm snout-vent length. The dorsal skin is granular, especially on the back and the dorsal surfaces of the legs, dorsal surfaces of forelimbs lightly granular, flanks and venter non-granular. Maxillary and premaxillary teeth present. Tongue gray, ovoid, attaching anteriorly. Head widest at jaw articulations, slightly wider than body in most individuals (head width at tympanum 105.8% of body width at axillae). Head width 32.0% of SVL. Snout truncate in dorsal and ventral view, sloping and rounded in lateral view. Canthus rostralis rounded, loreal region vertical. Nares situated and directed posterolaterally to the tip of snout; nares visible from front and below but not from above. Canthus rostralis sloped, slightly rounded; loreal region nearly vertical and slightly concave. Upper eyelid width is three-quarters of interorbital distance. Eye 4.8 mm in diameter and prominent, with a maximum diameter of 14.2% of the snout vent length; pupil rounded and horizontally elliptical. Interorbital distance greater width than superior upper eyelid. Tympanum 2.1 mm in diameter; circular, partially concealed posterodorsally, lacking tympanic annulus; tympanum width 43.8% of eye diameter. Supratympanic fold absent.

Hands relatively small, length 30.5% of SVL. Relative length of appressed fingers: III > IV > II ≈ I. Discs moderately expanded, disc on finger III 1.5 times width of finger below disc. A large, circular to ovoid outer metacarpal tubercle present on the median base of palm; a smaller inner metacarpal tubercle on the base of finger I; one well developed and prominent subarticular tubercle on fingers I and II, two on fingers III and IV.

Hind limbs are relatively short and small, femur 51.2% of SVL, tibia 55.0% 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 V barely expanded discs (much smaller than finger discs), and toes III and IV with discs expanded (disc 1.5–1.6 times broader than adjacent phalanx). Inner and a smaller outer metatarsal tubercle present, somewhat protuberant with rounded surfaces. One protuberant subarticular tubercle present on toes I and II, two on toes III, IV, and V. Interior subarticular tubercle of toe V smaller and partially raised. Hands and feet lacking supernumerary tubercles, lateral fringes, and webbing. No toe fringes.

In life, the holotype possessed bright yellow limbs and dorsal coloration (Fig. 9) and bluish-green ventral coloration. In preservative, the dorsum, limbs and venter are largely dark brown. The yellow dorsal coloration is faintly visible and is dull yellowish grey in preservative and concentrated on the head. The bluish-green ventral coloration in life is also weakly visible as a dark greyish-blue in preservative and concentrated in the venter near limbs (Fig 7).

Variation. Little to no sexual dimorphism is apparent except for males being slightly smaller, possessing vocal slits and a subgular vocal sac. Head widest at jaw articulations, slightly wider than body in most individuals (head width at tympanum 88.1–109.6% of body width at axillae); head width 29.1–32.0% of SVL. Eye large and prominent, with a maximum diameter of 11.5-14.2% of the snout vent length; tympanum width 43.8–61.0% of eye diameter. Hands relatively small, length 29.2–32.0% of SVL. Relative length of appressed fingers: III > IV > II ≈ I. Discs moderately expanded, disc on finger III 1.4–2.0 times width of finger below disc. Hind limbs are relatively short and small, femur 47.7–51.2 of SVL, tibia 50.2–55.0% 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 V barely expanded discs (much smaller than finger discs), and toes III and IV with discs expanded (disc 1.5–2.0) times broader than adjacent phalanx).

Coloration varies spatially and in the core of the range of this species (in the Cordillera Escalera), most individuals possess bright yellow dorsal coloration that covers the entire back. However, within these populations some individuals have intense orange coloration usually concentrated on the head (e.g. Fig 9f), occasionally the orange covers the entire dorsum (e.g., Fig 10f). At the periphery of this species' distribution, some individuals possess duller gold or chartreuse dorsal coloration (e.g. small populations observed near Sauce, Roque, and Alto Shilcayo nearby Tarapoto; Brown & Twomey 2009 Fig. 13). In most populations the extent of yellow coloration varies among individuals, with some frogs being completely yellow colored and others being partially yellow colored (Brown & Twomey 2009 Fig. 13g). The proportion of individuals that are completely colored also varies spatial and at the core of its distribution, most the dorsum are entirely yellow colored, whereas at some peripheral populations, complete yellow dorsal coloration is rare (e.g. at Alto Shilcayo nearby Tarapoto).

