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A taxonomic revision of the Neotropical poison frog genus *Ranitomeya* (Amphibia: Dendrobatidae)

JASON L. BROWN[1]*, EVAN TWOMEY[2], ADOLFO AMÉZQUITA[3], MOISÉS BARBOSA DE SOUZA[4], JANA-LEE P. CALDWELL[5], STEFAN LÖTTERS[6], RUDOLF VON MAY[7], PAULO ROBERTO MELO-SAMPAIO[4], DANIEL MEJÍA-VARGAS[8], PEDRO PEREZ-PEÑA[9], MARK PEPPER[10], ERIK H. POELMAN[11], MANUEL SANCHEZ-RODRIGUEZ[12] & KYLE SUMMERS[2]

1. Biology Department, Duke University, Durham NC 27701, USA
2. Biology Department, East Carolina University, Greenville NC 27858, USA
3. Universidad de los Andes, Department of Biological Sciences, Bogotá, Colombia
4. Universidade Federal do Acre, Centro de Ciências Biológicas e da Natureza, BR 364 km 04 Distrito Industrial, CEP 69.915-900 Rio Branco AC, Brazil
5. Sam Noble Oklahoma Museum of Natural History and Department of Zoology, University of Oklahoma, Norman, OK 73072, USA
6. Biogeography Department, Trier University, 54286 Trier, Germany
7. Department of Biological Sciences, Florida International University, Miami FL 33199, USA
8. Associate Researcher, Department of Biological Sciences, Universidad de los Andes, Bogotá, Colombia
9. Wildlife Conservation Society, Malecón Tarapaca 332, Iquitos Perú.
10. Understory Enterprises Inc., Charing Cross, Ontario Canada, N0P 1G0
11. Laboratory of Entomology, Wageningen University, P.O. Box 8031, 6700 EH Wageningen, the Netherlands
12. Understory Enterprises Inc., Iquitos, Peru
**jasonleebrown@gmail.com*

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Jason L. Brown, Evan Twomey, Adolfo Amézquita, Moisés Barbosa de Souza, Janalee P. Caldwell, Stefan Lötters, Rudolf von May, Paulo Roberto Melo-Sampaio, Daniel Mejía-Vargas, Pedro Perez-Peña, Mark Pepper, Erik H. Poelman, Manuel Sanchez-Rodriguez & Kyle Summers
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Abstract

The Neotropical poison frog genus *Ranitomeya* is revised, resulting in one new genus, one new species, five synonymies and one species classified as *nomen dubium*. We present an expanded molecular phylogeny that contains 235 terminals, 104 of which are new to this study. Notable additions to this phylogeny include seven of the 12 species in the *minuta* group, 15 *Ranitomeya amazonica*, 20 *R. lamasi*, two *R. sirensis*, 30 *R. ventrimaculata* and seven *R. uakarii*.

Previous researchers have long recognized two distinct, reciprocally monophyletic species groups contained within *Ranitomeya*, sensu Grant *et al.* 2006: the *ventrimaculata* group, which is distributed throughout much of the Amazon, and the *minuta* group of the northern Andes and Central America. We restrict *Ranitomeya* to the former group and erect a new genus, *Andinobates* Twomey, Brown, Amézquita & Mejía-Vargas **gen. nov**., for members of the *minuta* group. Other major taxonomic results of the current revision include the following: (i) A new species, *Ranitomeya toraro* Brown, Caldwell, Twomey, Melo-Sampaio & Souza **sp. nov.**, is described from western Brazil. This species has long been referred to as *R. ventrimaculata* but new morphological and phylogenetic data place it sister to *R. defleri*. (ii) Examination of the holotype of *R. ventrimaculata* revealed that this specimen is in fact a member of what is currently referred to as *R. duellmani*, therefore, *Dendrobates duellmani* Schulte 1999 is considered herein a junior synonym of *D. ventrimaculatus* Shreve 1935 (= *R. ventrimaculata*). (iii) For the frogs that were being called *R. ventrimaculata* prior to this revision, the oldest available and therefore applicable name is *R. variabilis*. Whereas previous definitions of *R. variabilis* were restricted to spotted highland frogs near Tarapoto, Peru, our data suggest that this color morph is conspecific with lowland striped counterparts. Therefore, the definition of *R. variabilis* is greatly expanded to include most frogs which were (prior to this revision) referred to as *R. ventrimaculata*. (iv) Phylogenetic and bioacoustic evidence support the retention of *R. amazonica* as a valid species related to *R. variabilis* as defined in this paper. Based on phylogenetic data, *R. amazonica* appears to be distributed throughout much of the lower Amazon, as far east as French Guiana and the Amazon Delta and as far west as Iquitos, Peru. (v) Behavioral and morphological data, as well as phylogenetic data which includes topotypic material of *R. sirensis* and numerous samples of *R. lamasi*, suggest that the names *sirensis, lamasi* and *biolat* are applicable to a single, widespread species that displays considerable morphological variation throughout its range. The oldest available name for this group is *sirensis* Aichinger; therefore, we expand the definition of *R. sirensis*. (vi) *Ranitomeya ignea* and *R. intermedia,* elevated to the species status in a previous revision, are placed as junior synonyms of *R. reticulata* and *R. imitator,* respectively. (vii) *Ranitomeya rubrocephala* is designated as *nomen dubium*.

In addition to taxonomic changes, this revision includes the following: (i) Explicit definitions of species groups that are consistent with our proposed taxonomy. (ii) A comprehensive dichotomous key for identification of 'small' aposematic poison frogs of South and Central America. (iii) Detailed distribution maps of all *Ranitomeya* species, including unpublished localities for most species. In some cases, these records result in substantial range extensions (e.g., *R. uakarii, R. fantastica*). (iv) Tadpole descriptions for *R. amazonica, R. flavovittata, R. imitator, R. toraro* sp. nov., *R. uakarii* and *R. variabilis;* plus a summary of tadpole morphological data for *Andinobates* and *Ranitomeya* species. (v) A summary of call data on most members of *Andinobates* and *Ranitomeya,* including call data of several species that have not been published before. (vi) A discussion on the continued impacts of the pet trade on poison frogs (vii) A discussion on several cases of potential Müllerian mimicry within the genus *Ranitomeya*. We also give opinions regarding the current debate on recent taxonomic changes and the use of the name *Ranitomeya*.

Key words: *Andinobates* gen. nov.*, Dendrobates, Ranitomeya toraro* sp. nov., systematics, Müllerian mimicry, phylogenetics

Resumen

Se hace una revisión del género de ranas venenosas neotropicales *Ranitomeya*, con el resultado de un nuevo género, una nueva especie, cinco sinonimias y una especie clasificada como *nomen dubium*. Presentamos una filogenia molecular amplia que contiene 235 terminales, de los cuales 104 son nuevos para este estudio. Las adiciones más importantes en este estudio incluyen a siete de las 12 especies del grupo *minuta*, 15 de *Ranitomeya amazonica*, 20 de *R. lamasi*, dos de *R. sirensis*, 30 de *R. ventrimaculata* y siete de *R. uakarii*.

Los pasados estudios han distinguido por un largo tiempo dos grupos de especies distintos, recíprocamente monofiléticos dentro del género *Ranitomeya*, sensu Grant *et al.* 2006: El grupo *ventrimaculata*, distribuido a lo largo de gran parte de la amazonia y el grupo *minuta*, del norte de los Andes y Centroamérica. Restringimos *Ranitomeya* al grupo *ventrimaculata* y erigimos un nuevo género, *Andinobates* Twomey, Brown, Amézquita & Mejía-Vargas **gen. nov**., para los miembros del grupo *minuta*. Se incluyen además los siguientes resultados taxonómicos mayores en esta revisión: (i) Se describe una nueva especie, *Ranitomeya toraro* Brown, Caldwell, Twomey, Melo-Sampaio & Souza **sp. nov.**, del occidente de Brasil. Esta especie ha sido por largo tiempo conocida como *R. ventrimaculata*, pero nuevos datos morfológicos y filogenéticos la sitúan como la especie hermana de *R. defleri*. (ii). El examen del holotípo de *R. ventrimaculata* reveló que este especímen es, de hecho, un miembro de lo que actualmente se conoce como *R. duellmani*, por lo que *Dendrobates du-*

ellmani Schulte 1999 se considera aquí como un sinónimo junior de *D. ventrimaculatus* Shreve 1935 (= *R. ventrimaculata*). (iii) Para las ranas que estaban siendo llamadas *R. ventrimaculata* antes de esta revisión, el nombre más antiguo y por tanto aplicable es *R. variabilis*. Mientras que las definiciones anteriores de *R. variabilis* la restringían a las ranas con puntos de tierras altas cerca a Tarapoto, nuestros datos sugieren que estas ranas son conespecíficas a sus contrapartes con líneas de tierras bajas. Por lo tanto, la definición de *R. variabilis* se expande ampliamente y se sugiere incluir muchas de las ranas que eran (anteriormente a esta revisión) referidas a *R. ventrimaculata.* (iv) La evidencia filogenética y bioacustica soporta la conservación de *R. amazonica* como una especie válida, aunque relacionada a otras. Basado en evidencia filogenética, *R. amazonica* parece distribuirse a lo largo de mucho del bajo Amazonas, de Guyana Francesa y el delta del Amazonas al occidente y desde Iquitos, Perú al occidente. (v) La evidencia comportamental y morfológica, aunada a nuestros resultados de análisis filogenéticos, que incluyen material topotípico de *R. sirensis*, así como numerosas muestras de *R. lamasi*, sugieren que los nombres *sirensis*, *lamasi* y *biolat* son aplicables a una única especie, ampliamente extendida, que muestra una variación morfológica considerable a lo largo de su distribución. El nombre más antiguo disponible para este grupo es *sirensis* Aichinger; por lo tanto, ampliamos la definición de *R. sirensis*. (vi) *Ranitomeya ignea* y *R. intermedia*, que fueron elevadas al nivel de especie en una revisión previa, son puestas como sinónimos junior de *R. reticulata* y *R. imitator* respectivamente. (vii) Se designa a *Ranitomeya rubrocephala* como *nomen dubium*.

En adición a los cambios taxonómicos, esta revisión incluye lo siguiente: (i) Definiciones explícitas de los grupos de especies que son consistentes con nuestra taxonomía propuesta. (ii) Una clave dicotómica completa para la identificación de ranas aposemáticas "pequeñas" de sur y centro América. (iii) Mapas de distribución detallados para todas las especies de *Ranitomeya*, que incluyen localidades no publicadas para muchas especies. En algunos casos, estos reportes proporcionan extensiones de rango considerables (por ejemplo *R. uakarii* y *R. fantastica*). (iv) Descripciones de los renacuajos de *R. amazonica, R. flavovittata, R. imitator, R. toraro* Brown, Caldwell, Twomey, Melo-Sampaio & Souza sp. nov., *R. uakarii* y *R. variabilis;* además de un compendio de los datos de morfología larvaria para las especies de *Andinobates* y *Ranitomeya*. (v) Una recopilación de los cantos de muchos de los miembros de *Andinobates* y *Ranitomeya*, que incluye los cantos de muchas especies que no habían sido publicadas. (vi) Una discusión sobre los impactos continuos del comercio de animales en las ranas venenosas. (vii) Introducimos varios casos potenciales de mímica Mülleriana dentro del género *Ranitomeya*. Además, opinamos acerca del debate actual sobre los recientes cambios taxonómicos y el uso del nombre *Ranitomeya*.

Resumo

Os sapos venenosos neotropicais do gênero *Ranitomeya* são revisados aqui, resultando em um novo gênero, uma nova espécie, cinco sinonímias e uma das espécies classificadas como *nomen dubium*. Apresentamos uma filogenia molecular expandida que contém 235 terminais, 104 dos quais são novos para este estudo. Incluem a essa filogenia adições notáveis para sete das 12 espécies do grupo *minuta*, 15 *Ranitomeya amazonica*, 20 *R. lamasi*, dois *R. sirensis*, 30 *R. ventrimaculata* e sete *R. uakarii*.

Outros pesquisadores já haviam reconhecido por muito tempo dois grupos reciprocamente distintos, de espécies monofiléticas contidas em *Ranitomeya* sensu Grant *et al.* 2006: o grupo *ventrimaculata*, que é distribuído pela maior parte da Amazônia, e o grupo *minuta* do norte dos Andes e da América Central. Nós restringimos *Ranitomeya* ao grupo *ventrimaculata* e elevamos um novo gênero, *Andinobates* Twomey, Brown, Amézquita & Mejía-Vargas **gen. nov.**, para os membros do grupo *minuta*. Outros importantes resultados taxonômicos da revisão em curso incluem: (i) Uma nova espécie, *Ranitomeya toraro* Brown, Caldwell, Twomey, Melo-Sampaio & Souza **sp. nov.**, é descrita para o Brasil ocidental. Esta espécie tem sido referida como *R. ventrimaculata*, mas novos dados morfológicos e filogenéticos colocam-na como espécie-irmã de *R. defleri*. (ii) O exame do holótipo de *R. ventrimaculata* revelou que o espécime é na verdade um membro do que é atualmente designado como *Dendrobates.duellmani* Schulte 1999, portanto, este é considerado aqui como sinônimo júnior de *D. ventrimaculatus* Shreve 1935. (iii) Para os anuros que estavam sendo chamados *R. ventrimaculata* antes desta revisão, o nome mais antigo disponível e, portanto, aplicável é *R.variabilis*. Considerando que as definições anteriores de *R. variabilis* eram restritas aos sapos manchados de altitude próxima a Tarapoto, Peru, nossos dados sugerem que estes sapos são da mesma espécie que seus homólogos listrados da planície. Portanto, a definição de *R. variabilis* é expandida e sugerimos incluir a maioria dos anuros que estavam (antes desta revisão) designados como *R. ventrimaculata*. (iv) Evidências bioacústicas e filogenéticas apoiam a manutenção de *R. amazonica* como uma espécie válida, mas com espécies relacionadas. Baseado em dados filogenéticos, *R. amazonica* parece ser distribuída em grande parte do baixo Amazonas, a leste, até a Guiana Francesa e do delta do Amazonas e no extremo oeste, até Iquitos, no Peru. (v) Dados morfológicos, comportamentais e análises filogenéticas dos nossos resultados, que incluem material topotípico de *R. sirensis* bem como numerosas amostras de *R. lamasi*, sugerem que os nomes *sirensis*, *lamasi* e *biolat* são aplicáveis a uma única espécie que apresenta ampla variação morfológica em toda a sua dsitribuição. O nome mais antigo disponível para este grupo é *Ranitomeya sirensis* Aichinger, portanto, podemos expandir a definição de *R.sirensis*. (vi) *Ranitomeya ignea* e *R. intermedia*, elevadas ao status de espécies em uma revisão anterior, são colocadas como sinônimos júnior de *R. reticulata* e *R.imitator*, respectivamente. (vii) *Ranitomeya rubrocephala* é designada como *nomen dubium*.

Além de mudanças taxonômicas, esta revisão inclui: (i) definições de grupos de espécies que são consistentes com a nossa taxonomia proposta. (ii) Uma chave para a identificação completa de 'pequenos' sapos venenosos aposemáticos da América Central e do Sul. (iii) Mapas de distribuição detalhada de todas as espécies de *Ranitomeya*, incluindo locais inéditos para a maioria das espécies. Em alguns casos, esses registros resultam no conjunto de extensões substanciais (para *R. uakarii*, *R. fantastica* por exemplo). (iv) Descrição dos girinos de *R. amazonica*, *R. flavovittata*, *R. imitator*, *R. toraro* sp. nov., *R. uakarii* e *R. variabilis* acrescido de um resumo dos dados morfológicos do girino para as espécie de *Andinobates* e *Ranitomeya*. (v) Um resumo dos dados das vocalizações da maioria dos membros *Andinobates* e *Ranitomeya* incluindo dados de vocalização de várias espécies que não tinham sido publicadas antes. (vi) Uma discussão sobre os impactos da continuidade do comércio de sapos venenosos como animais de estimação (vii) Introduzimos vários casos de potencial mimetismo Mülleriano dentro do gênero *Ranitomeya*. Também opinamos a respeito do debate atual sobre as recentes mudanças taxonômicas e o uso do nome *Ranitomeya*.

Résumé

La révision de la systématique des grenouilles vénéneuses du genre *Ranitomeya* résulte en un nouveau genre, une nouvelle espèce, cinq synonymes, et une espèce classifiée en tant que *nomen dubium*. Nous présentons une phylogénie moléculaire élargie contenant 235 terminaux, dont 104 sont exclusifs à cette étude. Parmi les ajouts notables à cette phylogénie il y a l'inclusion de sept des 12 espèces du groupe *minuta*, 15 *Ranitomeya amazonica*, 20 *R. lamasi*, deux *R. sirensis*, 30 *R. ventrimaculata* et sept *R. uakarii*.

Les scientifiques reconnaissent depuis longtemps deux groupes d'espèces distincts, caractérisés par leur monophylie réciproque, au sein du genre *Ranitomeya* sensu Grant *et al.* 2006: le groupe *ventrimaculata* distribué en Amazonie, et le groupe *minuta* du nord des Andes et de l'Amérique Centrale. Nous restreignons le genre *Ranitomeya* au groupe *ventrimaculata* et créons un nouveau genre, Twomey, Brown, Amézquita & Mejía-Vargas **gen. nov.**, pour les membres du groupe *minuta*. Parmi les changements taxonomiques majeurs découlant de la présente révision, il est à souligner : (i) Une nouvelle espèce, *Ranitomeya toraro* Brown, Caldwell, Twomey, Melo-Sampaio & Souza **sp. nov.**, provenant de l'ouest du Brésil est décrite. Cette espèce a longtemps été définie comme étant *R. ventrimaculata* mais de nouvelles données morphologiques et phylogénétiques la situent comme étant une espèce sœur de *R. defleri*. (ii) La réexamination de l'holotype de *R. ventrimaculata* a révélé que ce spécimen fait parti du groupe connu comme étant *R. duellmani*, et de fait, *Dendrobates duellmani* Schulte 1999 est considéré comme étant un synonyme de *D. ventrimaculatus* Shreve 1935. (iii) Pour les grenouilles appelées *R. ventrimaculata* avant cette révision, le plus vieux nom disponible, et de ce fait applicable, est *R. variabilis*. Alors que *R. variabilis* était antérieurement caractérisé comme étant une grenouille réticulée provenant des hautes altitudes près de Tarapoto, nos données suggèrent que ces grenouilles sont conspécifiques avec leurs congénères lignés et distribués dans les basses terres. Ainsi, la définition de *R. variabilis* est grandement élargie, suggérant que la majorité des grenouilles définies (avant cette étude) en tant que *R. ventrimculata* sont en fait des *R. variabilis*. (iv) Les données phylogénétiques et bioacoustiques maintiennent *R. amazonica* comme étant une espèce distincte, proche de *R. variabilis* tel que défini dans cet article. Selon ces données phylogénétiques, la distribution de *R. amazonica* semble s'étendre sur la majorité de l'Amazonie : de la Guyane Française et du delta du fleuve Amazone, jusqu'à Iquitos au Pérou. (v) Des données comportementales, morphologiques, ainsi que nos analyses phylogénétiques, incluant du matériel topotypique de *R. sirensis* ainsi que de nombreux échantillons de *R. lamasi*, suggèrent que les noms *sirensis*, *lamasi* et *biolat* sont applicables à une seule et même espèce ayant une grande distribution et démontrant de grandes variations morphologiques. Le nom le plus ancien pour ce groupe est *sirensis* Aichinger; nous élargissons donc la définition de *R. sirensis*. (vi) *Ranitomeya ignea* et *R. intermedia*, élevés au statut d'espèce dans une révision antérieure, sont classés comme étant des synonymes juniors de *R. reticulata* et *R. imitator* respectivement. (vii) *Ranitomeya rubrocephala* est désigné *nomen dubium*.