Vocalization. The advertisement call for *A. kuriinti* **sp. nov.** (Table 1) is a 'retarded trill' repeated 1.6–2.3 times per second for several minutes. Each note is short (mean 0.30 sec), with the dominant frequency from 2433.25–3000.00 Hz. This advertisement call is given most frequently in the morning and evening as males chorus back and forth in small groups. The call of *A. kuriinti* **sp. nov.** can be differentiated from the other species of the ABSG by the second-fastest repeated call rate, slower only than *A. yoshina*.

Description of larvae. Tadpoles are small (≥25 mm TL) with an ovoid body. In life, the dorsal surface is grey-brown, tail translucent with brown mottling, tail musculature grey-brown, belly brown. Cream spots are present between corners of the upper lip and nostrils (Supp. Fig. 1). Eyes dorsal; fin dorsally arched; not extending onto body, tail musculature broad. The LTRF is 2(2)/3; A-2 gap well defined, P3 slightly shorter than P2. The oral apparatus is oriented anteroventrally. The oral disk is emarginated. Anterior and posterior labium contains a single row of marginal papillae. Larvae feed on detritus and, when available, dead tadpoles. They complete metamorphosis in about 2 months and gain adult coloration months after completing metamorphosis. The overall external morphology of tadpoles in the ABSG is highly conserved, but *A. kuriinti* **sp. nov.** typically co-occur with other distinguishable congeneric species *Ameerega trivittata, Ameerega cainarachi, Ameerega pongoensis,* and *Ameerega altamazonica.* Previous ecological studies by Twomey *et al.* (2008a, 2008b) refer to *A. kuriinti* **sp. nov** as *A. bassleri*.

Distribution and natural history. *Ameerega kuriinti* **sp. nov.** is distributed throughout northern regions of San Martin throughout the Cordillera Escalera with a few populations extending south, across the Huallaga river near the buffer zone of Cordillera Azul National Park (e.g. at Sauce) and possibly extending into the park. This species occurs in the southern part of the Cordillera Escalera and is found at elevations of ca. 316–1278 m, which is statistically distinct from elevational distributions of both *A. pepperi* and *A. yoshina* within the ABSG (Fig. 5; Supplemental data). This species is common and can be locally abundant in undisturbed forested habitats that surround, or are nearby, small streams, which collectively provide refugia from the midday heat and habitat for reproduction.

A parasitic fly (*Notochaeta bufonivora*) has been found to use adult *A. kuriinti* **sp. nov.** as hosts (Hagman, 2005; Brown & Twomey, *pers. observ.*) (Fig. 10). After 1–4 days, infected frogs die and up to 30 fly larvae consume the dead frog. Within 48 hours of death, adult fly larvae pupate and after three weeks, the adults emerge (Brown and Twomey, *pers. observ.*).

Conservation status. Following the IUCN Red List criteria 3.1 (IUCN 2012), we suggest *A. kuriinti* **sp. nov.** be listed as Least Concern (LC) under the following criteria: (1) we estimate its extent of occurrence at 3,981 km^2 (as shown in Fig. 6), and part of this range lies in a large protected forest (Parque Regional Cordillera Escalera: 1,498 km^2) and the northern edge of Parque Nacional Cordillera Azul, a small communal reserve (Alto Shilcayo) and three private concession areas (ACP Juningue, Tambo Ilusión, Las Naranjas); (2) it occurs mostly in undisturbed habitats; (3) population sizes are unknown, but assumed to be large given the abundant forested habitats and tentative large range; (4) populations do not appear to be declining; and (5) demand for the pet trade is presumed to be moderate. Under the international CITES agreement it is listed under Appendix II, limiting international trade. Not until 2006 has this species been legally exported (as *A. bassleri*).

FIGURE 6. Species in the *Ameerega bassleri* species group. (a) Chrome-green morph of *Ameerega bassleri* (uncollected individual from 8.6 km E of San José de Sisa, San Martín, Peru) and is representative of the holotype described by Melin 1941; (b) *A. pepperi* (uncollected individual from 6.3 km N of Campanilla, San Martín, Peru); (c) *A. kuriinti* **sp. nov.** (uncollected individual from Cainarachi Valley, San Martín, Peru) and is a representative of the holotype (KU 211979) and described here; (d) Holotype of *A. yoshina* (MUSM 24945) collected by J. Brown 17.5 km NE Contamana at the western foothills of the Serranía de Contamana. Photos: J. Brown.

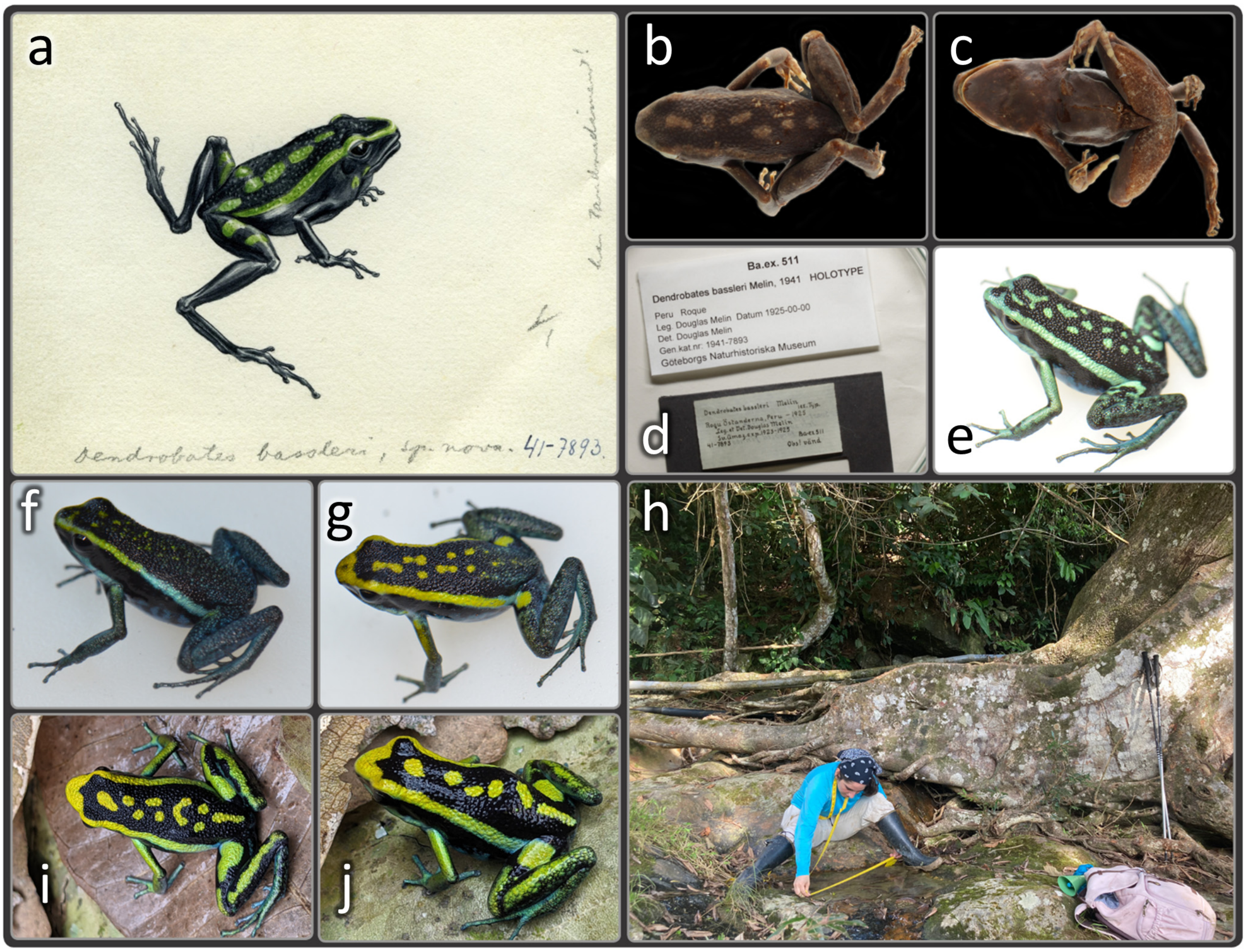

FIGURE 7. Updates to *Ameerega bassleri* biogeography and taxonomy. Holotype of *A. bassleri,* NHMG 511 collected 1925 by Melin in Roque, Peru: **A.** Painting, **B.** Dorsum, **C.** Venter, **D.** Original label "Dendrobates bassleri Melin lex.Typ., Roqu Östanderna, Peru - 1925, Leg. et Det. Douglas Melin, Su.Amaz.exp.1923-1925. 41-7893, ßa-ex511, Obs! vänd" **E.** Newly discovered population of *A. bassleri* from near Nuevo San Andreas, San Martín, Peru; **F.** & **G.**, Variation of *A. bassleri* from near Shima, San Martín, Peru. **H.** Breeding pool of *A. yoshina* near Shamboyacu, San Martín, Peru., **I.** & **J.** Newly discovered population of *A. bassleri* from Ojos de Agua Pucacaca, San Martín, Peru

Ameerega pepperi Brown and Twomey, 2009

Pepper's poison frog

Phyllobates bassleri: **Silverstone 1976** p. 45 (AMNH 42327, 42867, 43402 collected in 1926 and 1928 by H. Bassler at "Pachiza")