En plus des changements taxonomiques, cette révision inclut : (i) Des définitions explicites des différents groupes d'espèces définis dans la taxonomie proposée. (ii) Une clé dichotomique permettant l'identification de ces 'petites' grenouilles aposématiques d'Amérique Central et du Sud. (iii) Des cartes de distributions détaillées pour les différentes espèces de *Ranitomeya*, incluant de nouvelles localités pour la majorité des espèces. Dans certains cas, l'aire de répartition est substantiellement élargie (e.g., *R. uakarii*, *R. fantastica*). (iv) La description des têtards de *R. amazonica*, *R. flavovittata*, *R. imitator*, *R. toraro* sp. nov., *R. uakarii* et *R. variabilis*; ainsi qu'un résumé des données morphologiques pour les espèces d'*Andinobates* et *Ranitomeya*. (v) Un résumé des données de chants pour la majorité des membres des genres *Andinobates* et *Ranitomeya*, incluant des données jamais publiées auparavant pour plusieurs espèces. (vi) Une discussion de l'impact qu'a le braconnage des grenouilles vénéneuses qui sont destinées au marché animalier. (viii) La mention de plusieurs cas potentiels de mimétisme Müllerien au sein du genre *Ranitomeya*. Nous donnons également notre opinion en ce qui concerne le débat sur les changements taxonomiques récents et de l'utilisation du nom *Ranitomeya*.

Introduction

Difficulties of *Ranitomeya* taxonomy

In the early 1970s, as a graduate student, Philip A. Silverstone sorted through countless jars of small Neotropical frogs with the daunting task of clarifying the taxonomy of aposematic poison dart frogs (family Dendrobatidae). Many of the frogs he worked with and allocated to the genus *Dendrobates* are now considered to be members of the more recently erected genus *Ranitomeya*, a species-rich group of poison frogs characterized by their diminutive size. The initial classifications of members of *Ranitomeya*, without genetic, behavioral, or acoustic data, would have been extremely difficult. Therefore, it is easy to understand why early workers were careful and 'lumped' every small Amazonian specimen with pale limb reticulation under the single name *Dendrobates quinquevittatus*, which was suggested to be a highly variable species that exhibited a cline of morphology (see Fig. 14 in Silverstone 1975). Such levels of variation were certainly not unheard of in poison frogs. For example, *Oophaga pumilio*, *O. histrionica*, *Dendrobates tinctorius*, and *D. auratus* display dramatic levels of phenotypic variation over their geographic ranges— the alpha-taxonomic status of each of these species continues to be widely accepted today (e.g., Lötters *et al.* 2007). In 1982, Myers wrote that:

> *New material, as well as closer attention to morphological details and evidence of sympatry, convinces me that* Dendrobates quinquevittatus *Steindachner,* sensu *Silverstone, is a composite of five or more species of distinctively colored frogs.*
>
> C.W. Myers 1982, p. 3

Interestingly, almost a decade later, Caldwell & Myers (1990) would point out that, in fact, none of those species was actually *Dendrobates quinquevittatus* sensu stricto. They stated that:

> *Myers erred in concluding that the restricted* quinquevittatus *remained "indeed a widespread and variable species." We correct that mistake by further restricting the name* Dendrobates quinquevittatus *Steindachner to a not particularly variable species confined to the southwestern section of Amazonia and by formally resurrecting the name* Dendrobates ventrimaculatus *Shreve for the residue of what recently has been called* quinquevittatus*. We emphasize that* Dendrobates ventrimaculatus *sensu lato becomes the new composite species of this complex, but we urge caution in dealing with it systematically. We are aware that* "ventrimaculatus" *contains more than one species, some of which may be difficult to separate even when sympatric…Attempts at taxonomic diagnosis based on literature and/or terrarium specimens of vague provenance seem likely to be fruitless at best… or, more seriously, to create needless confusion arising from nomenclatural irresponsibility.*
>
> J.P. Caldwell & C.W. Myers 1990, p. 11

Today, 13 species are recognized that were considered by Silverstone (1975) as *D. quinquevittatus*. *Dendrobates quinquevittatus* is just one example of how this group has perplexed taxonomists for the last half-century, and, despite the fact that many researchers have suspected that this group was composed of many more species (e.g., Myers 1982; Caldwell & Myers 1990; Noonan & Wray 2006; Brown *et al.* 2006; Twomey & Brown 2009), defining species boundaries has proven to be extremely difficult. This confusion, naturally, slowed the rate at which species have been described (Fig. 1). Furthermore, this group's variation appeared to be limitless, with every unexplored valley or mountain seeming to contain new forms, many times muddling the distinction between previously distinct forms. Christmann (2004) lamented "From excursion to excursion, our desire to see the largest number of populations in their biotype increases. However, at the same time—with each new find, our feelings of helplessness grow. Will it ever be possible to recognize some kind of order in this multitude of species?" Myers (1982) commented "But we are gradually realizing that there always will be another poison frog to be sought on the next mountain or across the next river. So, the new names are offered in hope of encouraging others who find it interesting to pursue small frogs in obscure places." The vital piece of the *quinquevittatus* puzzle that was previously lacking was not morphological data (of which there was plenty), but acoustic, genetic and behavioral data, and firsthand experience with these species in their natural habitats throughout their entire ranges.

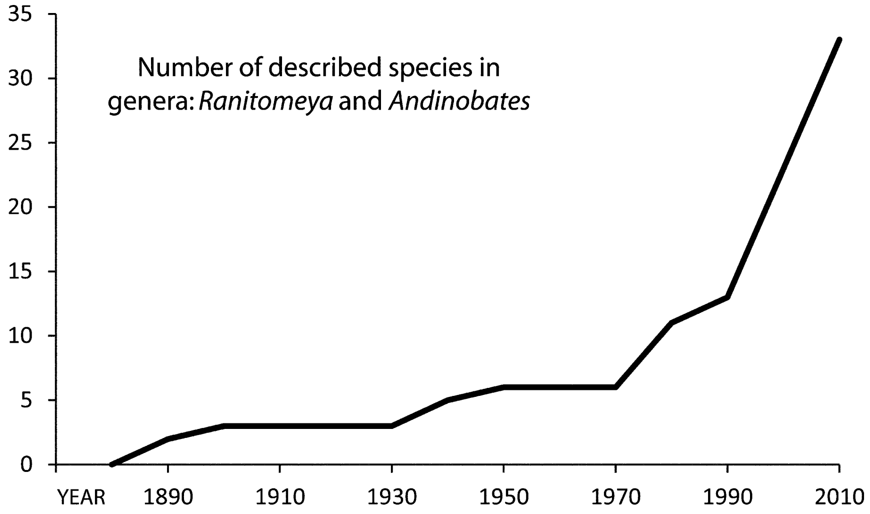

FIGURE 1. Accumulation of described species in genera *Ranitomeya* and *Andinobates*.

This last point is particularly crucial because most of the alpha-taxonomic problems in *Ranitomeya* stem from the fact that many species could not be diagnosed with certainty based on coloration (or, at least, reliable characters were not apparent), and other diagnostic morphological characters (e.g., osteology) seemed to be insufficiently variable for diagnoses below the genus level. Many species show extensive variation between populations (e.g., *R. imitator, R. fantastica, R. amazonica*), whereas other species display only subtle differences when compared to their sister taxa (e.g., *R. flavovittata* and *R. vanzolinii*).

One cause for the varying levels of intraspecific diversity in Amazonian species (and resulting taxonomic confusion), is due to at least one, and perhaps multiple, occurrences of Müllerian mimicry (see Symula *et al.* 2001 and the mimicry section in discussion of this paper). For example, in some localities in north-central Peru, three species have converged (at least partially) on a single phenotype (i.e., *Ranitomeya imitator, R. variabilis* sensu this paper and *R. fantastica* near Pongo de Cainarachi, Department San Martin), making it easier for local predators to recognize the similarly toxic species (Ruxton *et al.* 2004). On the other hand, nearby populations of the same species appear so dissimilar (having converged on the color and pattern of a different model species) that they are not easily identified as conspecific unless acoustic and genetic data are available.

This group's taxonomic classification was further complicated by the shy nature of many species and their typically high species diversity at any given site, with two to three species usually occurring in sympatry, often appearing similar in color and pattern. Furthermore, in many species, advertisement calls can be easily overlooked, often being quiet, infrequent, and insect-like. Nevertheless, advertisement calls are important characters in the classification of the main groups within *Ranitomeya* (see Table 5; Erdtmann & Amézquita 2009). In addition, the size of a species' distribution seems to bear little significance in determining specific units, and some species appear to have extremely small ranges (e.g., *R. summersi*), whereas other species appeared to be distributed across much of the Amazon, from French Guiana to Peru (e.g., *R. amazonica* and *R. uakarii*).

Recently, the use of molecular phylogenetics has elucidated many of these problems and in some instances exposed flaws in previously accepted taxonomies (see for example the species accounts of *R. ventrimaculata*, *R. variabilis*, *R. sirensis* in this paper). Using these methods, researchers have been able to focus their taxonomic studies on closely related species groups, rather than higher-level groups that may have been easier to diagnose based on morphology.

History of *Ranitomeya*

George A. Boulenger, more than a century ago, described the first species in this group, *Dendrobates fantasticus* and *D. reticulatus* (Boulenger 1884 "1883"). In 1975, Philip A. Silverstone published the first comprehensive monograph dealing with specific relationships of the genus *Dendrobates* (a group containing *Ranitomeya* sensu Grant *et al.* 2006). Using adult and tadpole morphology he proposed the *minutus* group, containing six species:

altobueyensis, fulguritus, minutus, opisthomelas, *quinquevittatus* and *steyermarki*. The main characters used to define this group were larval: emarginate (laterally indented) oral disc and dextral anus (though he lacked data for *quinquevittatus* and *steyermarki*). Soon after, Charles W. Myers and John W. Daly began publishing their seminal research on the systematics of Central and South American dendrobatids. Their addition of alkaloid profiles, vocalization data and behavioral data to traditional taxonomic methods clarified many of the coarse relationships within this group and led to the description of numerous new species. In 1980, they described *Dendrobates bombetes* and resurrected *D. reticulatus*, assigning them and an undescribed species that was eventually named *D. claudiae* by Jungfer *et al.* (2000) to Silverstone's *minutus* group. Furthermore, they hypothesized that *abditus*, *bombetes* and *opisthomelas* formed a monophyletic group delimited by 'median gap that interrupts the papillate fringe on the posterior (lower) edge of the oral disc' (Myers & Daly 1980). Shortly after, Myers removed *D. fantasticus* from synonymy with *D. quinquevittatus* and placed *D. vanzolinii*, *D. fantasticus*, *D. captivus*, *D. quinquevittatus*, and *D. reticulatus* (removing the latter two from the *minutus* group) in a suggested monophyletic assemblage delimited by 'distinctively reticulated limbs,' which was dubbed the *quinquevittatus* group (Myers 1982).

Five years later, Myers placed the remaining members of the *minutus* group into a new genus, *Minyobates* (with *steyermarki* as the type species), based on the following characters: cephalic amplexus present, very small size (12–19.5 mm snout to vent length), oblique lateral stripe present (though he qualified this by noting that this feature is also absent in some *Minyobates*), and larvae with lateral indentations of the oral disc of the mouth and a dextral anus (Myers 1987). The establishment of a new genus was hurried to preceed the expected name *Ranitomeya*, which shortly after was coined by Luc Bauer, a Dutch amateur herpetologist, in a privately published paper (Bauer 1988). *Ranitomeya* at that time contained the former *Dendrobates* species *reticulatus* (as the type species), *captivus*, *fantasticus*, *imitator*, *mysteriosus*, *quinquevittatus* and *vanzolinii*, and was completely ignored in the scientific literature, presumably because it posed several problems under the International Code of Zoological Nomenclature (ICZN, see Grant *et al.* 2006 for a detailed discussion).

Caldwell & Myers (1990) further restricted *D. quinquevittatus* and the *quinquevittatus* group to *D. quinquevittatus* sensu stricto and its suggested sister taxon *D. castaneoticus*, united by their shared absence of the inner metacarpal tubercle. They placed this group as sister to the clade united by pale limb reticulation (i.e., *Ranitomeya* of Grant *et al.* 2006). This clade was referred to as the *ventrimaculatus* group, and it comprised all other members of the *quinquevittatus* group exclusive of *quinquevittatus* sensu stricto, but the authors did not propose additional synapomorphies to support this arrangement. More than a decade later, Rainer Schulte privately published a book on Peruvian dendrobatids in which he described five new species and proposed several novel systematic relationships, including the designation of eight species groups (Schulte 1999). His classifications did not consider much of the works of previous authors (not allowing him to classify all taxa in previously established groups) and some proposed groups were paraphyletic in the illustrated diagrams. More importantly, synapomorphies and the criteria from which the groups were designated were largely not mentioned. A fair scientific assessment of these groups cannot be made and these groups will not be considered herein (see Table 1); for a detailed discussion of Schulte's work see Lötters & Vences (2000).

In the late 1990s, Kyle Summers and collaborators started using molecular phylogenetics to look at the specific relationships among a few members of the genus *Ranitomeya* (Summers *et al.* 1997). Since, numerous studies have addressed the molecular phylogenetics of this group (e.g., Summers *et al.* 1999; Clough & Summers 2000; Vences *et al.* 2000; Symula *et al.* 2001, 2003; Santos *et al.* 2003, 2009; Darst & Cannatella 2004; Brown *et al.* 2006, 2008c; Grant *et al.* 2006; Noonan & Wray 2006; Roberts *et al.* 2006a; Twomey & Brown 2008).

Using primarily molecular phylogenetics, Grant *et al.* (2006) revised the entire family Dendrobatidae, dividing *Dendrobates* sensu Silverstone (1975) into five genera: *Adelphobates*, *Dendrobates*, *Minyobates*, *Oophaga*, and *Ranitomeya*. Grant *et al.* (2006) placed the former members of the *minutus* group sensu Myers (1982), minus *Minyobates steyermarki*, as well as most members of the *ventrimaculatus* group sensu Caldwell & Myers (1990), minus *captivus* and *mysteriosus*, in the genus *Ranitomeya* (an available name under the ICZN). Only *steyermarki* was retained in *Minyobates*. These placements were well supported by prior phylogenies (Vences *et al.* 2000, 2003; Noonan & Wray 2006; Roberts *et al.* 2006a). The definition of *Ranitomeya* contained 24 species (Table 1) and is currently the most widely accepted taxonomy for this group (though see below). In 2008, Twomey & Brown described a new genus, *Excidobates*, removing *captivus* from *Adelphobates* and placing it in its own group together with *mysteriosus* (an affinity originally suggested by Myers 1982), which was sister to the genus *Ranitomeya* (Twomey & Brown 2008). They also suggested that future taxonomies may be better off by restricting the use of

Ranitomeya to the *ventrimaculata* group sensu Caldwell & Myers (1990) and placing the *minuta* group into a separate, at that time, unnamed genus. Roberts *et al.* (2006a) and Twomey & Brown (2008), collectively, further subdivided the *ventrimaculata* group into three smaller groups: *reticulata*, *vanzolinii* and *ventrimaculata* (Table 1), in part to help accommodate the numerous new species being described within this genus.

More recently, in online supplemental material, Santos *et al.* (2009) proposed to synonymize *Adelphobates*, *Dendrobates*, *Excidobates*, *Minyobates*, *Oophaga* and *Ranitomeya* back into *Dendrobates*. We will use here the previously described taxonomy following Grant *et al.* (2006) and Twomey & Brown (2008). For further comments on this matter see discussion.

The genus *Ranitomeya* currently comprises two reciprocally monophyletic clades: the *minuta* group and a clade containing the *ventrimaculata*, *reticulata* and *vanzolinii* groups. The *minuta* group is trans-Andean; its members have long, rattle-like advertisement calls and typically possess dark limbs and coarsely blotched venters. The *ventrimaculata*, *reticulata* and *vanzolinii* groups comprise a motley clade of Amazonian frogs, most of which possess pale limb reticulation and some permutation of dorsolateral stripes.

Goals of This Paper

Based on results from our molecular phylogenetic analyses, accompanied by morphological (adult and larval), behavioral and acoustic data, and natural history information, we:

(i) restrict *Ranitomeya* to the *ventrimaculata*, *reticulata* and *vanzolinii* groups and redefine (in one case rename) these groups and erect a fourth species group. We also reevaluate the taxonomic status of all taxa contained within this genus, resulting in the description of one new species and the redefinitions of others, as well as several synonymies.

(ii) describe a new genus, *Andinobates*, for species in the *minuta* group. At the same time we restrict the *minuta* group to *claudiae* and *minuta* and erect two species groups for the remaining species in the new genus.

Materials and methods

Species examination. Measurements were made with mechanical calipers and a dissecting microscope to the nearest 0.01 mm following Myers (1982) and Brown *et al.* (2006): snout to 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 thighs extended at a 90 degree angle from body (respective to each side), forming a straight line between both (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 occipitum to tip of snout (HL), head width between tympanum (HW), body width under axilla (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 III just below disc (W3F). All tadpole measurements are in mm. All SVL measurements are based on adult individuals unless stated otherwise.

All voucher specimens morphologically examined in this paper were deposited in the Museu Paraense Emílio Goeldi and Ministério da Ciência e Tecnologia do Brasil, Belém, Pará, Brazil (MPEG) and in the Sam Noble Oklahoma Museum of Natural History, Norman, OK, USA (OMNH). As follows are abbreviations of museums mentioned: California Academy of Sciences, San Francisco, CA, USA (CAS); Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA (MCZ); Smithsonian National Museum of Natural History, Washington, DC, USA (USNM); Museo de Historia Natural 'Javier Prado' de la Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM); Natural History Museum, London, United Kingdom (NHML); Muséum d'histoire naturelle de la Ville de Genève, Geneva, Switzerland (MHNG); Natural History Museum, University of Kansas, Lawrence, KS, USA (KU); Centro de Ornitología y Biodiversidad, Surco-Lima, Peru (CORBIDI); Rainer Schulte Private Collection, Tarapoto, Peru (CRS); Naturhistorisches Museum Wien, Vienna, Austria (NHMW); Museum of Zoology of the University of São Paulo, São Paulo, Brazil (MZUSP); Museo de la Facultad de Ciencias Biológicas de la Universidad Nacional de la Amazonía Peruana, Iquitos, Peru (MZUNAP); Museum national d'histoire naturelle, Paris, France (MNHN); Los Angeles County Museum of Natural History, Los Angeles, CA, USA (LACM); Naturhistoriska Riksmuseet, Göteborg, Sweden (NHMG); Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany (SMNS); Pontificia Universidad Javeriana in Bogotá, Colombia (PUJB).

Tadpoles (n = 5) of *R. toraro* sp. nov were collected from the backs of male parent frogs, preserved in 10% formalin for description and staged according to Gosner (1960). All other tadpoles were from the following sources: the backs of male parent frogs or offspring of captive frogs from known localities (typically from parents that are F^2s; the tadpoles were either preserved, as described above, or measured alive). Tadpoles that were measured alive were anesthetized by placing a small drop of benzocaine on the top of head and allowed to recover after measurements. The Labial Tooth Row Formula (LTRF) follows Altig & McDiarmid (1999). Adult morphological characters used herein are the same as used in Grant *et al.* (2006) with the exception that we classify the stripe that extends longitudinally down the back (above the vertebral column) as the middorsal stripe versus medial stripe in Grant *et al.* (2006), see Figure 2.

An estimate of conservation priority based on IUCN Red List categories and criteria (2010) was performed for all species for which taxonomic classification changed considerably. The geographic range of *Ranitomeya* was predicted using the ecological niche modeling algorithm and software (employing default settings) Maxent 3.3.3c of Phillips *et al.* (2006). Climatic data for model building were obtained through the WORLDCLIM website (http://www.worldclim.org/).

DNA extraction, amplification and sequencing. Tissue samples, collected from toe clippings from adult frogs and from tips of tadpole tails, were preserved in a buffer solution of 20% DMSO saturated with sodium chloride and EDTA. Genomic DNA was extracted from tissue samples using the Qiagen DNeasy Tissue Kit. The cytochrome-b gene (*cytb*), 12S ribosomal RNA (*12S*) and 16S ribosomal RNA (*16S*) regions were amplified using the following primer sets for a total of 1011 base pairs: *cytb*: CB1-L, CB2-H (Kocher *et al.* 1989); KSCYB1(A)-L, KSCYB1-H (Clough & Summers 2000); *12S*: 12SA-L (Palumbi *et al.*1991), 12SK-H (Goebel *et al.*1999); *16S*: LGL 286, LGL 381 (Palumbi *et al.* 1991). All loci used are from the mitochondrial genome. PCR amplifications and DNA sequencing protocols followed Roberts *et al.* (2006b). Samples were sequenced in both directions and aligned using Sequencher version 1.4.0 (ABI 1995). Sequences in both the nuclear and mitochondrial analyses were aligned using MUSCLE 3.6 (Edgar 2004). All sequences were translated to confirm proper reading frame and absence of stop codons.

Mitochondrial phylogenetic analyses. Much of the sequence data used in this analysis were derived from previous studies (Summers *et al.* 1999; Clough & Summers 2000; Summers & Symula 2001; Santos *et al.* 2003; Symula *et al.* 2003; Darst & Cannatella 2004; Graham *et al.* 2004; Grant *et al.* 2006; Noonan & Wray 2006; Roberts *et al.* 2006a; Brown *et al.* 2008c, Santos *et al.* 2009). Newly determined sequences were deposited in Genbank under accession numbers JN651247–JN651274 and JN635752–JN635962 (see appendix I for details). Representative species of the genera *Colostethus*, *Hyloxalus* and *Phyllobates* (all sensu Grant *et al.* 2006) were used as outgroups for a phylogenetic analysis using Bayesian inference (Huelsenbeck & Ronquist 2001). The dataset was partitioned into codon-position specific sets of nucleotides (1st, 2nd, and 3rd positions for *cytb*, with a separate, single partition each for *12S* and *16S*). MrModeltest version 2.3 (Nylander 2004) was used to identify a substitution model, nucleotide frequencies and optimal priors for the gamma parameter and the proportion of invariant sites for each partition. Sequence data may better be explained by partitioning a dataset than by applying an average model across genes and codon positions, as indicated by higher model likelihood scores in partitioned analyses (Nylander *et al.* 2004). MrBayes version 3.1.1 (Huelsenbeck & Ronquist 2001) was run for 25 million generations using the following mixed models: *12S* (nst = 6, I+Γ), *16S* (nst = 6, I+ Γ), *cytb*-1st (nst = 1, equal), *cytb*-2nd (nst = 6, Γ), and *cytb*-3rd (nst = 6, Γ). All analyses were run in parallel on 8 CPUs, each chain on a separate processor, selected from available CPUs that are part of an 800+ cluster of computers at Duke University. Negative log-likelihood (-ln) scores were used to identify the burn-in phase at 12 million generations, after which all trees (n = 11,540) were summed. To ensure that the burn-in phase was properly defined in all runs, Bayesian parameter files were also analyzed in TRACER 1.3 (Rambout & Drummond 2006). The Bayesian analysis standard deviation of split frequencies reached < 0.01 to ensure consistency of the resulting tree topology.

Nuclear phylogenetic analyses. All the sequence data used in this analysis were derived from Grant *et al.* (2006). A total of 2262 characters were used from five nuclear genes/markers: rhodopsin exon 1 (*Rhod*), recombination activating gene 1 (*RAG1*), histone H3 (*H3*), 28S rDNA (*28S*) and seventh in absentia (*SIA*). Representative species of the genera *Hyloxalus* and *Phyllobates* were used as outgroups for a phylogenetic analysis using Bayesian inference, as described above. The dataset was partitioned into codon-position specific sets of nucleotides (1st, 2nd, and 3rd positions for *Rhod, RAG1*, *SIA* and *H3* with a separate, single partition for *28S*). MrModeltest version 2.3 (Nylander 2004) was used to identify a substitution model, nucleotide frequencies and optimal priors for the gamma parameter and the proportion of invariant sites for each partition. MrBayes version 3.1.1 (Huelsenbeck & Ronquist 2001) was run for 15 million generations using the following mixed models: *Rhod*-1st (nst = 1, equal), *Rhod*-2nd (nst = 1, equal), *Rhod*- 3rd (nst = 6, propinv), *RAG1*-1st (nst = 1, equal), *RAG1*-2nd (nst = 1, equal), *RAG1*-3rd (nst = 6, Γ), *SIA*-1st (nst = 1, equal), *SIA*-2nd (nst = 2, Γ), *SIA*-3rd (nst = 6, equal), *H3*-1st (nst = 1, equal), *H3*-2nd (nst = 2, Γ), *H3*-3rd (nst = 6, equal), and *28S* (nst = 1, I+Γ). Negative log-likelihood (-ln) scores were used to identify the burn-in phase at 4 million generations, after which all trees (n = 10,500) were summed. The Bayesian analysis standard deviation of split frequencies reached < 0.01 to ensure consistency of the resulting tree topology.

We also used Maximum Parsimony in PAUP* (Swofford 2002) to estimate the phylogenetic relationships using the same dataset. All resulting trees (n = 820) were used to generate a consensus tree.

Character state reconstructions. Character state reconstruction methods used to diagnose lineages was performed in PAUP* using ACCTRAN optimization (Swofford 2002). All unambiguous characters were mapped for the node of interest.

Monophyly testing. To test the monophyly of groups we used Bayes Factor Analyses (BFA). This method differs from other traditional tests because it does not offer a criterion for absolute rejection of a null hypothesis, but instead it evaluates the phylogenetic evidence in favor of the null hypothesis. Bayes factor analyses were done in MrBayes by generating constraint trees of each test topology. The constraint trees each consisted of a tree containing at least, two hypothetical clades (both polytomies), one of which is the test group (e.g., a genus), while the other consists of all other taxa included in the analysis. This arrangement resulted in an absolute prior (= 100) for test topology. The predictive value of the constrained post burn-in harmonic mean likelihoods (H_0) were then compared to the original, unconstrained post burn-in likelihoods (H_A) using a Bayes factor comparison: 2 (Harmonic Mean Ln Likelihood H_A − Harmonic Mean Ln Likelihood H_0; Kass & Raftery 1995). Values above 10 were interpreted as strong evidence against H_0. Values between 0 and 10 were interpreted as support for both hypotheses, and values less than 0 were interpreted as support against H_A (Kass & Raftery 1995; Brandley *et al.* 2005; Suchard *et al.* 2005).

Recent criticisms have challenged the use of harmonic means to calculate the marginal likelihood for model estimation; in particular, harmonic means can favor more parameter-rich models (Lartillot & Philippe 2006) and they can possess a systematic bias capable of significantly skewing Bayes factors (Calderhead & Girolami 2009). Given that the calculation of more robust estimates of the marginal likelihood (i.e., thermodynamic integration and path sampling) is statistically non-trivial, we chose to continue to use harmonic means, though we limit our interpretation of these results. Further, we compared our results to other published studies using other tests of monophyly. In many cases the estimated marginal likelihoods varied considerably for hypotheses regarding a particular clade: the hypothesis most similar to our unconstrained topology had an estimated marginal likelihood similar to the unconstrained tree and those with more dramatic changes were much larger.

We evaluated the following 16 hypotheses (Table 2) using BFA: H_1, *Ranitomeya* and *Andinobates* as reciprocally monophyletic clades using the nuclear dataset; H_2, *Ranitomeya* (sensu this paper) monophyletic; H_3, *Andinobates* monophyletic; H_4, *Andinobates* sister to *Excidobates*; H_5, *Andinobates* sister to the *vanzolinii* group; H_6, *Andinobates* sister to a clade comprising the *defleri*, *ventrimaculata* and *reticulata* groups; H_7, *Ranitomeya biolat* and *R. lamasi* (including *R. sirensis*) as reciprocally monophyletic clades; H_8, *R. biolat* within *R. lamasi* (including *R. sirensis*); H_9, *R. sirensis* and *R. lamasi* (including *R. biolat*) as reciprocally monophyletic clades; H_{10}, *R. sirensis* within *R. lamasi* (including *R. biolat*); H_{11}, *R. ventrimaculata* (sensu this paper) monophyletic; H_{12}, *R. amazonica* (sensu this paper) monophyletic; H_{13}, *R. variabilis* (containing only individuals from Cainarachi Valley) monophyletic; H_{14}, *R. variabilis* and *R. variabilis cf.* (all spotted *R. ventrimaculata*) monophyletic; H_{15}, *R. amazonica* individuals from French Guiana and all other *R. amazonica* individuals as reciprocally monophyletic sister clades; H_{16}, *R. flavovittata* monophyletic.

TABLE 1A (continued on next page). Currently accepted taxa (based on Frost *et al.* 2011). History of alpha-taxonomic and species group (in parentheses) classification of taxa in the genera *Ranitomeya* and *Andinobates*. *Dendrobates (minutus)** = by implication, "+" species which were not described at the time of classification, "*" species which were not acknowledged by the authors.

Specific Epithet	Description (authors and date)	Classification: Genus (group)			
		Silverstone 1975	Myers & Daly 1980	Myers 1982	Myers 1987
fantasticus	Boulenger, 1884 “1883”	*Dendrobates* (*minutus*)* Fig. 14: I, h?, l, m	*	*Dendrobates (quinquevittatus)*	*Dendrobates (quinquevittatus)*
reticulatus	Boulenger, 1884 “1883”	*Dendrobates (minutus)** Fig. 14: a, b, c	*Dendrobates (minutus)*	*Dendrobates (quinquevittatus)*	*Dendrobates (quinquevittatus)*
opisthomelas	Boulenger, 1899	*Dendrobates (minutus)*	*Dendrobates (minutus)*	*Dendrobates (minutus)*	*Minyobates*
minutus	Shreve, 1935	*Dendrobates (minutus)*	*Dendrobates (minutus)*	*Dendrobates (minutus)*	*Minyobates*
ventrimaculatus	Shreve, 1935	*Dendrobates (minutus)** Fig. 14 j	*	*	*
igneus	Melin, 1941	*Dendrobates (minutus)** pg. 34	*	*	*
altobueyensis	Silverstone, 1975	*Dendrobates (minutus)*	*Dendrobates (minutus)*	*Dendrobates (minutus)*	*Minyobates*
fulguritus	Silverstone, 1975	*Dendrobates (minutus)*	*Dendrobates (minutus)*	*Dendrobates (minutus)*	*Minyobates*
abditus	Myers & Daly, 1976	+	*Dendrobates (minutus)*	*Dendrobates (minutus)*	*Minyobates*
vanzolinii	Myers, 1982	*Dendrobates (minutus)** Fig. 14 e	+	*Dendrobates (quinquevittatus)*	*Dendrobates (quinquevittatus)*
viridis	Myers & Daly, 1976	+	*Dendrobates (minutus)*	*Dendrobates (minutus)*	*Minyobates*
bombetes	Myers & Daly, 1980	+	*Dendrobates (minutus)*	*Dendrobates (minutus)*	*Minyobates*
imitator	Schulte, 1988	+	+	+	+
variabilis	Zimmermann & Zimmermann, 1988	+	+	+	+
sirensis	Aichinger, 1991	+	+	+	+
biolat	Morales, 1992	+	+	+	+
lamasi	Morales, 1992	+	+	+	+
virolinensis	Ruiz-Carranza & Ramírez-Pinilla, 1992	+	+	+	+
amazonicus	Schulte, 1999	+	+	+	+
duellmani	Schulte, 1999	+	+	+	+
flavovittatus	Schulte, 1999	+	+	+	+
intermedius	Schulte, 1999	+	+	+	+
rubrocephalus	Schulte, 1999	+	+	+	+
claudiae	Jungfer, Lötters & Jörgens, 2000	+	*Dendrobates (minutus)**	*Dendrobates (minutus)**	*Minyobates**
daleswansoni	Rueda-Almonacid, Rada, Sánchez-Pacheco, Velásquez-Álvarez & Quevedo-Gil, 2006	+	+	+	+
dorisswansonae	Rueda-Almonacid, Rada, Sánchez-Pacheco, Velásquez-Álvarez & Quevedo-Gil, 2006	+	+	+	+
uakarii	Brown, Schulte & Summers, 2006	*Dendrobates (minutus)** pg. 34	+	+	+
tolimense	Bernal-Bautista, Luna-Mora, Gallego & Quevedo-Gil, 2007	+	+	+	+
benedicta	Brown, Twomey, Pepper & Sanchez-Rodriguez, 2008	*Dendrobates (minutus)** Fig. 14 k	+	+	+
summersi	Brown, Twomey, Pepper & Sanchez-Rodriguez, 2008	*Dendrobates (minutus)** Fig. 14: h?, g	+	+	+
cyanovittata	Perez-Peña, Chavez, Twomey & Brown, 2010	+	+	+	+
defleri	Twomey & Brown, 2009	*Dendrobates (minutus)** Fig. 14 f	+	+	+
yavaricola	Perez-Peña, Chavez, Twomey & Brown, 2010	+	+	+	+
steyermarki	Rivero, 1971	*Dendrobates (minutus)*	*Dendrobates (minutus)*	*Dendrobates (minutus)*	*Minyobates*
quinquevittatus	Steindachner, 1864	*Dendrobates (minutus)*	*Dendrobates (minutus)*	*Dendrobates (quinquevittatus)*	*Dendrobates (quinquevittatus)*

TABLE 1B (continued from previous page).