Ameerega pepperi: **Brown & Twomey 2009** (by implication) p. 1-38; **Kahn *et al.* 2016** (by implication) p. 177-181; **Grant *et al.* 2017** (by implication) p. 1-90 (appendix s2: iso1); **Serrano-Rojas *et al.* 2017** (by implication) p. 71-94 (appendix 2: FJ752283, FJ752287, FJ752280, FJ752281); **Neves *et al.* 2017** (by implication) p. 485-493 (supplementary table 1: FJ752280, FJ752281, FJ752282, FJ752283, FJ752284, FJ752285, FJ752286, FJ752287, FJ752288); **Claessens *et al.* 2020** (partim) p. 158-162 (supplemental); **Guillory *et al.* 2020** (partim) p. 1-8 (supplemental table 1: 0296, 0209, 0295); **Guillory & Brown 2021** (by implication) p. 1033-1045 (supplemental)

Ameerega bassleri: **Grant *et al.* 2006** (partim) p. 1-262 (Figure 66-67: AMNH 43402; appendix 6: AMNH 42327, AMNH 42333, AMNH 43402); **Claessens *et al.* 2020** (partim) p. 158-162 (supplemental material)

Holotype. MUSM 2640, an adult male, collected in 2006 by M. Pepper in Provincia Tocache, Departamento San Martín, Peru, 2 km NE of San Francisco, 980 m elevation, 8° 18' 30.3" S, 76° 40' 37.6" W. Found on the ground near a small waterfall.

Background information. This species was originally described by Brown & Twomey (2009) largely on the basis of advertisement calls. In the original description, a phylogeny based on mtDNA rendered *A. bassleri* paraphyletic. Guillory et al. (2020), using nuclear markers, supported the monophyly of this species and others in the ABSG. Here, based on a greatly expanded phylogenetic sampling, we provide additional information on the vocalization, larvae, distribution, conservation status, and evolutionary relationships of this species.

Vocalization. The advertisement call of *A. pepperi* (Table 1) is categorized as a 'retarded trill' based on Lötters *et al*. (2003). The call comprises a sequence of musical notes that resemble brief 'whistles,' occurring at a note interval of 0.63–1.31 per min/sec. Each note lasts between 0.21–0.44 sec and is separated by intervals of 0.40–1.03 sec, with an overall dominant frequency of 3011.48 Hz. The call of *A. pepperi* can be differentiated from the other species of the ABSG by the slowest repeated call rate.

Description of larvae. Tadpoles are small (≥25 mm TL) with an ovoid body. In life, the dorsal surface is grey-brown, tail translucent with brown mottling, tail musculature grey-brown, belly brown. Cream spots are present between corners of the upper lip and nostrils (Supp. Fig. 1). Eyes dorsal; fin dorsally arched; not extending onto body, tail musculature broad. The LTRF is 2(2)/3; A-2 gap well defined, P3 slightly shorter than P2. The oral apparatus is oriented anteroventrally. The oral disk is emarginated. Anterior and posterior labium contains a single row of marginal papillae. Larvae feed on detritus and, when available, dead tadpoles. They complete metamorphosis in about 2 months and gain adult coloration months after completing metamorphosis. The overall external morphology of tadpoles in the ABSG is highly conserved, but *A. pepperi* typically co-occur with other distinguishable congeneric species *Ameerega trivittata* and *Ameerega altamazonica.*

Distribution and natural history. *Ameerega pepperi* occupies premontane elevations (407–825 m) throughout the upper Huallaga Valley from south of Río Huayabamba near Huicungo to the southern San Martín border. Most records lie along the road between Tingo María and Juanjui on the river's eastern bank (western slope of Cordillera Azul), but populations also exist on the western bank (eastern Andean slope) at San Francisco and Huicungo. *Ameerega pepperi* is strictly riparian, inhabiting primary and secondary premontane forest within ~30 m of streams, though it tolerates moderate disturbance if riparian shade remains. By day, adults shelter among streamside boulders; calling peaks at dusk, with males vocalizing from elevated rocks. Courtship and oviposition occur on leaf litter, where males guard clutches of 22–44 eggs that hatch in ~18 days (Brown & Twomey 2009). Tadpoles develop in shallow eddies or clay-bottomed pools left by receding flows, often burying in sediment during hot afternoons.

Conservation status. Following the IUCN Red List criteria 3.1 (IUCN 2012), we suggest *A. pepperi* be listed as Vulnerable (VU) under the following criteria: (1) we estimate its extent of occurrence at 1,539 km^2 (Fig. 1), with only a small part of its known range within a large National protected forest, Parque Nacional Río Abiseo, however this distribution of this species is in this area has not been confirmed. Areas between most known populations are heavily fragmented and deforested. (2) it occurs in undisturbed habitat and moderately disturbed habitats; (3) population sizes are unknown, but assumed to be moderately sized, with some populations exceeding hundreds of individuals (4) populations do not appear to be declining; and (5) demand for the pet trade is presumed to be moderate. Under the international CITES agreement it is listed under Appendix II; limiting international trade. Not until 2007 had legally exported samples entered availability in North America, however the availability in the US and European hobby markets is quite limited.

Ameerega yoshina Brown and Twomey, 2009

Phantom poison frog

Ameerega yoshina: **Brown & Twomey 2009** (by implication) p. 1-38; **Kahn *et al.* 2016** (by implication) p. 230-234; **Grant *et al.* 2017** (by implication) p. 1-90 (appendix s2: iso5); **Serrano-Rojas *et al.* 2017** (by implication) p. 71-94 (appendix 2: FJ752274, FJ752275, FJ752278, FJ752279); **Neves *et al.* 2017** (by implication) p. 485-493 (supplementary table 1: FJ752274, FJ752275, FJ752276, FJ752277, FJ752278); **Guillory *et al.* 2020** (by implication) p. 1-8 (supplemental table 1: 0587, 0230, 0229, 0447); **Guillory & Brown 2021** (by implication) p. 1033-1045 (supplemental)

Holotype. MUSM 24945, an adult female, collected in 2006 by Jason L. Brown in Departamento Loreto, Peru, 17.5 km NE Contamana at the western foot of the Serranía de Contamana, 310 m elevation, 7° 11’ 7.43” S, 74° 57’ 13.12” W. Found near El Unión, on the ground near a small creek flowing into the coldwater stream.

Background information. This species was originally described by Brown & Twomey (2009) on the basis of its advertisement call, which is emitted at a markedly higher rate compared to *A. pepperi* and *A. bassleri*. Although this species was polyphyletic in the mtDNA phylogeny provided in its description, recent work based on nuclear markers has found that *A. yoshina* is monophyletic (Guillory et al. 2020). Here, we document *A. yoshina* from several new localities, provide expanded phylogenetic results for the species, and provide additional information on its vocalizations, larvae, and conservation status.

Vocalization. The advertisement call of *A. yoshina* (Table 1) is categorized as a ‘retarded trill’ based on Lötters *et al.* (2003). The call comprises a sequence of musical notes that resemble brief ‘whistles,’ occurring at a note interval of 0.24–0.49 per sec. Each note lasts between 0.20-–0.33 sec and is separated by intervals of 0.01–0.15 sec, with an overall dominant frequency of 3046.01 Hz. The call of *A. yoshina* can be differentiated from the other species of the ABSG by the fastest call repetition rate.

Description of larvae. Tadpoles are small (≥25 mm TL) with an ovoid body. In life, the dorsal surface is grey-brown, tail translucent with brown mottling, tail musculature grey-brown, belly brown. Cream spots are usually present between corners of the upper lip and nostrils. At Shamboyacu, some tadpoles lack cream spots (Supp. Fig. 1). Eyes dorsal; fin dorsally arched; not extending onto body, tail musculature broad. The LTRF is 2(2)/3; A-2 gap well defined, P3 slightly shorter than P2. The oral apparatus is oriented anteroventrally. The oral disk is emarginated. Anterior and posterior labium contains a single row of marginal papillae. Larvae feed on detritus and, when available, dead tadpoles. They complete metamorphosis in about 2 months and gain adult coloration months after completing metamorphosis. The overall external morphology of tadpoles in the ABSG is highly conserved, but *A. yoshina* typically co-occur with other distinguishable congeneric species *Ameerega trivittata, Ameerega ignipedis, Ameerega cainarachi,* and *Ameerega altamazonica.*

Distribution and natural history. *Ameerega yoshina* is known from two premontane regions with an elevational range of 195-873 meters: east of Ucayali River in the Serranía de Contamana (near the Sierra del Divisor National Park) and then west of the Ucayali River in the northern Cordillera Azul. Within Cordillera Azul it is found at two disjunct locations: Callanayacu in the northern Cordillera Azul near the Huallaga River, and near Shamboyacu at two isolated sites. Near Callanayacu, *A. kuriinti* **sp. nov.** occurs only north of the Huallaga River, while *A. yoshina* is only known from a small stream, Quebrada Pucayacu, south of the Huallaga River. In the southernmost localities, near Shamboyacu, this species is restricted to rocky and steep gallery forests due to extensive deforestation surrounding more accessible habitats. At all known localities, this species is absent from surrounding lowland habitats and appears to be confined to these upland forests adjacent to small and medium-sized streams. We expect that this species occurs at other localities within north-central Cordillera Azul, however this is unverified, as much of this area has not been surveyed. Further, even if an area is surveyed, this species is often exceedingly difficult to observe.