Specific Epithet	Classification: Genus (group)					Current alpha-taxonomic status
	Caldwell & Myers 1990	Schulte 1999	Grant *et al.* 2006	Twomey & Brown 2008	This paper	
fantasticus	*Dendrobates (ventrimaculatus)*	*Dendrobates* (Group 1)	*Ranitomeya (ventrimaculata)*	*Ranitomeya (reticulata)*	*Ranitomeya (reticulata)*	*fantastica*
reticulatus	*Dendrobates (ventrimaculatus)*	*Dendrobates* (Group 6)	*Ranitomeya (ventrimaculata)*	*Ranitomeya (reticulata)*	*Ranitomeya (reticulata)*	*reticulata*
opisthomelas	*Minyobates*	*	*Ranitomeya (minuta)*	*	*Andinobates (bombetes)*	*opisthomelas*
minutus	*Minyobates*	*	*Ranitomeya (minuta)*	*Ranitomeya (minuta)*	*Andinobates (minutus)*	*minutus*
ventrimaculatus	*Dendrobates (ventrimaculatus)*	*Dendrobates* (Group 5)	*Ranitomeya (ventrimaculata)*	*Ranitomeya (ventrimaculata)*	*Ranitomeya (ventrimaculata)*	*ventrimaculata*
igneus	*	*	*Ranitomeya (ventrimaculata)*	*	*Ranitomeya (reticulata)*	*reticulata*
altobueyensis	*Minyobates*	*	*Ranitomeya (minuta)*	*	*Andinobates (fulguritus)*	*altobueyensis*
fulguritus	*Minyobates*	*	*Ranitomeya (minuta)*	*Ranitomeya (ventrimaculata)*	*Andinobates (fulguritus)*	*fulguritus*
abditus	*Minyobates*	*	*Ranitomeya (minuta)*	*	*Andinobates (bombetes)*	*abditus*
vanzolinii	*Dendrobates (ventrimaculatus)*	*Dendrobates* (Group 4)	*Ranitomeya (ventrimaculata)*	*Ranitomeya (vanzolinii)*	*Ranitomeya (vanzolinii)*	*vanzolinii*
viridis	*Minyobates*	*	*Ranitomeya (minuta)*	*	*Andinobates (fulguritus)*	*viridis*
bombetes	*Minyobates*	*	*Ranitomeya (minuta)*	*	*Andinobates (bombetes)*	*bombetes*
imitator	*	*Dendrobates* (Group 3)	*Ranitomeya (ventrimaculata)*	*Ranitomeya (vanzolinii)*	*Ranitomeya (vanzolinii)*	*imitator*
variabilis	*Dendrobates (ventrimaculatus)*	*Dendrobates* (Group 1)	*Ranitomeya (ventrimaculata)*	*Ranitomeya (ventrimaculata)*	*Ranitomeya (ventrimaculata)*	*variabilis*
sirensis	$^{+}$	*Dendrobates* (Group 6)	*Ranitomeya (ventrimaculata)*	*Ranitomeya (vanzolinii)*	*Ranitomeya (vanzolinii)*	*sirensis*
biolat	$^{+}$	*Dendrobates* (Group 4)	*Ranitomeya (ventrimaculata)*	*Ranitomeya (vanzolinii)*	*Ranitomeya (vanzolinii)*	*sirensis*
lamasi	$^{+}$	*Dendrobates* (Group 4)	*Ranitomeya (ventrimaculata)*	*Ranitomeya (vanzolinii)*	*Ranitomeya (vanzolinii)*	*sirensis*
virolinensis	$^{+}$	*Dendrobates* (Group 6)	*Ranitomeya (minuta)*	*	*Andinobates (bombetes)*	*virolinensis*
amazonicus	$^{+}$	*Dendrobates* (Group 1)	*Ranitomeya (ventrimaculata)*	*Ranitomeya (ventrimaculata)*	*Ranitomeya (ventrimaculata)*	*amazonica*
duellmani	$^{+}$	*Dendrobates* (Group 1)	*Ranitomeya (ventrimaculata)*	*Ranitomeya (reticulata)*	*Ranitomeya (reticulata)*	*ventrimaculata*
flavovittatus	$^{+}$	*Dendrobates* (Group 2)	*Ranitomeya (ventrimaculata)*	*Ranitomeya (vanzolinii)*	*Ranitomeya (vanzolinii)*	*flavovittata*
intermedius	$^{+}$	*Dendrobates* (Group 3)	*Ranitomeya (ventrimaculata)*	*Ranitomeya (vanzolinii)*	*Ranitomeya (vanzolinii)*	*imitator*
rubrocephalus	$^{+}$	*Dendrobates* (Group 6)	*Ranitomeya (ventrimaculata)*	*Ranitomeya*	*Ranitomeya*	*nomen dubium*
claudiae	*Minyobates**	*	*Ranitomeya (minuta)*	*Ranitomeya (minuta)*	*Andinobates (minutus)*	*claudiae*
daleswansoni	$^{+}$	$^{+}$	*	*	*Andinobates (bombetes)*	*daleswansoni*
dorisswansonae	$^{+}$	$^{+}$	*	*	*Andinobates (bombetes)*	*dorisswansonae*
uakarii	$^{+}$	$^{+}$	*	*Ranitomeya (reticulata)*	*Ranitomeya (reticulata)*	*uakarii*
tolimense	$^{+}$	$^{+}$	$^{+}$	$^{+}$	*Andinobates (bombetes)*	*tolimensis*
benedicta	$^{+}$	$^{+}$	$^{+}$	$^{+}$	*Ranitomeya (reticulata)*	*benedicta*
summersi	$^{+}$	$^{+}$	$^{+}$	*Ranitomeya (reticulata)**	*Ranitomeya (reticulata)*	*summersi*
cyanovittata	$^{+}$	$^{+}$	$^{+}$	$^{+}$	*Ranitomeya (vanzolinii)*	*cyanovittata*
defleri	$^{+}$	$^{+}$	$^{+}$	$^{+}$	*Ranitomeya (reticulata)*	*defleri*
yavaricola	$^{+}$	$^{+}$	$^{+}$	$^{+}$	*Ranitomeya (vanzolinii)*	*yavaricola*
steyermarki	*Minyobates*	*Dendrobates* (Group 6)	*Minyobates*	*Minyobates*	*Minyobates*	*steyermarki*
quinquevittatus	*Dendrobates (quinquevittatus)*	*Dendrobates* (Group 2)	*Adelphobates*	*Adelphobates*	*Adelphobates*	*quinquevittatus*

Due to the aforementioned concerns regarding BFA, we additionally performed Shimodaira-Hasegawa tests for many of the 16 hypotheses (see Table 3), though given the differences between methods and the resulting tests, some hypotheses are not identical and some caution should be taken when comparing these results. These analyses were performed in PAUP* (Swofford 2002) and test topologies were generated in MacClade (Maddison & Maddison, 2001).

Bioacoustic analysis. We gathered call data from 21 species of *Andinobates* and *Ranitomeya*. For four of these species, we relied solely on previously published data. For the remaining 17 species, we analyzed new calls in addition to previously published data. Of these 17 species, 12 are having their calls described herein for the first time. In total, we obtained calls from 66 individuals of 17 species. Calls were recorded by six different people. Recordings by J.L. Brown and E. Twomey used either a Sony TCM 5000 EV tape recorder or a Marantz PMD660 solid state digital recorder with a Sennheiser ME 66-K6 microphone. Recordings by D. Mejia-Vargas used a Sony TCM-5000 EV cassette recorder. E. Poelman made available recordings from Marty & Gaucher (1999) of French Guianan *R. amazonica*. Recordings by Adolfo Amézquita used a Marantz PMD660 solid state digital recorder with a Sennheiser ME 64 unidirectional microphone. Recordings by T. Ostrowski used a Sony Professional walkman (WM-D6C) and a Sennheiser MKH 416 P48 microphone, or an iPhone4 in combination with the software Record Pad 5.04. For details on calls originating from previous publications, see references provided in Table 5.

The following bioacoustic variables were analyzed: dominant frequency (frequency at which peak amplitude occurs), note length (length in seconds of a note, where a note is as a discrete bundle of pulses), pulses per note (where each pulse is defined as a burst of energy, several of which together comprise a note), pulse rate (pulses per second, calculated as pulse count for a note divided by note length), internote interval (the amount of time from the end of one note to the beginning of the following note), and notes per minute (number of notes given during 1 minute, if the recording was less than one minute this was extrapolated from the available recording). In addition, we provided verbal descriptions of each call type. For the purposes of statistical analysis of call parameters between *Ranitomeya amazonica* and *R. variabilis*, the unit of replication is an individual frog, i.e., multiple measurements taken from the same individual were averaged to a single value. Calls were analyzed in Raven Pro 1.4 (Charif 2010).

Results

Phylogenetics. Our mitochondrial phylogenetic topology is similar to recent studies (e.g. Grant *et al.* 2006 and Santos *et al.* 2009) and all major groups are well supported (Fig. 3, see discussion for comments on *Minyobates*). Increased sampling reveals a more detailed phylogeography of many species throughout their known ranges. Within *Ranitomeya*, there exist four major monophyletic groups which we herein define as species groups: the *variabilis*, *reticulata, defleri* and *vanzolinii* groups (Fig. 3).

In the *variabilis* group, there exist two reciprocally monophyletic clades (classified herein as *R. amazonica* and *R. variabilis*). Within *R. variabilis* (not to be confused with the *variabilis* group), there exists a deep divergence among populations predominantly from areas surrounding the upper Huallaga river (individuals 40-46) and all other populations (individuals 1-39). Similar biogeographic divergence is observed in other dendrobatids (e.g. between *Ameerega pepperi* and *A. bassleri*, and between *R. fantastica* and *R. summersi*), suggesting a barrier existed between upper Huallaga river populations and other populations in recent history. In the two cases mentioned, this likely resulted in allopatric speciation. For *Ranitomeya variabilis*, though minor morphological differences exist, these populations do not appear to be different species and it appears ancestors to these individuals have radiated northward, as far as Rio Marañón (individual 47) and east to the Serranía de Contamana (individual 42), mixing with local populations.

In the *reticulata* group, there is deep divergence among the clade containing *R. reticulata*/*R. ventrimaculata*, the clade containing *R. fantastica*/*R. summersi*/*R. benedicta* and the *R. uakarii* clade. Within *R. uakarii* a north-south break exists between Tournavista, PE/Porto Walter, BZ and Tamshiyacu-Tahuayo, PE.

In *Ranitomeya*, the deepest genetic divergence between sister taxa exists between *R. toraro* sp. nov. and *R. defleri*. Both species comprise the *defleri* group, a group that is sister to the *reticulata* group which form a clade sister to the *variabilis* group. The *vanzolinii* group, a group sister to all other *Ranitomeya* groups, contains two divergent clades. One clade contains *R. sirensis* and the other contains the remaining five species in the group.

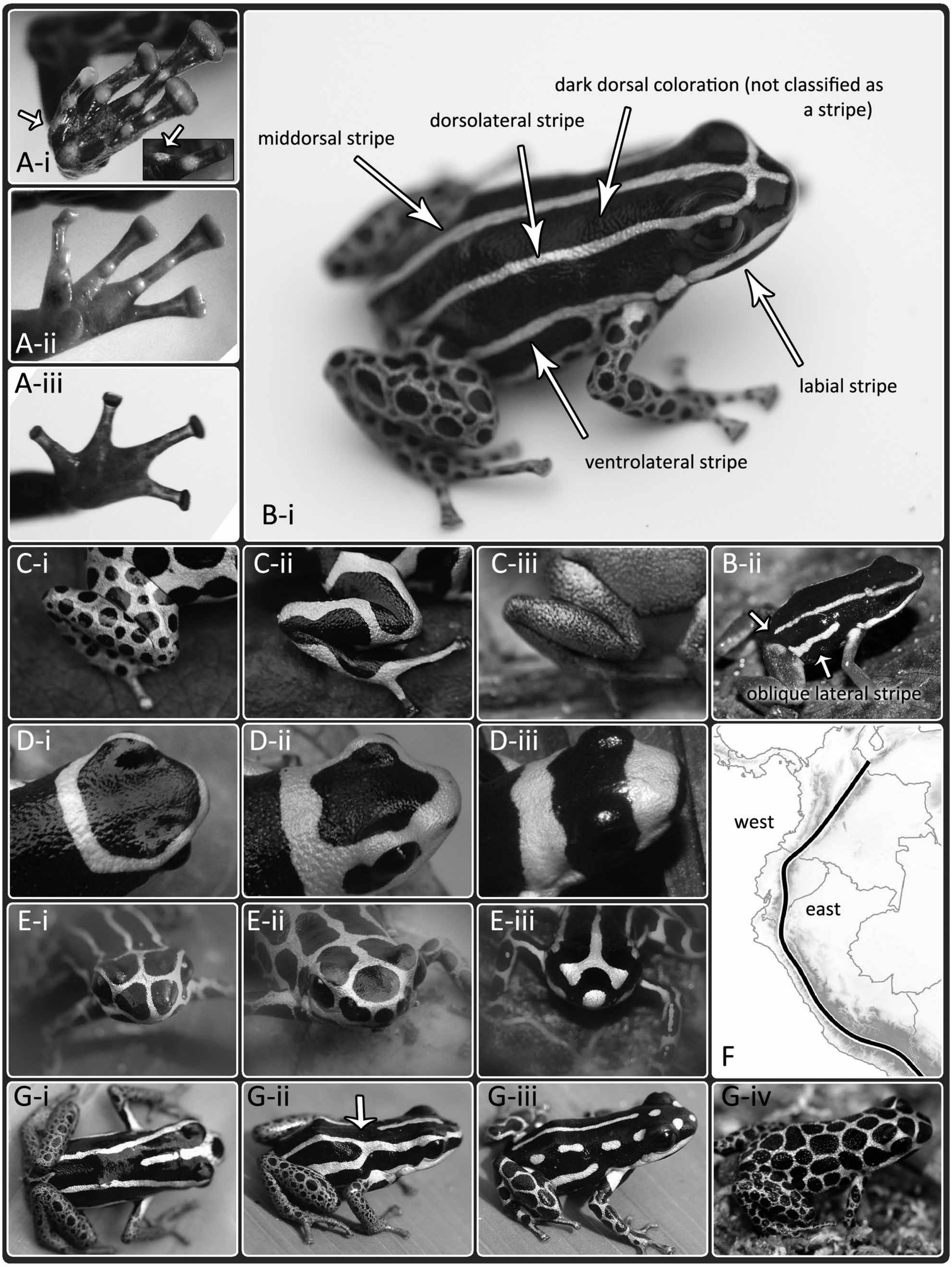

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FIGURE 2. Illustrated guide to morphological terminology. A. Finger and hand morphology: i. Finger I (far left) < Finger II, thenar tubercle (= inner metacarpal tubercle) present (depicted by arrow), and greatly expanded finger discs in Fingers II-IV. Inset depicts Finger I and a thenar tubercle which is clearly visible. Note that in some *Ranitomeya* this is trait reduced and difficult to view (as in main picture) (*Ranitomeya variabilis* pictured, inset of *R. benedicta*). **ii.** Finger I ≈ Finger II, thenar tubercle absent. (*Adelphobates quinquevittatus* pictured) **iii**. Weakly expanded finger discs in Fingers II-IV (*Excidobates captivus* pictured). **B. Stripes: i.** Mid-dorsal (follows vertebral column), dorsolateral (extends from eye to either upper thigh, as pictured, or to vent), ventrolateral (running from groin to axilla) and labial stripe (stripe that extends from shoulder around upper lip)(*R. sirensis* pictured). **ii.**. Oblique lateral stripe (extends from groin to eye, as in picture stripe is incomplete anteriorly). Unlabeled arrow depicts a dorsolateral stripe that does not reach thigh, a characteristic of certain species of *Andinobates* (type 'A' in Grant *et al.* 2006). *(Andinobates claudiae* pictured). **C. Limb patterns: i.** Distinct limb reticulation/spotting (characteristic of most species of *Ranitomeya*) (*R. variabilis* pictured). **ii.** Wavy stripes (not classified as distinct limb reticulation) (*R. summersi* pictured). **iii**. Patternless. Typical of most *Andinobates* species (*R. sirensis* pictured). **D. Diagnostic head patterns**: **i.** Large black "oval" on head (*R. imitator* pictured). **ii.** Large black "pentagon" or "five-point star" on head (*R. summersi* pictured). **iii.** Black band across head entirely covering eyes (known only in a single population of this species near the Pongo de Manseriche, Peru) (*R. fantastica* pictured). **E. Nose spots. i.** Two nose spots (*R. imitator* pictured). **ii.** Single nose spot. (*R. variabilis* pictured). **iii.** Frontward-turned "U" on the tip of snout. (*R. toraro* pictured). **F. Geographical distribution.** West: distribution within Andes, west of Andes, or in Central America. East: distribution east of Andes (including Guiana Shield) or in east-Andean versant. **G. Dorsal patterns**: **i.**"Y-shape". Space between stripes create black pattern which forms a black Y on the back. (*R. variabilis* pictured). **ii**. Merging of the obliquelateral and dorsolateral stripes (*R. variabilis* pictured). **iii**. Broken dorsolateral stripes (*R. flavovittata* pictured). **iv.** Spotting (*R. imitator* pictured). **H. Key ventral characters: i.** Distinctive throat coloration and ventral reticulation (also shown in H-ii & H-iii) (*R. reticulata* pictured). **ii.** Belly patch (*R. sirensis* pictured). **iii.** Gular spots (single or paired dark spots at corner of mouth) (*R. amazonica* pictured). **iv.** Marbled pattern (not classified as reticulation) (*Andinobates virolinensis* pictured).

In *Andinobates* gen. nov, there appear to be three distinct clades (classified herein as species groups): *bombetes*, *fulguritus* and *minutus*. The *minutus* group is sister to both the *fulguritus* and *bombetes* groups. Within the *bombetes* group, there is little phylogenetic distinction between *A. bombetes* and *A. virolinensis*, suggesting they may be different morphs of the same species or have diverged recently. There is strong phylogenetic support for the placement of *A. dorisswansonae* as a member of the *bombetes* group, a species which, along with *A. daleswansoni*, was thought to deserve allocation to a new genus (Rueda-Almonacid *et al.* 2006) based on its unique foot morphology.

Bioacoustics. Call data is summarized in Table 5. Within the genus *Ranitomeya*, we recognize three main call types: *reticulata* group calls, *variabilis* group calls, and *vanzolinii* group calls. Calls of the *reticulata* group and *variabilis* group sound similar, with the main difference that notes are given much more rapidly in the *reticulata* group. The *vanzolinii* group has a distinct call, consisting of a tonal trill. The call of *R. defleri* is similar to calls from the *variabilis* group, while the call of *R. toraro* remains unknown. Within *Andinobates* gen. nov, it seems that all calls are some permutation of a buzz or rattle. The two main call groups appear to correspond to the Andean and Chocoan clades. Both species in the *minutus* group (*A. claudiae* and *A. minutus*), as well as *A. fulguritus* (and likely *A. viridis*) have similar calls consisting of short buzzes with varying levels of tonality and relatively high energy. Species in the *bombetes* group have long, atonal calls sounding like a buzz or rattle. These calls are typically longer than 1 sec, whereas calls of the Chocoan *Andinobates* gen. nov have calls typically shorter than 1 sec.

Within *Ranitomeya*, there is a strong correspondence of call type to species group, and three of the four species groups can be readily identified by call type. Differences between species within groups are more subtle; in some cases they can be diagnostic (see for example *R. benedicta*, Brown *et al.* 2008), whereas in other cases calls within a group appear to be relatively homogenous (for example, within the *vanzolinii* group). However, the overall trend is low call variation within, and high call variation between species groups. Within *Andinobates* gen. nov, the call groups appear to be less distinct, and in many cases our analyses are based on a single individual of a species, thus our understanding of intraspecific vs. interspecific variation is incomplete.

Morphology. Gross morphology in this group is of limited use in determining relationships below genus level. While *Andinobates* gen. nov and *Ranitomeya* can be diagnosed from each other on the basis of several characters (e.g., vertebrae 2 & 3 fused in *Andinobates* gen. nov, limb reticulation present in *Ranitomeya*), differences between species groups within each genus are less obvious and better resolved using bioacoustic and phylogenetic data. Within *Ranitomeya*, the *vanzolinii* group is the most distinctive morphologically, but the only unambiguous synapomorphy, as far as we can tell, is egg color (white in the *vanzolinii* group vs. dark grey or black in all other *Ranitomeya*). Within species groups, color pattern can be of some use in differentiating species, but determining which characters are useful is often made apparent in light of a molecular phylogeny. This problem is compounded by the fact that Müllerian mimicry appears to be widespread throughout *Ranitomeya* and often distant relatives appear to be morphologically identical. Even in species which are not mimetic, such as *R. sirensis*, intraspecific variation in color pattern is so high that previous authors considered different color morphs to be distinct species.

Within *Andinobates* gen. nov, the *bombetes* group can be diagnosed from the *fulguritus* + *minutus* group on the basis of a wide medial gap in the papillae on the posterior labium of larvae (gap present in *bombetes* group). We have tentatively defined the *fulguritus* group on their shared green dorsal coloration, however *A. viridis* and *A. altobueyensis* have not yet been sequenced, so the validity of this arrangement needs to be confirmed with molecular data.

Key to the 'small' aposematic poison frogs of South America

This key is designed to be useful in the field with only basic, easily observable characters such as hand and foot morphology and color pattern. Because it is designed to be a field key, some knowledge of the geographic distribution is expected. Notes in brackets indicate additional information that can be useful for identification.

1a. First finger approximately equal in length or longer than second finger (Fig. 2a-ii) 2
1b. First finger shorter than second finger (Fig. 2a-i) 6
2a. Thenar tubercle absent (Fig. 2a-ii) 3
2b. Thenar tubercle present (Fig. 2a-ii) 4
3a. White spots or dashes on dorsum . . . . *Adelphobates castaneoticus*
[bright orange flash marks onupper surfaces of limbs; distribution in state of Mato Grosso and Para, Brazil]
3b. White stripes on dorsum . . . . *Adelphobates quinquevittatus*
[limbs orange with black spots; distribution in States of Rondônia and Amazonas, Brazil and parts of Pando, Bolivia]
4a. SVL greater than 25 mm, entire body covered with white spots . . . . *Excidobates mysteriosus*
[distribution in Cordillera del Condor north of Bagua, Peru]
4b. SVL less than 18 mm 5
5a. Flash marks absent . . . . *Minyobates steyermarki*
[dorsum and venter essentially solid red or reddish-brown, sometimes with faint dorsolateral stripes; known only from Cerro de Yapacana, Venezuela]
5b. Yellow flash marks present above axilla and groin . . . . *Excidobates captivus*
[dorsum with distinct reddish orange markings in the form of elongated dashes, dorsolateral stripes, or heavy flecking; venter with distinct yellow blotches; distribution in upper Río Marañón drainage in northern Peru and southeastern Ecuador]
6a. Distinct limb reticulation absent (Fig. 2c-ii and iii) 7
6b. Distinct limb reticulation/spotting present (Fig. 2c-i) 25
7a. Distribution in Andes or west of Andes (i.e., Chocoan Ecuador or Colombia), or in Central America (Fig. 2f, see "west") . . . 8
7b. Distribution east of Andes (including Guiana Shield) or in east-Andean versant (Fig. 2f, see "east") 20
8a. Four toes on foot 9
8b. Five toes on foot 10
9a. Head entirely red, body dull gold or brown . . . . *Andinobates daleswansoni* [distribution in Caldas, Colombia]
9b. Body black with red vermiculations or spots . . . . *Andinobates dorisswansonae*
[some individuals with yellow spots on flanks; distribution in Tolima, Colombia]
10a. Dorsolateral stripes present (in some species these stripes are sometimes faint and/or incomplete) 11
10b. Dorsolateral stripes absent 14
11a. Distinct, well-defined yellow or green dorsolateral and middorsal stripes (occasionally stripes can be orange or with a broken mid-dorsal stripe) 12
11b. Dorsal stripes diffuse; reddish or orange 13
12a. Limbs pale brown, dorsal stripes tan to bright yellow . . . . *Andinobates claudiae*
[SVL less than 14 mm; distribution in Bocas del Toro Province of Panama]
12b. Limbs black with distinct marbling identical in color to dorsal coloration; body bicolored (typically green, yellowish or bronze) . . . . *Andinobates fulguritus* [distribution in eastern Panama and lowlands of western Colombia]

13a. Stripes bright red, broad, usually on anterior half of dorsum, pale blue markings often present on flanks . . . . *Andinobates bombetes* [distribution in Valle del Cauca, Quindío and Risaralda, Colombia]
13b. Stripes run nearly length of entire dorsum, typically orange-red, distinct stripe present extending along flank . . . . *Andinobates minutus* [distribution in central and eastern Panama, extending into Chocoan Colombia]
14a. Dorsum uniformly colored, lacking markings 15
14b. Dorsum with black markings 19
15a. Entire body one color (except for axilla and groin) 16
15b. Body two or more colors 17
16a. Entire body emerald green . . . . . *Andinobates viridis* [distribution in western slope of Colombian Andes and southern Chocó]
16b. Entire body yellow or metallic gold . . . . *Andinobates altobueyensis* [known only from the summit of Alto del Buey, Chocó, Colombia]
17a. Dorsum solid red, venter brown, flanks often reticulated blue and black . . . . *Andinobates opisthomelas* [distribution in Antioquia, Caldas, Córdoba, and Chocó, Colombia]
17b. Dorsum dull orange-red, distinct orange labial stripe and markings on upper surface of thigh and upper arms . . . . *Andinobates minutus* [distribution in central and eastern Panama, extending into Chocoan Colombia]
17c. Dorsal coloration fades from a brightly colored head to a dull posterior 18
18a. Head yellow, fading to brown . . . . *Andinobates tolimensis* [distribution in Tolima, Colombia]
18b. Head and most of body bright crimson red, fading to brown on rump, venter blue with black reticulation . . . . *Andinobates virolinensis* [distribution in Cudinamarca and Santander, Colombia]
19a. Spots very small, body color yellow or metallic gold . . . . *Andinobates altobueyensis* [known only from the summit of Alto del Buey, Chocó, Colombia]
19b. Spots elongated, large, body mostly bright green . . . . *Andinobates fulguritus* [distribution in eastern Panama and lowlands of western Colombia]
20a. Body and limbs one solid color . . . . *Andinobates abditus* [body and limbs bronzy brown or black, orange markings in axilla and groin, known only from Volcán Reventador, Ecuador]
20b. Body and limbs different colors 21
21a. Limbs bicolored 22
21b. Limbs one solid color, lacking distinct markings 24
22a. Head orange, large black “oval” on head (Fig. 2d-i), call consisting of a musical “trill” . . . . *Ranitomeya imitator* [this morph is a Müllerian mimic of *R. summersi*, therefore, diagnosis is difficult without call data; occurs near the towns of Chazuta and Sauce, San Martín, Peru]
22b. Black band across head entirely covering eyes (Fig. 2d-iii) . . . . *Ranitomeya fantastica* [similar morphologically to *R. summersi;* this morph is known only from the Pongo de Manseriche, Loreto, Peru]
22c. Head orange, large black “pentagon” present on head (Fig. 2d-ii) 23
23a. White lines on posterior half of body . . . . *Ranitomeya fantastica* [morph known from vicinity of Tarapoto, Peru]
23b. Orange lines on posterior half of body *Ranitomeya summersi* [occurs near the towns of Chazuta and Sauce, San Martín, Peru]
24a. Dorsum red, large red blotch on belly, legs metallic turquoise-green . . . . *Ranitomeya sirensis* [nominotypical morph, known from the Cordillera El Sira, Peru]
24b. Black dorsum with pale greenish-blue spots, legs solid bronze . . . . *Ranitomeya yavaricola* [known from Rio Yavari region of Peru]
24c. Legs solid blue or black (some individuals with blue-black gradient), conspicuous red head . . . . *Ranitomeya benedicta* [this morph occurs along the Río Ucayali and parts of the Cordillera Azul in southern Loreto, Peru]
25a. Dorsum with regular, complete, longitudinal stripes 26
25b. Dorsum with irregular, broken stripes and/or spots 35
25c. Dorsum with neither stripes, spots, nor dashes 41
26a. Stripes create black pattern which forms a distinct Y-shape on the back (Fig. 2g-i) (the colored middorsal stripe is typically incomplete, confined to anterior half of body) 27
26b. Stripes essentially parallel, middorsal stripe complete (Fig. 2b-i) 28
27a. From the Iquitos region and has red or orange stripes, or from the Guiana Shield and has yellow stripes . . . . *Ranitomeya amazonica*
27b. Stripes yellow or green, distribution in Peru, Ecuador, or Colombia (east Andean versant and Amazonian lowlands) . . . . *Ranitomeya variabilis*
28a. Stripes blue on black background . . . . . *Ranitomeya cyanovittata* [known only from Sierra del Divisor region of eastern Peru]
28b. Stripes green on black background . . . . *Ranitomeya sirensis* [this morph has been found near the towns of Contamana, Loreto, Peru and Codo del Pozuzo, Huánuco, Peru]
28c. Stripes yellow on black background 29
28d. Stripes red or orange on black background 32
29a. Yellow patch on belly present . . . . *Ranitomeya sirensis* [occurs widely throughout much of central Peru]
29b. No patch on belly 30
30a. Distribution in lowlands near Tarapoto and Yurimaguas, Peru . . . . *Ranitomeya imitator* [musical trill call]
30b. Distribution east of Río Ucayali in Peru, throughout much of western Brazil 31
31a. Frontward-turned ‘U’ on tip of snout (Fig. 2e-iii) . . . . *Ranitomeya toraro* sp. nov. [stripes straight and parallel]
31b. Round black spot on tip of snout (Fig. 2e-ii), stripes often wavy . . . . *Ranitomeya uakarii* [yellow-striped morph known only from Río Los Amigos in southern Peru and Porto Walter in western Brazil]

32a. Yellow, orange, or red patch on belly present . . . *Ranitomeya sirensis* [known from the vicinity of Puerto Inca, Huánuco, Peru]
32b. No patch on belly 33
33a. Yellow oblique lateral stripe present . . . . *Ranitomeya uakarii* [known from Río Tahuayo region of northern Peru and one locality in the Río Pachitea drainage in central Peru]
33b. No yellow oblique lateral stripe 34
34a. SVL greater than 17 mm . . . . *Ranitomeya ventrimaculata* [known from northern Peru, near the Ecuadorian border and from southern Ecuador]
34b. SVL less than 17 mm . . . . *Ranitomeya reticulata* [striped individuals of this species are typically rare; occurs near Iquitos, Loreto, Peru]
35a. Dorsum with black spots or dashes on bright background 36
35b. Dorsum with yellow spots or dashes on black background 39
36a. Dorsum mostly red, few black spots present. . . . . *Ranitomeya reticulata* [spotted adults are rare, but this pattern is fairly common in juveniles; distribution near Iquitos, Peru]
36b. Dorsum mostly yellow, green, or blue with black spots present. 37
37a. Belly patch present . . . . *Ranitomeya sirensis* [this morph is known from highlands of the upper Rio Iscozacín and Río Cacazú drainages, Pasco, Peru]
37b. Belly patch absent 38
38a. One nose-spot (Fig. 2e-ii), insect-like buzz call . . . . *Ranitomeya variabilis* [this morph is typically found in montane regions in the east Andean versant of Peru and Ecuador]
38b. Two nose-spots (Fig. 2e-i), musical trill call. . . . . *Ranitomeya imitator* [nominotypical morph, known from the Cainarachi valley near Tarapoto, Peru]
39a. Belly patch present; spots yellow, small and circular . . . . *Ranitomeya vanzolinii* [some individuals have an irregular middorsal stripe; distribution east of Río Ucayali in central Peru and extreme western Brazil]
39b. Belly patch absent; spots yellow, irregular; dashes or broken stripes also present 40
40a. Limb and ventral reticulation bright blue, distribution near Río Apaporis, Colombia . . . . . . *Ranitomeya defleri* [call is an insect-like buzz]
40b. Limb and ventral reticulation grayish-white, sometimes pale sky blue, distributed near Iquitos, Peru . . . . *Ranitomeya flavovittata* [call is a musical trill]
41a. Bright coloration on dorsum is about equal in area to black, dorsal coloration is bright orange,electric blue reticulation on limbs, trill call . . . . *Ranitomeya imitator* [this morph is only known from San Gabriel de Varadero, west of Yurimaguas, Peru]
41b. Bright coloration on dorsum confined to the head 42
41c. Dorsum almost entirely brightly colored 43
42a. Head coloration brilliant red, red coloration not extending to upper arms . . . . *Ranitomeya benedicta* [body and limbs black with bright blue reticulation, distribution east of Río Huallaga and west of Río Ucayali in north-central Peru]
42b. Head coloration orange to copper, extending onto upper arms. . . . . *Ranitomeya fantastica* [body black with light blue or white reticulation; known from Río Paranapura west of Yurimaguas, Peru and Cainarachi valley, north of Tarapoto, Peru]
43a. Dorsum bright red, SVL less than 17 mm. . . . . *Ranitomeya reticulata* [this is the most common morph, having a solid red dorsum; distribution near Iquitos, Peru]
43b. Dorsum reddish orange, SVL greater than 17 mm . . . . *Ranitomeya amazonica* [this morph is only known from a few undisclosed localities in Loreto, Peru]

Systematics

Andinobates Twomey, Brown, Amézquita & Mejía-Vargas, gen. nov.

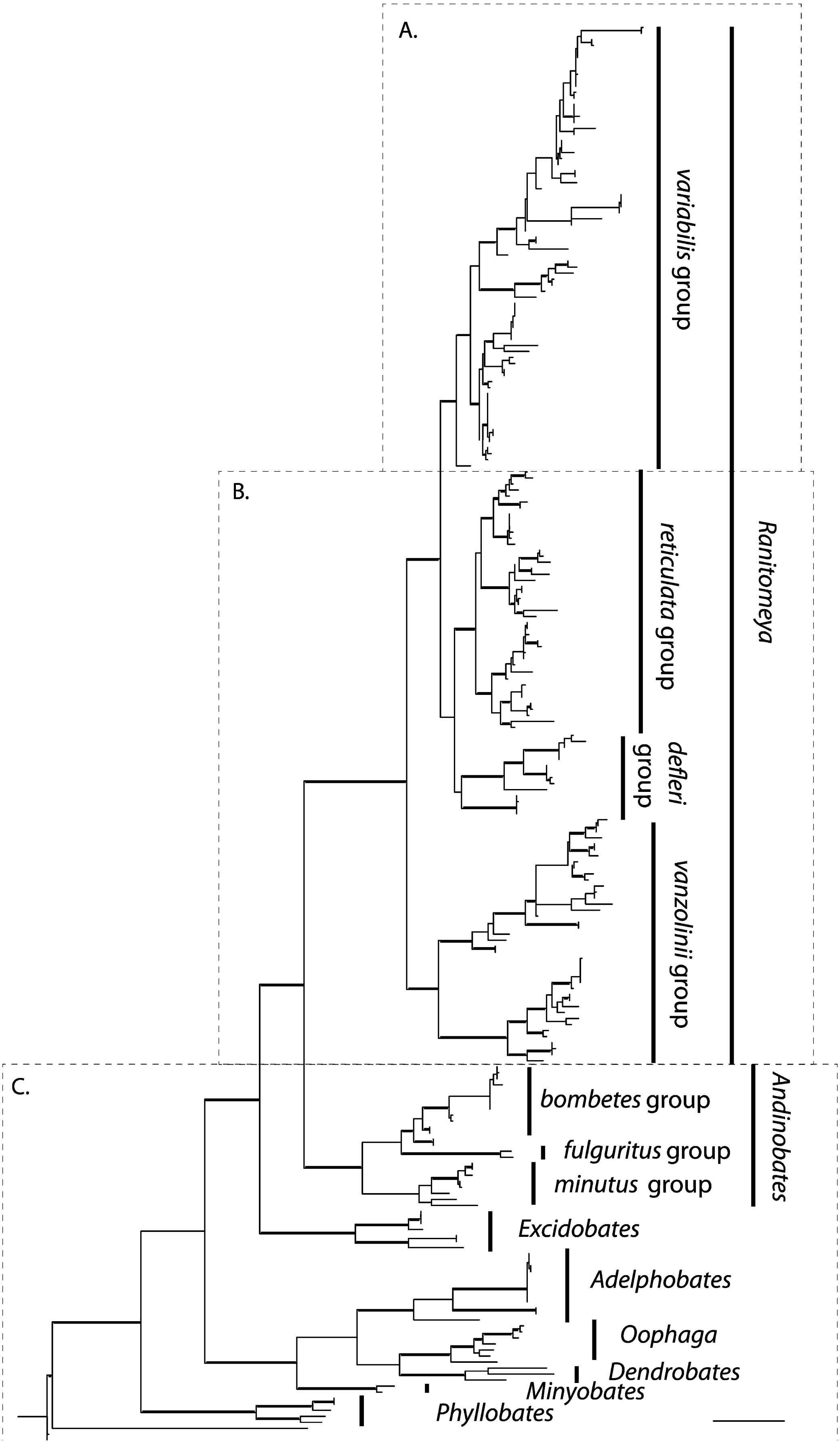
Account authors: E. Twomey, J.L. Brown, A. Amézquita, D. Mejía-Vargas
Figs. 3–8
Tables 2–6

Type species. *Dendrobates bombetes* Myers & Daly 1980

Etymology. From the Spanish adjective *Andino* (of the Andes) + the Greek *bates* (a walker), referring to the distribution of this genus, being primarily in the northern Andes. Gender masculine. The second half of the name is common among dendrobatine poison frogs.