In late July 2021, B. Geralds and J. Brown surveyed the forests between Shamboyacu and Tocache in Alto Biavo District of San Martin, with the particular aim of discovering additional populations of *A. yoshina* (and perhaps *A. pepperi*). We surveyed the road SM108 from Bellavista until the road became impassable at km. 53 (7°31’37.4”S 76°18’49.9”W, before the town of Nuevo Arica), we also surveyed a side road, the road to Israel Uriate (Valle de Pavo), and traveled past the village until km. 44 where the road was blocked by the high waters of a small river (ca. 7°23’17.3”S 76°14’20.6”W). During the three days of survey, we only observed larvae of *A. trivittata*, which was also occasionally calling along the road. No other dendrobatid (adult or larvae) was observed or heard calling. Based on these observations, it does not appear that members of ABSG are abundant in this region during the time of our survey. Elsewhere in San Martin, adult *A. yoshina* are frequently heard calling at multiple sites and routinely observed as tadpoles.

Conservation status. Following the IUCN Red List criteria 3.1 (IUCN 2012), we suggest *A. yoshina* be listed as Endangered (EN) under the following criteria: (1) we estimate its extent of occurrence at 1,163 km^2 (as shown in Fig. 1), however only four populations have been confirmed to be this species across its entire range (our map has two additional locations marked with * that are likely *A. yoshina* and are coordinates for other researchers/databases. However, when we surveyed these sites, we did not find any evidence of this species’ existence). However, this species likely occurs in two large reserves: Parque Nacional Cordillera Azul and Parque Nacional Sierra del Divisor, which have not been extensively surveyed for this shy species; (2) it only occurs largely undisturbed habitat (3); population sizes are small in known habitats likely range from 100-1000 adult individuals; (4) populations do not appear to be declining in areas where habitat is protected and (5) demand for the pet trade is presumed to be moderate to low. Under the international CITES agreement this species is listed under Appendix II; limiting international trade. Currently this species has never been legally exported, nor been observed in the US and European hobby markets.

FIGURE 8. Type series of *Ameerega kuriinti* **sp. nov.** Top row: L-R, KU 209400, KU 209401, KU 209399; Bottom row: KU 219979 [holotype], KU 211978. **A**. dorsal view and **B**. ventral view. **C.** Color in life (KU 219979, photo: W. E. Duellman).

Conclusion

Here we propose two taxonomic changes to the ABSG. Based on our molecular phylogenetic analyses, we restrict *A. bassleri* to populations northwest of Rio Huallaga, southwest of Rio Mayo, and north of Rio Abiseo. This includes populations immediately south of Roque, San Martin, Peru (the type locality of *A. bassleri*; Melin, 1941). The second taxonomic change elevates *A. bassleri* Yellow morph lineage to a specific status, *A. kuriinti* **sp. nov**. These populations were assigned to *A. bassleri* by Brown and Twomey (2009) using a Bayesian phylogenetic analysis of three mitochondrial regions (12S, 16S, and Cytb). Our analyses are based on increased spatial sampling, more populations sampled and individuals within previously sampled populations, as well as intense sampling around each type locality (including topotypic material), and dramatically more genetic loci (genome-wide UCEs representing 3,003 loci and the entire mitogenome). All analyses of these data fully support the existence of two lineages with distinct morphologies and unique distributions formerly contained with *A. bassleri* (sensu Brown & Twomey, 2009). Under this rearrangement, both species form well-supported monophyletic groups and all species in the ABSG are monophyletic.