Proposed sister group. *Ranitomeya.*

Definition and diagnosis. Unambiguous synapomorphies include: 15 nuclear and 11 mitochondrial synapomorphies (based upon the dataset used in this study, Fig. 3, Tables 2 and 3); vertebrae 2 and 3 fused (known only in *A. claudiae*, *A. minuta*, *A. opisthomelas*, and *A. virolinensis*; trait also present in *Oophaga*). Other characteristics include: adult SVL less than 20 mm; adults typically with bright coloration, often with bright red, green, or yellow dorsal coloration (either uniform or as stripes); *Andinobates abditus* an exception, dorsum mostly black or brown,



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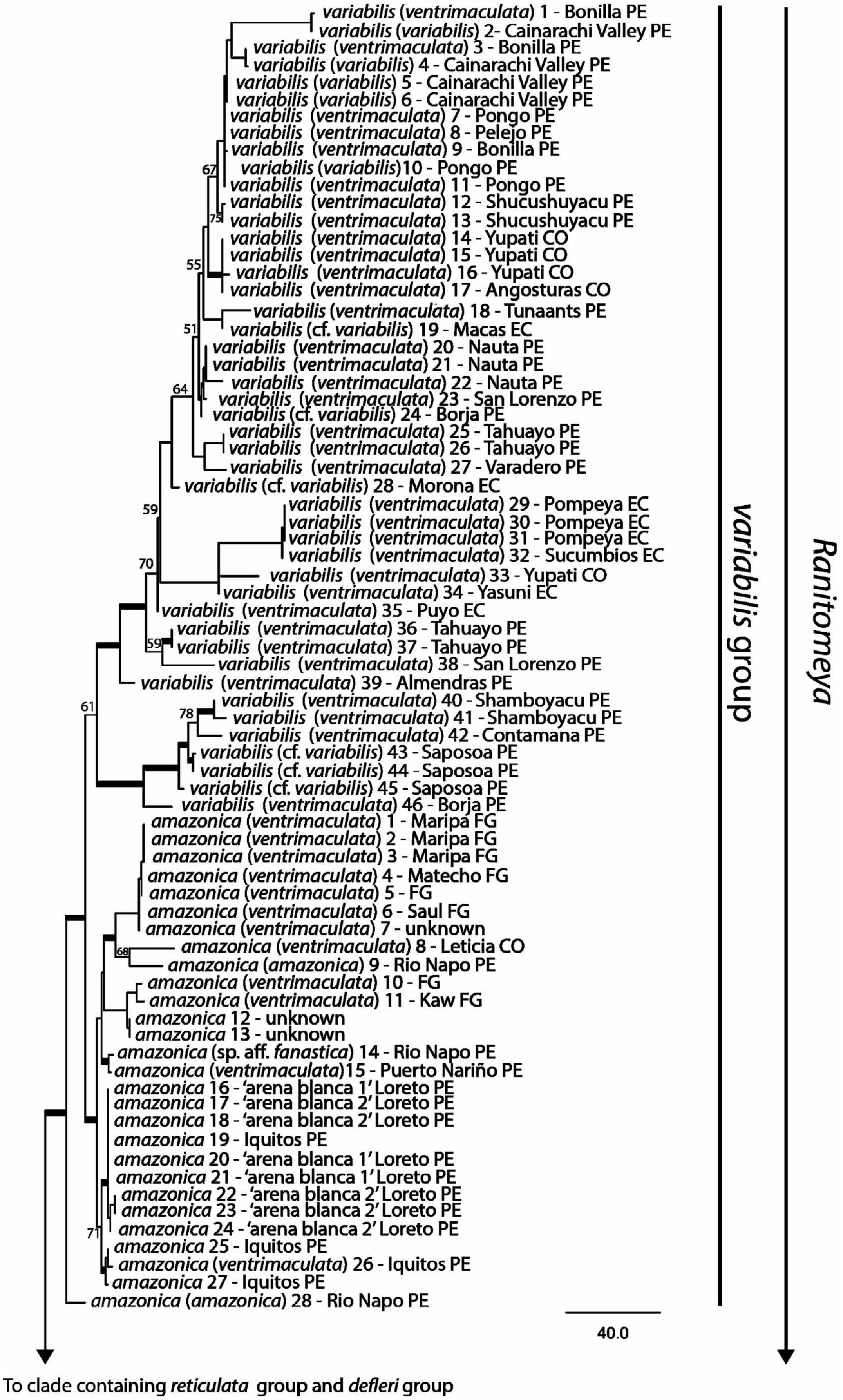

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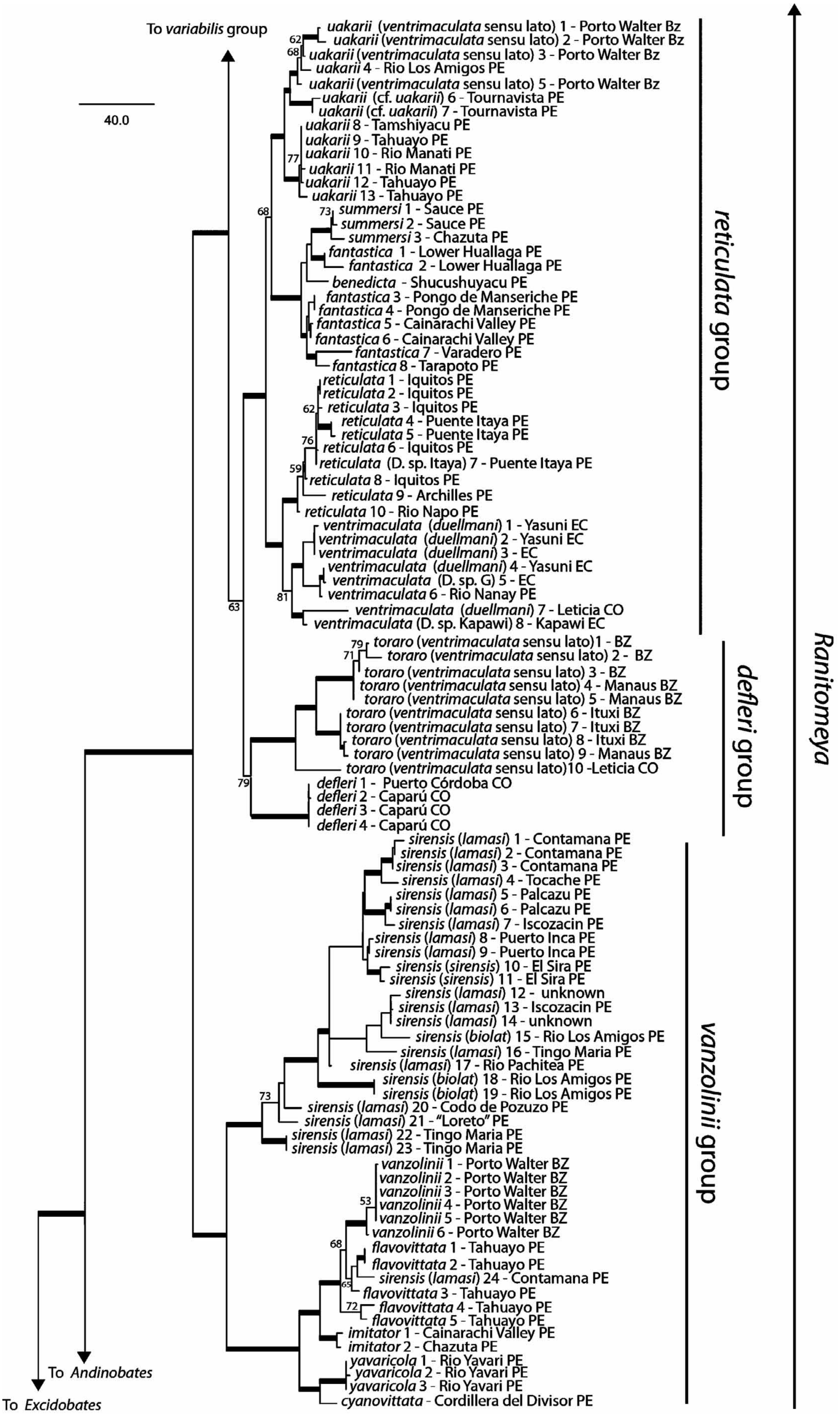

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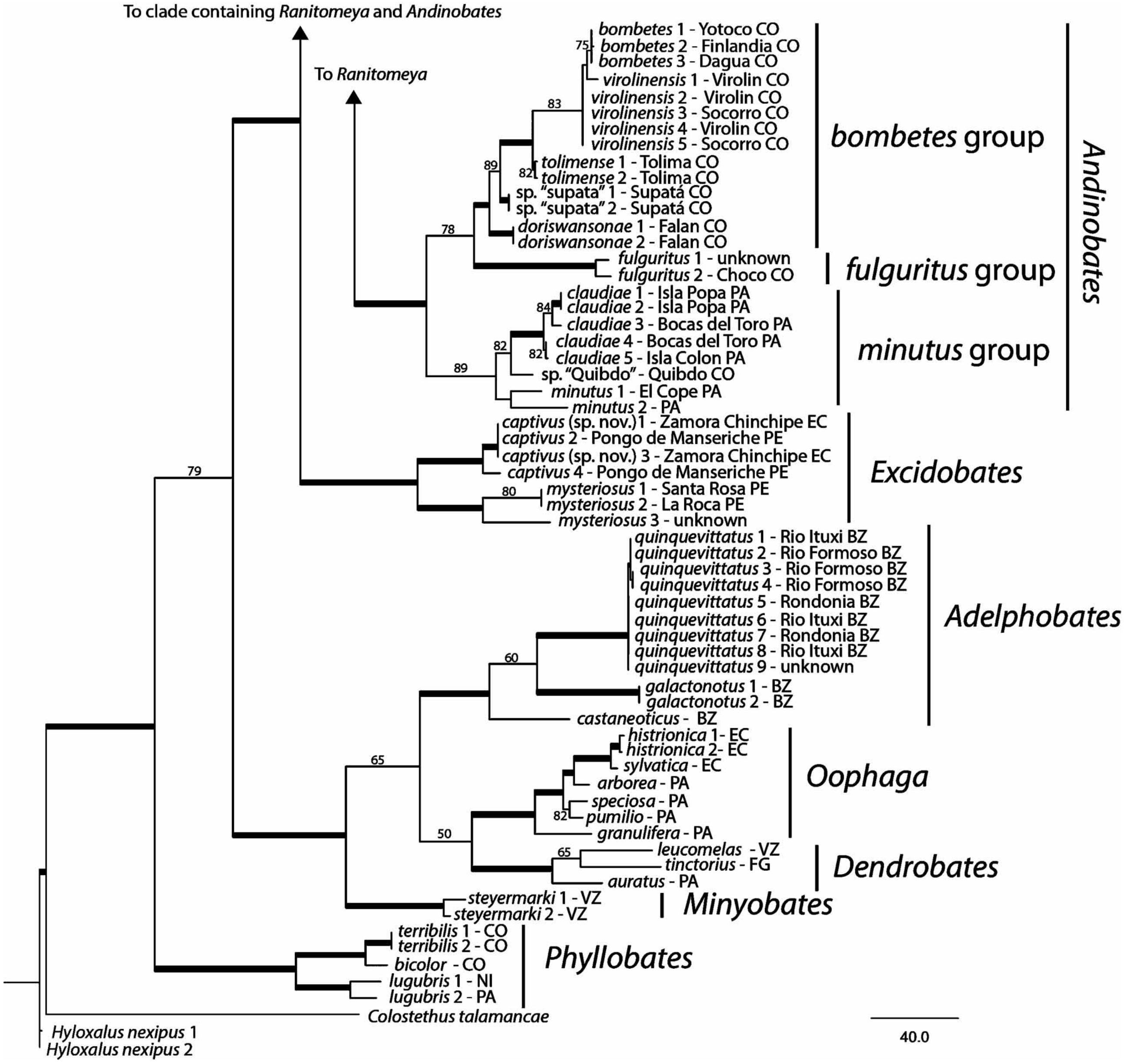

FIGURE 3. A consensus Bayesian phylogeny based on 1011 base pairs of aligned mitochondrial DNA sequences of the *12S* (12s rRNA), *16S* (16s rRNA) and cytb (cytochrome-b gene) regions. Thickened branches represent nodes with posterior probabilities 90 and greater, other values are shown on nodes. Taxon labels depict current specific epithet, number in tree, the epithet being used prior to this revision (contained in parentheses), and the collection locality. A. Top segment. B. Middle segment. C. Bottom segment of phylogeny.

orange spots in axilla and groin. When present, complete dorsolateral stripe ending before thigh (type 'A' in Grant *et al*. 2006); ventrolateral stripe absent; when present, oblique lateral stripe incomplete. Limbs usually dark with or without pale longitudinal stripes, lacking discrete pale reticulation as in most species of *Ranitomeya*. Ventral coloration variable, usually with distinct, bright markings. Colored throat patch absent. Head narrower than body; teeth absent; vocal slits present in males. First finger distinctly shorter than second; finger discs II and III weakly to moderately expanded; toe disc III and IV weakly expanded; toe V unexpanded; toe webbing absent; median lingual process absent; tadpoles with LTRF 2(2)/3 (sometimes with gap in first posterior row, Table 4); larval oral disc emarginated; larvae with complete papillae on the posterior labium (so far known in *A. minuta* and *A. claudiae*) or wide medial gap in papillae on posterior labium (so far known in *A. abditus*, *A. bombetes*, *A. opisthomelas*, *A. virolinensis* and *A. tolimensis*).

Distribution. This genus occurs within the rainforests of Colombia (Departments: Antioquia, Chocó, Santander, Cundinamarca, Caldas, Cauca, Córdoba, Tolima, Valle del Cauca, Quindío, Risaralda), Ecuador (Provinces: Napo) and Panama (Provinces: Bocas del Toro, Colón, Coclé, Kuna Yala, Veraguas).

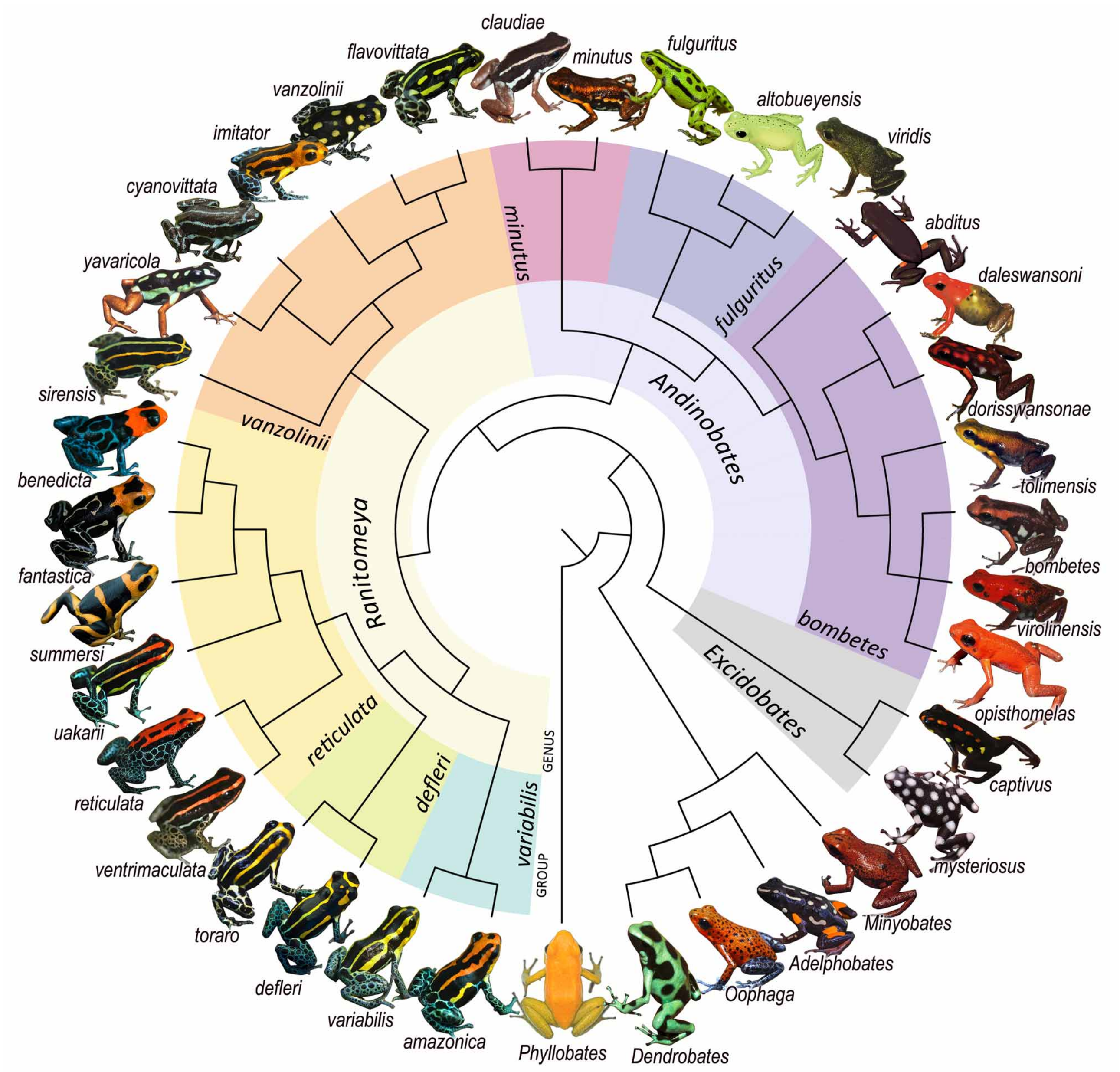

FIGURE 4. Putative species tree for *Andinobates*, *Excidobates*, and *Ranitomeya*. Placement of species where molecular data were lacking (*A. altobueyensis*, *A. viridis*, *A. abditus*, *A. daleswansoni* and *R. opisthomelas*) was based on morphology. *Andinobates altobueyensis* and *A. viridis* were placed as sister taxa due to the absence of dark pigmentation on dorsal body and limbs and overall similar dorsal coloration and patterning. These species were placed as sister to *A. fulguritus* (sequenced) on the basis of similar dorsal coloration (bright green to greenish-yellow). *Andinobates opisthomelas* was placed in the *bombetes* group in a polytomy with *A. bombetes* and *A. virolinensis* (both sequenced) due to their similar advertisement calls and morphology, particularly their red dorsal pattern and marbled venter. *Andinobates daleswansoni* was placed as sister to *A. dorisswansonae* due to the absence of a well-defined first toe in both species. *Andinobates abditus* was placed in the *bombetes* group based on a larval synapomorphy which appears to be diagnostic of that group (wide medial gap in the papillae on the posterior labium). However, *A. abditus* was placed as the sister species to all other members of the *bombetes* group due to the absence of bright dorsal coloration and isolated geographic distribution. *Andinobates abditus* is currently the only species of its genus known to occur in the east-Andean versant, thus its placement remains speculative until molecular data become available. Photo credits: Thomas Ostrowski, Karl-Heinz Jungfer, Victor Luna-Mora, Giovanni Chaves-Portilla.

TABLE 2. Bayes Factor Analyses. Bayes factor values above 10 were interpreted as strong evidence against H_0. Values between 0 and 10 were interpreted as support for both hypotheses, and values less than 0 were interpreted as support against H_A. H_A= an unconstrained phylogeny. Often when Bayes factor values were between 0-10, H_o consensus topologies where similar to H_A. Lower values often resulted in identical consensus topologies (differing only by branch lengths). * Includes *R. sirensis* sensu Aichinger 1991 $^+$includes *R. biolat* sensu Morales 1992

Hypothesis (H_0)	LnL: unconstrained	LnL: constrained	LnL: difference	Bayes factor [2ln(B_{10})]
Nuclear Dataset				
H_1: *Ranitomeya* and *Andinobates* reciprocally monophyletic sister clades	-5760.52	-5759.44	-1.08	-2.16
Mitochondrial Dataset				
H_2: *Ranitomeya* monophyletic (sensu this paper)	-13781.76	-13786.02	4.26	**8.52**
H_3: *Andinobates* monophyletic	-13781.76	-13786.74	4.98	**9.96**
H_4: *Andinobates* within *Excidobates*	-13781.76	-13839.19	57.43	114.86
H_5: *Andinobates* sister to the *vanzolinii* group	-13781.76	-13797.16	15.40	30.80
H_6: *Andinobates* sister to a clade comprising the *defleri, variabilis* and *reticulata* groups	-13781.76	-13796.73	14.98	29.95
H_7: *R. biolat* sensu Morales 1992 and *R. lamasi sensu Morales 1992 as reciprocally monophyletic sister clades**	-13781.76	-13797.36	15.60	31.19
H_8: *R. biolat* sensu Morales 1992 within *R. lamasi sensu Morales 1992**	-13781.76	-13781.91	0.15	**0.30**
H_9: *R. sirensis* sensu Aichinger 1991 sister to *R. lamasi*$^+$ sensu Morales 1992	-13781.76	-13812.23	30.47	60.94
H_{10}: *R. sirensis* sensu Aichinger 1991 within *R. lamasi*$^+$ sensu Morales 1992	-13781.76	-13781.91	0.15	**0.30**
H_{11}: *R. ventrimaculata* monophyletic (sensu this paper)	-13781.76	-13785.22	3.46	**6.91**
H_{12}: *R. amazonica* monophyletic (sensu this paper)	-13781.76	-13784.14	2.76	**4.76**
H_{13}: *R. variabilis* sensu Zimmermann & Zimmermann 1988 monophyletic (only individuals from Cainarachi Valley, Peru)	-13781.76	-13780.06	1.70	**3.41**
H_{14}: All spotted and striped *R. variabilis* as reciprocally monophyletic sister clades	-13781.76	-13831.16	49.40	98.80
H_{15}: *R. amazonica* individuals from French Guiana and all other *R. amazonica* individuals as reciprocally monophyletic sister clades	-13781.76	-13781.41	-0.35	**-0.71**
H_{16}: *R. flavovittata* monophyletic	-13781.76	-13799.24	17.48	34.97

TABLE 3. Shimodaira-Hasegawa tests. * Includes *R. sirensis* sensu Aichinger. [+]includes *R. biolat* sensu Morales [&]excludes a *R. amazonica* individual 28 that falls as the base of this group. [$] *R. fantastica* (including the two individuals from lower Huallaga) and *R. summersi* as sister taxa, which is sister to *R. benedicta*. [x]*R. summersi* sister to *R. fantastica* individuals that are finely reticulated in orange (i.e., individuals from the lower Huallaga valley) which are then sister to *R. benedicta*. This group forms a sister clade to all other *R. fantastica*.[-]parsimony tree length difference of 1. [=] parsimony tree length difference of 13. Unconstrained topology is from the Bayesian analysis (Fig. 3).

Hypothesis (H$_0$)	LnL: unconstrained	LnL: constrained	LnL: difference	P value
Mitochondrial Dataset: this paper				
H$_4$: *Andinobates* within *Excidobates*	17048.31	17064.13	15.82	**0.049**
H$_5$: *Andinobates* sister to the *vanzolinii* group	17048.31	17099.80	51.49	**<0.001**
H$_6$: *Andinobates* sister to a clade comprising the *defleri, variabilis* and *reticulata* groups	17048.31	17100.77	52.46	**<0.001**
H$_7$: *R. biolat* sensu Morales 1992 and *R. lamasi* sensu Morales 1992* as reciprocally monophyletic sister clades	17048.31	17174.21	125.90	**<0.001**
H$_9$: *R. sirensis* sensu Aichinger 1991 and *R. lamasi* sensu Morales 1992[+] as reciprocally monophyletic sister clades	17048.31	17062.23	13.87	**0.043**
H$_{13}$: *R. variabilis* (only individuals from Cainarachi Valley, Peru) reciprocally monophyletic to all other striped *R. variabilis*	17048.31	17219.48	171.17	**<0.001**
H$_{14}$: All spotted *R. variabilis* reciprocally monophyletic to all other (striped) *R. variabilis*	17048.31	17379.14	330.83	**<0.001**
H$_{15}$: *R. amazonica* individuals from French Guiana and all other *R. amazonica* individuals as reciprocally monophyletic sister clades	17048.31	17040.05	21.75	**0.026**
H$_{16}$: *R. flavovittata* and *R. vanzolinii* as reciprocally monophyletic sister clades	17048.31	17118.58	70.27	**<0.001**
H$_{17}$: *R. fantastica* complex sensu Brown *et al.* 2008[$]	17048.31	14048.87	1.85	**0.491**[-]
Mitochondrial Dataset from Brown *et al.* 2008				
H$_{18}$: *R. fantastica* complex sensu this paper[x]	3071.48	3025.64	45.84	**0.012**[=]

TABLE 4A (continued on next page). Basic Tadpole Morphology.

Genus	Species	Body color	Tooth Row Formula	Marginal Papillae	Oral disc
Andinobates	*abditus*	gray	2(2)/3(1)	incomplete: absent dorsally and wide ventral gap	emarginate
Andinobates	*altobueyensis*	gray	*	*	emarginate
Andinobates	*bombetes*	gray	2(2)/3	incomplete: absent dorsally and wide ventral gap	emarginate
Andinobates	*claudiae*	gray	2(2)/3(1)	incomplete: wide dorsal gap	emarginate
Andinobates	*daleswansoni*	gray	*	*	*
Andinobates	*dorisswansonae*	gray	*	*	*
Andinobates	*fulguritus*	gray	*	*	emarginate
Andinobates	*minutus*	gray	2(2)/3	incomplete: wide dorsal gap	emarginate
Andinobates	*opisthomelas*	gray	2(2)/3(1)	incomplete: absent dorsally and wide ventral gap	emarginate
Andinobates	*tolimensis*	gray	2(2)/3 (1)	incomplete: absent dorsally and wide ventral gap	emarginate
Andinobates	*viridis*	*	*	*	*
Andinobates	*virolinensis*	dark brown	2(2)/3	incomplete: wide dorsal and ventral gap	emarginate
Ranitomeya	*amazonica*	gray	2(2)/3 (1)	incomplete: wide dorsal gap	emarginate
Ranitomeya	*benedicta*	gray	2(2)/3	incomplete: wide dorsal gap	emarginate
Ranitomeya	*cyanovittata*	*	*	*	*
Ranitomeya	*defleri*	gray	2(2)/3(1)	incomplete: wide dorsal gap	emarginate
Ranitomeya	*fantastica*	gray	2(2)/3	incomplete: wide dorsal gap	emarginate
Ranitomeya	*flavovittata*	whitish	2(2)/3(1)	incomplete: wide dorsal gap	emarginate
Ranitomeya	*imitator*	whitish	2(2)/3(1)	incomplete: wide dorsal gap	emarginate
Ranitomeya	*reticulata*	gray	2(2)/3(1)	incomplete: wide dorsal gap	emarginate
Ranitomeya	*sirensis*	whitish	2(2)/3(1)	incomplete: wide dorsal gap	emarginate
Ranitomeya	*summersi*	gray	2(2)/3	incomplete: wide dorsal gap	emarginate
Ranitomeya	*toraro*	gray	2(2)/2(1)	incomplete: wide dorsal gap	emarginate
Ranitomeya	*uakarii*	gray	2(2)/3(1)	incomplete: wide dorsal gap	emarginate
Ranitomeya	*vanzolinii*	gray to dark gray	2(2)/3 (1)	incomplete: wide dorsal gap	emarginate
Ranitomeya	*variabilis*	gray	2(2)/3 (1)	incomplete: wide dorsal gap	emarginate
Ranitomeya	*ventrimaculata*	gray	*	*	*
Ranitomeya	*yavaricola*	whitish	2(2)/3 (1)	incomplete: wide dorsal gap	emarginate

TABLE 4B (continued from previous page). Basic Tadpole Morphology.

Genus	Species	Nursery Pool Type	Larvae Diet	Citation
Andinobates	*abditus*	large phytotelmata	*	Myers & Daly 1976
Andinobates	*altobueyensis*	large phytotelmata: axils of large aroids. Species ID uncertain, possibly *minutus*	*	Silverstone 1975
Andinobates	*bombetes*	phytotelmata: bromeliads	*	Myers & Daly 1980
Andinobates	*claudiae*	phytotelmata: i.e., bamboo, "water filled leaf axils"	*	Jungfer *et al.* 2000; Unpub. data Thomas Ostrowski
Andinobates	*daleswansoni*	phytotelmata: epiphytic bromeliads	*	Rueda-Almonacid *et al.* 2006
Andinobates	*dorisswansonae*	phytotelmata: epiphytic bromeliads	*	Rueda-Almonacid *et al.* 2006
Andinobates	*fulguritus*	phytotelmata: epiphytic bromeliads	*	Silverstone 1975
Andinobates	*minutus*	phytotelmata: epiphytic bromeliads	*	Silverstone 1975
Andinobates	*opisthomelas*	large phytotelmata: bromeliads	*	Silverstone 1975
Andinobates	*tolimensis*	*	*	Bernal-Bautista *et al.* 2007
Andinobates	*viridis*	*	*	-
Andinobates	*virolinensis*	large phytotelmata: large *Tillandisa* spp. and *Guzmania* spp.	*	Ruiz-Carranza & Ramírez-Pinilla, 1992
Ranitomeya	*amazonica*	phytotelmata: typically bromeliads (e.g., *Pitcairnia geykessi*, *Aechmea aquilega*, *Catopsis berteroniana*)	detritivorous, predaceous, oophagous	this paper
Ranitomeya	*benedicta*	phytotelmata: bromeliads	detritivorous, predaceous	Brown *et al.* 2008c
Ranitomeya	*cyanovittata*	*	*	-
Ranitomeya	*defleri*	medium size phytotelmata: bromeliads	detritivorous, likely predaceous	Twomey & Brown 2009
Ranitomeya	*fantastica*	large phytotelmata: *Aechmea* bromeliads and tree holes	detritivorous, predaceous	Brown *et al.* 2008c
Ranitomeya	*flavovittata*	medium phytotelmata: bromeliads	detritivorous, predaceous	this paper
Ranitomeya	*imitator*	small to medium phytotelmata: i.e., *Heliconia*, *Dieffenbachia* and small tree holes	detritivorous, predaceous, oophagous	this paper
Ranitomeya	*reticulata*	small phytotelmata: i.e., bromeliads and seed capsules	detritivorous, predaceous	Werner *et al.* 2010, J.L. Brown, unpub. data
Ranitomeya	*sirensis*	Medium phytotelmata: i.e., bromeliads, *Xanthosoma*, bamboo internodes	detritivorous, predaceous	von May *et al.* 2008b; J.L. Brown unpub. data
Ranitomeya	*summersi*	small-medium phytotelmata: i.e., *Dieffenbachia*	detritivorous, predaceous	Brown *et al.* 2008c
Ranitomeya	*toraro*	Phytotelmata of bromeliads i.e., *Aechmea* cf. *bromeliifolia*) and palms (i.e., *Phenakospermum guyanense*)	detritivorous, predaceous	this paper
Ranitomeya	*uakarii*	Medium phytotelmata: i.e., *Guzmania* bromeliads	detritivorous, predaceous	this paper
Ranitomeya	*vanzolinii*	small phytotelmata: i.e., tree holes, within woody vines	detritivorous, predaceous, oophagous	Caldwell & de Oliveira 1999
Ranitomeya	*variabilis*	Medium phytotelmata: *Aechmea* and *Guzmania* bromeliads, *Dieffenbachia*	detritivorous, predaceous, oophagous (variable)	this paper
Ranitomeya	*ventrimaculata*	*	*	-
Ranitomeya	*yavaricola*	small phytotelmata: i.e., bromeliads	detritivorous, predaceous	Perez-Peña *et al.* 2010

Vocalizations. Two main call groups within *Andinobates* correspond to the Andean and Chocoan clades (Fig. 8, Table 5). Species in the former (*A. bombetes, A. opisthomelas, A. daleswansoni, A. dorisswansonae, A. tolimensis, A. virolinensis*) produce calls that can be described as an extended rattle or buzz. These calls are typically over 1 sec in length and are relatively atonal with low energy. Chocoan species (*A. claudiae, A. fulguritus, A. minutus*) produce high-energy, short calls (less than 1 sec.) that are more reminiscent of calls produced by *Ranitomeya* species of the *variabilis* group. Data on *A. abditus, A. viridis, A. virolinensis* and *A. altobueyensis* are lacking.

Species included (12). *Dendrobates abditus* Myers & Daly 1976; *Dendrobates altobueyensis* Silverstone 1975; *Dendrobates bombetes* Myers & Daly 1980; *Dendrobates claudiae* Jungfer, Lötters & Jörgens 2000; *Dendrobates daleswansoni* Rueda-Almonacid, Rada, Sánchez-Pacheco, Velásquez-Álvarez & Quevedo-Gil 2006; *Dendrobates dorisswansonae* Rueda-Almonacid, Rada, Sánchez-Pacheco, Velásquez-Álvarez & Quevedo-Gil 2006; *Dendrobates fulguritus* Silverstone 1975; *Dendrobates minutus* Shreve 1935; *Dendrobates opisthomelas* Boulenger 1899; *Ranitomeya tolimensis* Bernal-Bautista, Luna-Mora, Gallego & Quevedo-Gil 2007; *Dendrobates viridis* Myers & Daly 1976; *Dendrobates virolinensis* Ruiz-Carranza & Ramírez-Pinilla 1992.

Remarks. Our definition of *Andinobates* is essentially equal to Myers' (1987) definition of *Minyobates* minus *steyermarki*. When molecular data became available for *Minyobates steyermarki* (Vences *et al*. 2003; Roberts *et al*. 2006a), it was evident that this species was not affiliated with the other members of *Minyobates* sensu Myers (1987), but rather was more closely related to the *Oophaga* + *Dendrobates* + *Adelphobates* clade (see discussion for more information). The ancestor to *Andinobates* apparently diverged during the mid-Miocene from *Excidobates* about 17 mya and from *Ranitomeya* sensu this paper about 14 mya (Santos *et al*. 2009).

Species groups contained within *Andinobates*

Andinobates minutus species group

Figs. 3–5 (a–m), 8
Tables 4–6

A monophyletic assemblage of two divergent species: *Andinobates minutus* (Shreve 1935) comb. nov. and *A. claudiae* (Jungfer, Lötters & Jörgens 2000) comb. nov.

Definition and diagnosis. SVL 13–16 mm; dark brown or black dorsum; largely complete light colored dorsolateral stripes not extending to thigh and oblique lateral stripes present, typically incomplete and not extending to eye; large spots near body on upper surface of legs and forearms; limbs and venter black with pale marbling on venter; LTRF either 2(2)/3(1) (*A. claudiae*) or 2(2)/3 (*A. minutus*); larvae with complete papillae on posterior labium and wide gap in papillae on anterior labium; oral disc emarginated (Table 4); larvae gray; eggs dark (Table 6). Vocalizations short, tonal buzz-notes, notes less than 1 sec in length, repeated at 3–17 notes per minute (Fig. 8, Table 5).

Andinobates fulguritus species group

Figs. 3–5 (n–v), 6 (a–d), 8
Tables 2–4

An assemblage of three species: *Andinobates altobueyensis* (Silverstone 1975) comb. nov., *A. fulguritus* (Silverstone 1975) comb. nov. and *A. viridis* (Myers & Daly 1976) comb. nov.

Definition and diagnosis. SVL 14–17 mm; body uniform yellow to dark green dorsally; *A. fulguritus* with black dorsolateral stripes and black oblique lateral stripes; *A. altobueyensis* lacking dorsal stripes but with fine black irregular spots on dorsum; *A. viridis* green with no black markings on dorsum; venter spotted or marbled in gray. Limbs identical to dorsal pattern and color. Vocalization data only available for *A. fulguritus* (Fig. 8, Table 5). Call consisting of short buzzes, notes 0.19–0.34 sec in length, repeated at 11–16 notes per minute. Call of *A. viridis* sounds similar to that of *A. fulguritus*, although recordings are lacking (D. Mejía-Vargas unpub. data, Table 5).

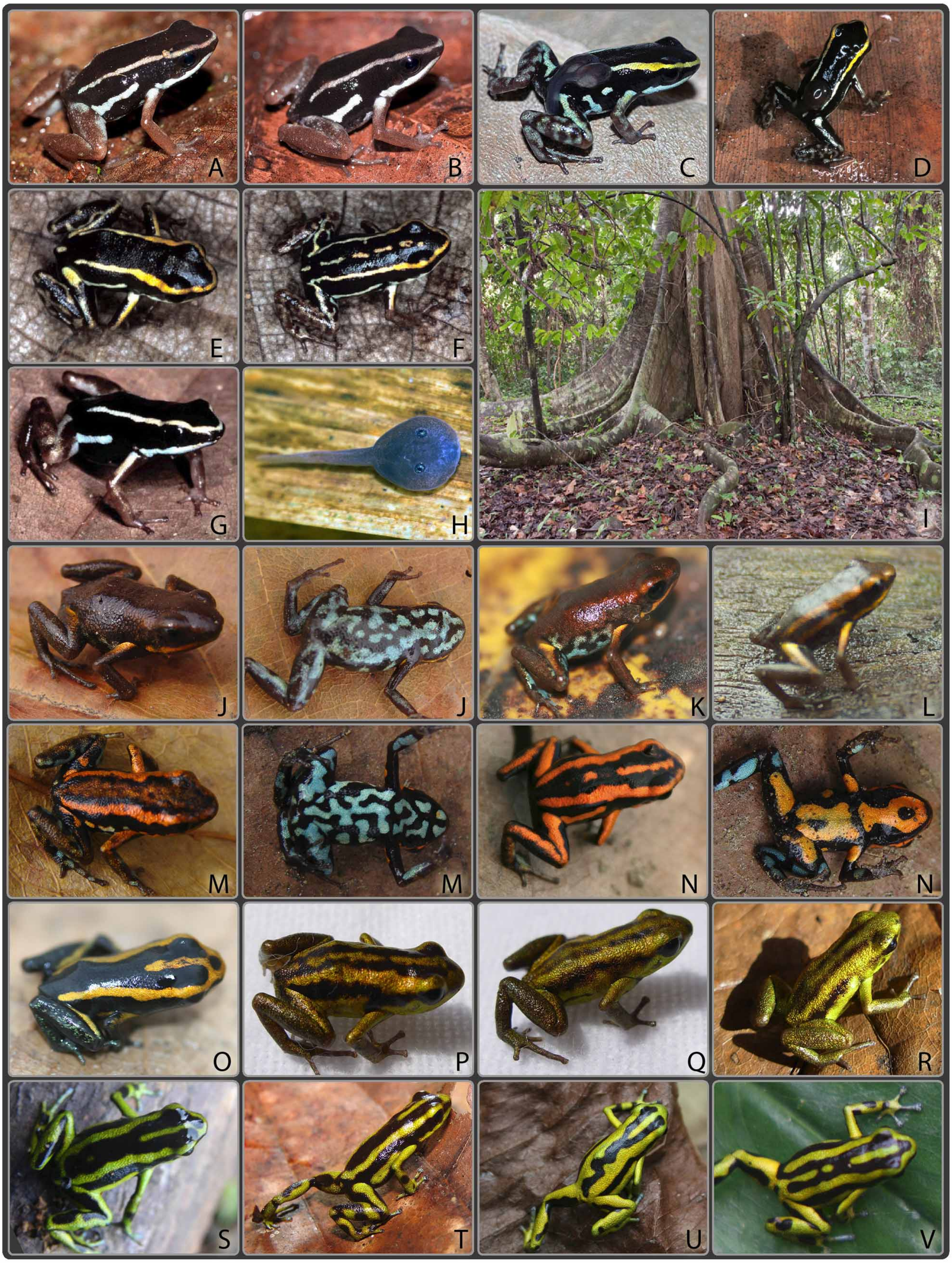

FIGURE 5. ***Andinobates*** **Plate 1.** minutus group: **A–G:** ***Andinobates claudiae*** and habitat (all from Bocas del Toro, Panama. Photos T. Ostrowski); A & B: Buena Esperanza; C–F: Isla Colon; G: Cerro Brujo; H: tadpole in phytotelm; I: habitat in Bocas del Toro, Panama. **J–M:** ***Andinobates minutus*** (all from Colombia. Photos DMV unless noted): J & K: Buenaventura, Valle del Cauca; L: Quibdó, Chocó; M: Baudó, Chocó (photo J. Mejía-Vargas). fulguritus group: **N–V:** ***Andinobates fulguritus*** (all from Colombia, photos DMV unless noted): N: Baudó, Chocó (photo J. Mejía-Vargas); O: Playa de Oro, Chocó (type locality); P–R: Uraba, Chocó. S–V: Anchicayá, Valle del Cauca. (nΦ = number of individual in phylogeny, Ω = population sampled in phylogeny).