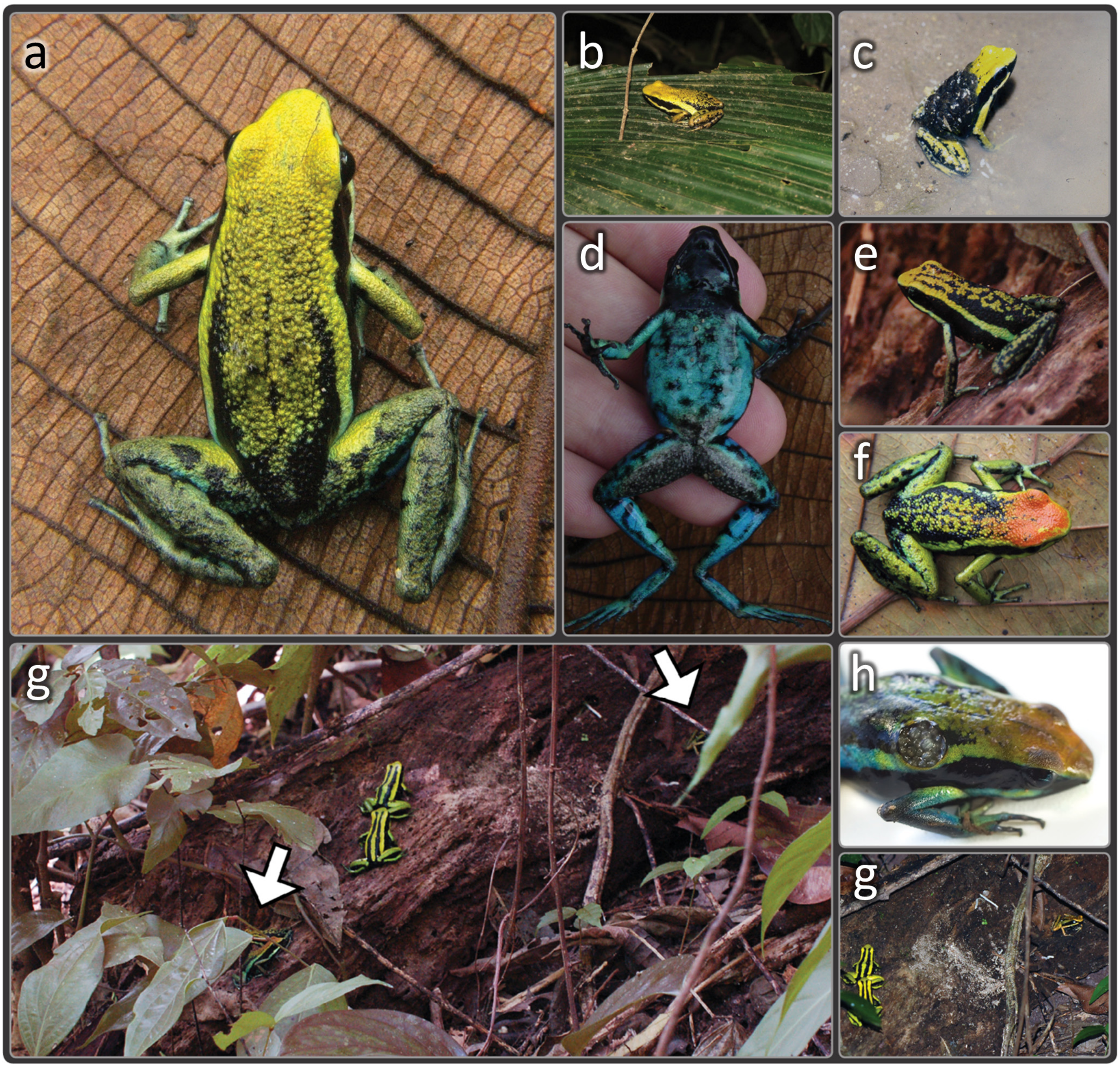

FIGURE 9. Coloration, parasites, and natural history of *A. kuriinti* **sp. nov. A.** *Ameerega kuriinti* **sp. nov.** from near Sauce, San Martín, Peru. **B.** Adult sleeping on a plant surface. **C.** Adult male depositing tapdoles. **D.** Venter of *Ameerega kuriinti* **sp. nov.** from near Sauce, San Martín, Peru. **E.** Adult from near Chazuta, San Martín, Peru; **F.** Adult from Cainarachi Valley, San Martín, Peru. **G.** Population of *Ameerega* frogs *in situ* near Chazuta, San Martín, Peru. Five *Ameerega spp.* are visible in this picture: 2 *A. trivittata* and 3 *A. kuriinti* **sp. nov.** (highlighted with arrows, see smaller G for view of the third individual). At this site *A. cainarachi* and *A. altamazonica* were also frequently observed. **H.** *A. kuriinti* **sp. nov.** has been observed to be infected by a parasitic flesh eating fly (Diptera, Sarcophagidae).

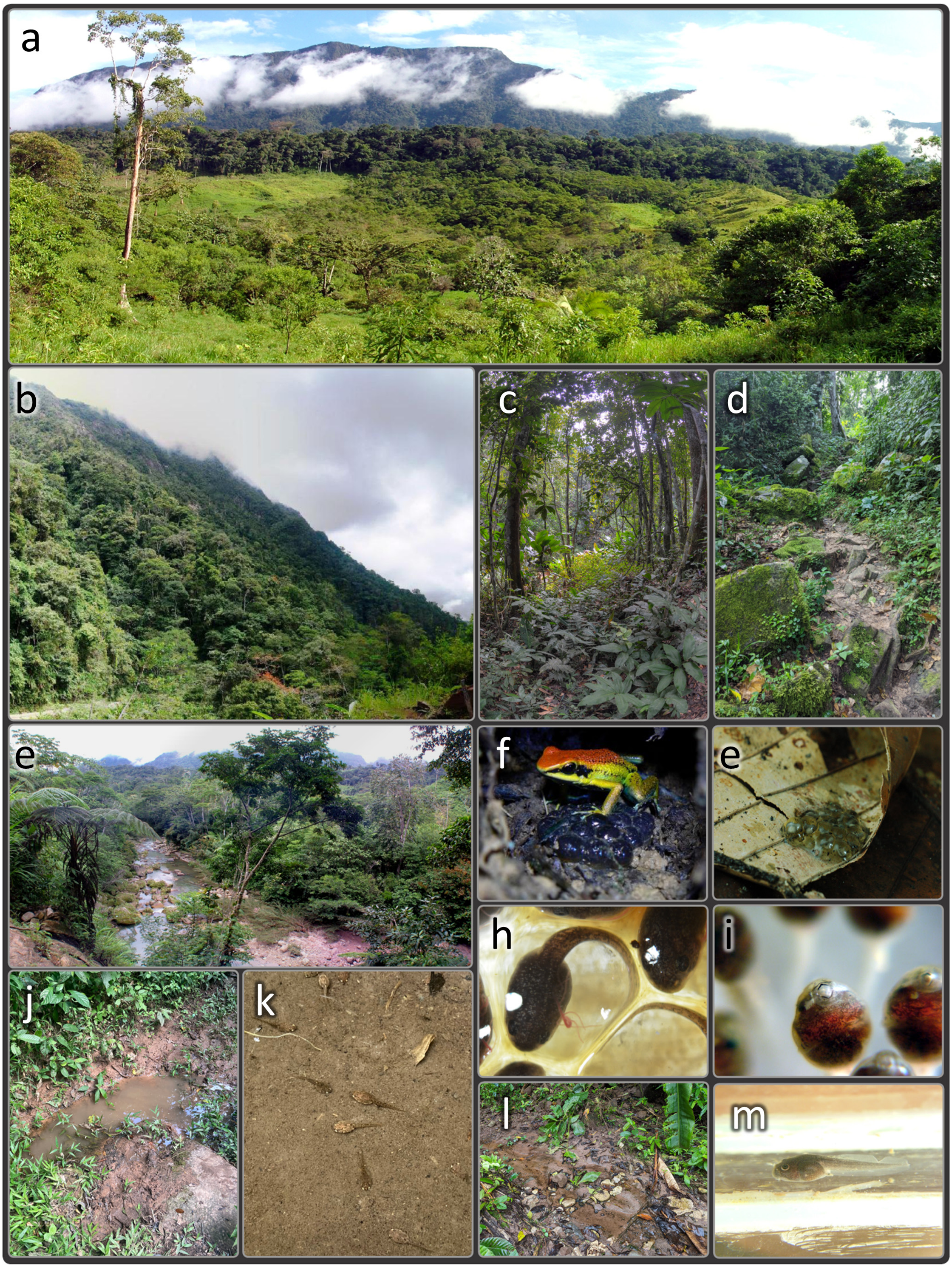

FIGURE 10. Habitat, reproductive ecology, and larvae of *A. kuriinti* **sp. nov. A.** Forests in on western versant of the Cainarachi Valley. The type locality is located in the center of this image at middle elevations. **B.** Habitat at type locality **C.** Forest understory in the central Cainarachi Valley, a locality where *A. kuriinti* **sp. nov.** is commonly found. **D.** Habitat of this species at Alto Shilcayo preserve near Tarapoto. **E.** Cainarachi River in the central Cainarachi Valley. *Ameerega kuriinti* **sp. nov.** is rarely found along the main river, however this species is common within the secondary and tertiary streams that flow into this river. **F.** *Ameerega kuriinti* **sp. nov.** guarding eggs (photo by M. Ramírez Zárate), **G.** Eggs of *A. kuriinti* **sp. nov.** on the surface of a leaf in leaf litter. **H.** Larvae in captivity. **I.** Mouth coloration *in situ.* **J & L.** Terrestrial pool used for tadpole deposition **K.** Close-up of tadpoles within pool **M.** *A. kuriinti* **sp.nov.** tadpole.

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