FIGURE 6. ***Andinobates*** **Plate 2.** fulguritus group: **A–D:** ***Andinobates fulguritus*** (all from Risaralda, Colombia. photos DMV). bombetes group: **E:** ***Andinobates abditus*** type locality (photo W.E. Duellman). **F–I:** ***Andinobates daleswansoni*** and habitat (photos J. Mejía-Vargas); F & G: from type locality; H: type locality habitat; I: overview of habitat – human encroachment continues to threaten the habitat of this species. **J–M:** ***Andinobates dorisswansonae*** from Tolima, Colombia (photos DMV and T. Ostrowski). **N–P:** ***Andinobates tolimense*** from Tolima, Colombia (photos V. Mora-Luna). **Q–R:** ***Andinobates*** **sp. aff.** ***tolimense*** from Supatá, Colombia (photos G. Chaves-Portilla and T. Ostrowski).

FIGURE 7. ***Andinobates*** **Plate 3.** bombetes group: **A–B: *Andinobates* sp. aff. *tolimense***; A: from Supatá, Colombia (Photo credits: G. Chaves-Portilla); B: Tolima, Colombia (Photo credits: Fundacion ProAves-Alonso Quevedo). **C–H: *Andinobates bombetes***, all from Colombia (photo credits: DMV and T. Ostrowski); C: Quebrada a la Chapa, Boyacá; D-E: Valle del Cauca, T. Ostrowski; F: Yotoco, Valle del Cauca; G: Lowland habitat of *A. bombetes* near Quebrada a la Chapa; H: Yotoco, Valle del Cauca. **I: *Andinobates* sp. aff. *bombetes*** undisclosed locality in Colombia (photo credits: Dennis Nilsson and DMV). **J–N: *Andinobates virolinensis***; Charalá, Virolin, Colombia . **O–Q: *Andinobates opisthomelas***. O: Guatape, Antioquia, Colombia (photo credits: Dennis Nilsson and DMV); P-Q: Carmen de Atrato, Choco, Colombia.

Table 5A (continued on following page). Summary of acoustic data in *Ranitomeya* and *Andinobates*.

Species	Description	Dominant frequency	Note length	Pulses per note
Andinobates altobueyensis	unknown			
Andinobates claudiae	buzz	5773–6079 Hz	0.85–1.03 sec	55–65
Andinobates fulguritus	short buzz	4834–5161 Hz	0.19–0.34 sec	28–52
Andinobates viridis	similar to *fulguritus*			
Andinobates minutus	tonal buzz	5400–6400 Hz	0.2–1.1 sec	20–71
Andinobates abditus	unknown			
Andinobates bombetes	long buzz	4000–4800 Hz	0.9–1.7 sec	160 (estimate)
Andinobates opisthomelas	long buzz	5000–5500 Hz	1.6–2.3 sec	215–224
Andinobates daleswansoni	very similar to *dorisswansonae*			
Andinobates dorisswansonae	long buzz	4100–4200 Hz	1.4–1.6 sec	72–78
Andinobates virolinensis	long buzz			
Andinobates tolimensis	buzz	4730–5220 Hz	0.84–0.99 sec	n/a
Ranitomeya amazonica	buzz	4200–5800 Hz	0.16–0.36 sec	20–49
Ranitomeya variabilis	buzz	4386–5624 Hz	0.14–0.44 sec	19–116
Ranitomeya defleri	buzz	5319–5415 Hz	0.41–0.62 sec	40–61
Ranitomeya toraro	unknown			
Ranitomeya benedicta	rapid buzz	3190–4240 Hz	0.10–0.17 sec	n/a
Ranitomeya fantastica	rapid buzz	2950–3790 Hz	0.18–0.32 sec	10–13 pulses
Ranitomeya reticulata	rapid buzz	4140–4480 Hz	0.18–0.29 sec	48–94 pulses
Ranitomeya summersi	rapid buzz	2760–3220 Hz	0.38–0.50 sec	14–16
Ranitomeya uakarii	rapid buzz	3790–4130 Hz	0.26–0.29 sec	14–16 pulses
Ranitomeya ventrimaculata	rapid buzz	4190–4400 Hz	0.32–0.38 sec	58–63
Ranitomeya cyanovittata	unknown			
Ranitomeya flavovittata	trill	5928–5950 Hz	0.81–1.06 sec	24–31 pulses
Ranitomeya imitator	trill	4710–5660 Hz	0.44–1.07 sec	16–32 pulses
Ranitomeya sirensis	trill	5010–5690 Hz	0.88–2.2 sec	21–55 pulses
Ranitomeya vanzolinii	trill	5350–5440 Hz	0.57–0.64 sec	16–17 pulses
Ranitomeya yavaricola	trill	5400–6000 Hz	0.63–0.88 sec	20–27 pulses

Table 5B (continued from previous page). Summary of acoustic data in *Ranitomeya* and *Andinobates*.

Species	Pulse rate	Inter-note interval	Notes per minute (extrapolated)	Source
Andinobates altobueyensis				
Andinobates claudiae	62–64 pulses/sec	18–24 sec	3 notes	this study (unpub data, D. Mejía-Vargas)
Andinobates fulguritus	130–157 pulses/sec	3.1–5.9 sec	11–16 notes	this study (calls courtesy T. Ostrowski and D. Mejía-Vargas)
Andinobates viridis				this study (unpub data, D. Mejía-Vargas)
Andinobates minutus	63–125 pulses/sec	1.2–3.2 sec	17 notes	Myers & Daly 1976; this study (calls courtesy D. Mejía-Vargas)
Andinobates abditus				
Andinobates bombetes	113–134 pulses/sec	8.8 sec	5.76	Myers & Daly 1980; this study (calls courtesy D. Mejía-Vargas)
Andinobates opisthomelas	92–95 pulses/sec	6–9 sec	6 notes	Myers & Daly 1980; this study (calls courtesy A. Amézquita)
Andinobates daleswansoni				this study (unpub data, D. Mejía-Vargas)
Andinobates dorisswansonae	47–52 pulses/sec	6.5 sec	7.5	this study (unpub data, D. Mejía-Vargas)
Andinobates virolinensis				this study (unpub data, D. Mejía-Vargas)
Andinobates tolimensis	n/a	2.5 sec (estimate)	16.5 (estimate)	Bernal *et al.* 2007
Ranitomeya amazonica	85–138 pulses/sec	0.75–3.3 sec	24–70 notes	this study
Ranitomeya variabilis	106–297 pulses/sec	0.6–2.0 sec	34–62 notes	this study
Ranitomeya defleri	94–104 pulses/sec	0.8–2.1 sec	27 notes	Twomey & Brown 2009
Ranitomeya toraro				
Ranitomeya benedicta	n/a	0.13–0.18 sec	200 notes	Brown *et al.* 2008c
Ranitomeya fantastica	41–57 pulses/sec	0.17–0.34 sec	107–146 notes	this study
Ranitomeya reticulata	270–382 pulses/sec	0.12–0.15 sec	145–172 notes	this study
Ranitomeya summersi	39–40 pulses/sec	0.10–0.19 sec	104 notes	Brown *et al.* 2008c
Ranitomeya uakarii	50–58 pulses/sec	0.10–0.11 sec	168 notes	Brown *et al.* 2006; this study
Ranitomeya ventrimaculata	166–181 pulses/sec	0.12–0.13 sec	124 notes	this study (call courtesy Thomas Ostrowski)
Ranitomeya cyanovittata				
Ranitomeya flavovittata	29–30 pulses/sec	22–46 sec	1.7 notes	this study
Ranitomeya imitator	29–38 pulses/sec	4–20 sec	7–11 notes	this study
Ranitomeya sirensis	24–30 pulses/sec	2–10 sec	6–14 notes	this study
Ranitomeya vanzolinii	26–28 pulses/sec	approx. 14 sec	approx. 4 notes	this study
Ranitomeya yavaricola	31–32 pulses/sec	7–37 sec	2–7 notes	Perez-Peña *et al.* 2010

Andinobates bombetes group

Figs. 3, 4, 6 (e–r), 7 (a–q), 8
Tables 4–6

An assemblage of seven species: *Andinobates abditus* (Myers & Daly 1976) comb. nov., *A. bombetes* (Myers & Daly 1980) comb. nov., *A. daleswansoni* (Rueda-Almonacid, Rada, Sánchez-Pacheco, Velásquez-Álvarez & Quevedo-Gil 2006) comb. nov., *A. dorisswansonae* (Rueda-Almonacid, Rada, Sánchez-Pacheco, Velásquez-Álvarez & Quevedo-Gil 2006) comb. nov., *A. opisthomelas* (Boulenger 1899) comb. nov., *A. tolimensis* (Bernal-Bautista, Luna-Mora, Gallego & Quevedo-Gil 2007) comb. nov. and *A. virolinensis* (Ruiz-Carranza & Ramírez-Pinilla 1992) comb. nov.

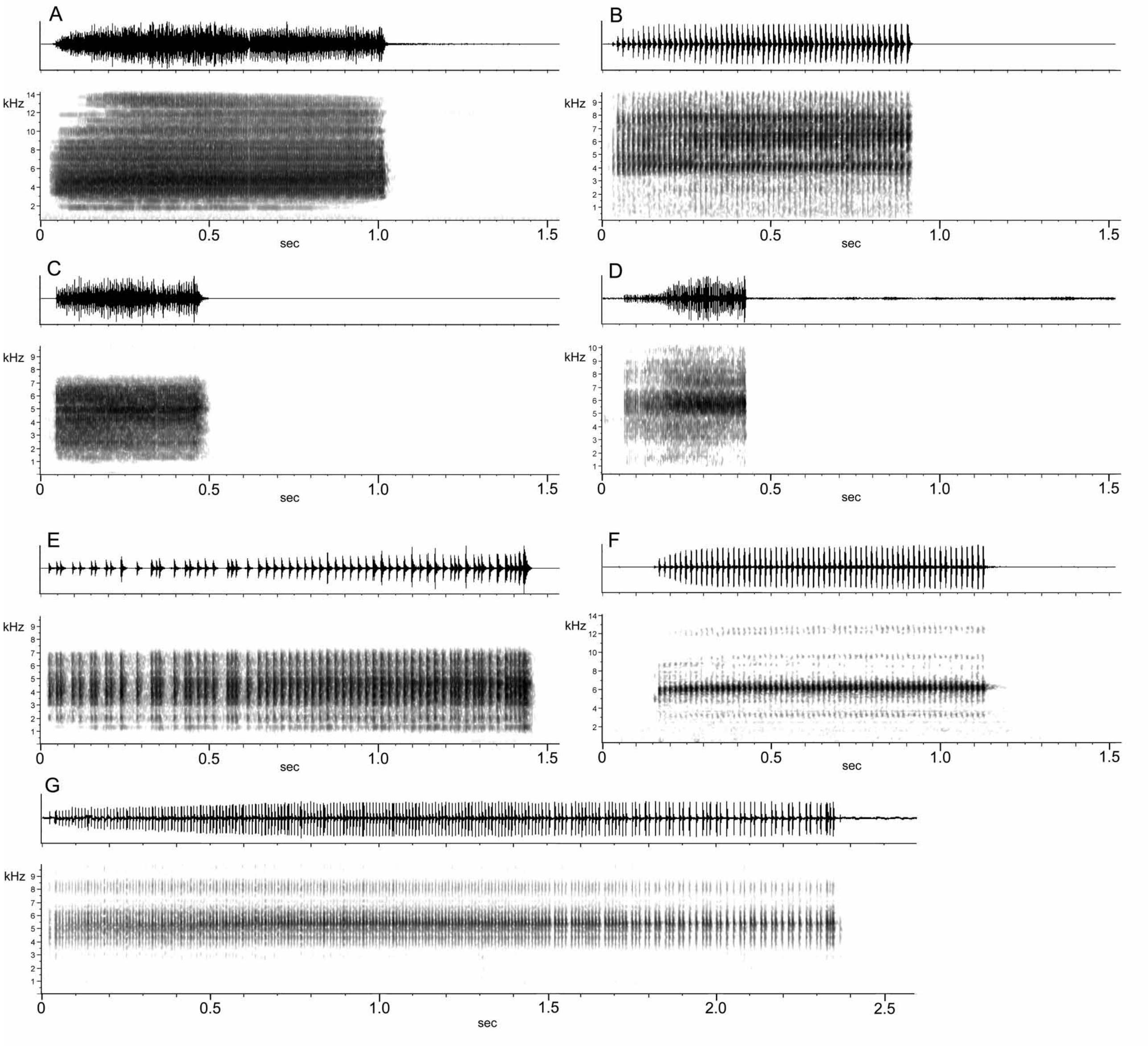

FIGURE 8. Advertisement calls for species of *Andinobates*. A. *Andinobates bombetes* from Bosque Yotoco, Valle del Cauca, Colombia (type locality), recorded at 18-20° C; **B.** *Andinobates claudiae* from Isla Colón, Panama, recorded at 25° C (call courtesy Thomas Ostrowski); **C.** *Andinobates fulguritus* from Itauri, Colombia, unknown temperature; **D.** *Andinobates fulguritus* from Kuna Yala, Panama, recorded in captivity at 24° C (call courtesy T. Ostrowski); **E.** *Andinobates dorisswansonae* from "El Estadero", Caldas, Colombia (type locality), recorded at 19-20° C; **F.** *Andinobates minutus*, unknown locality or temperature; **G.** *Andinobates opisthomelas* from Guatapé, Antioquia, Colombia, unknown temperature.

Table 6A (continued on next page). Life History Traits. **= we recognise some of the observations may reflect actual deposition strategies, and could in some cases be the result of cannibalism. Black horizontal line depicts different genera.

Specific epithet	Mating system	Parental care	Trophic egg feeding	Clutch number/ deposition sites	Deposition strategy
abditus	-	-	-	terrestrial bromeliads (possibly)	individually (possibly)
altobueyensis	-	-	-	-	individually**
bombetes	-	male parental	absent	-	individually
claudiae	-	male parental	absent	3-4 eggs deposited in leaf litter	1-2 per phytotelm
daleswansoni	-	-	-	-	communally, “1-6 larvae in different states… were found inside a bromeliad”
dorisswansonae	-	-	-	-	-
fulguritus	-	male parental	absent	1-5 eggs	individually
minutus		male parental	absent	1-4 eggs	-
opisthomelas	-	-	-	-	-
tolimensis	-	-	-	-	-
viridis	-	-	-	-	-
virolinensis	promiscuous	male parental	absent	-	individually
amazonica	promiscuous	male parental	absent or temporally dependent; see account	1-6 eggs, at water surface (or just below) in phytotelmata	individually
benedicta	promiscuous	male parental	absent	4-6 eggs, in leaf litter on forest floor	individually
cyanovittata	-	-	-	-	-
defleri	-	-	-	-	individually
fantastica	promiscuous	male parental	absent	2-6 eggs	individually
flavovittata	-	-	-	1-3 eggs deposited vertically above phytotelm	individually
imitator	monogamous	biparental care	present	1-4 eggs; away from water, > 14 cm above pool.	individually
reticulata		male parental	absent	1-4 eggs in leaf litter, often hidden.	individually; occasionally, multiple in single phytotelm
sirensis	promiscuous	male parental	absent	1-3 eggs per clutch, deposited on inner wall, above the water, of bamboo internodes or other phytotelmata.	individually
summersi	promiscuous	male parental	absent	4-9 eggs; in leaf litter on forest floor	individually
toraro	-	-	-	1-2 eggs, above phytotelm, ca. 5-20 cm. above pool	individually
uakarii	promiscuous	male parental	absent	2-5 eggs at surface of (or just above) water level in phytotelm or away from phytotelm in leaf litter, often hidden.	Individually; occasionally, entire clutch is abandoned in single phytotelm
vanzolinii	monogamous	biparental care	present	1-2 eggs, above phytotelm	individually
variabilis	promiscuous	male parental	absent	2-6 eggs at surface of water level (or just below) in phytotelm	individually, if not, entire clutch is abandoned in single phytotelm.
ventrimaculata	-	male parental	-	-	-
yavaricola	-	-	-	-	individually

Table 6B (continued from previous page). Life History Traits.

Specific epithet	Additional notes	Citation
abditus	-	Myers & Daly 1976
altobueyensis	Species ID uncertain, possibly *minutus*	Silverstone 1975
bombetes	High territoriality, presumed to be strictly terrestrial, observed transporting 1-3 tadpoles	Myers & Daly 1980
claudiae	observed transporting 1-2 tadpoles	Jungfer *et al.* 2000; unpub. data Thomas Ostrowski
daleswansoni	-	Rueda-Almonacid *et al.* 2006
dorisswansonae	Observed transporting 1-2 tadpoles	-
fulguritus	-	Silverstone 1975
minutus	-	Silverstone 1975, unpub. data Thomas Ostrowski
opisthomelas	-	
tolimensis	-	Bernal-Bautista *et al.* 2007
viridis	-	-
virolinensis	Predominantly terrestrial, observed transporting 1-2 tadpoles, no territoriality observed, single bromeliads could contain up to 5 individuals.	Ruiz-Carranza & Ramírez-Pinilla, 1992
amazonica	In French Guiana populations, researchers observed this species change its food-provisioning strategy; early in breeding season, tadpoles subsist predominantly on food within phytotelm, whereas later in the breeding season (likely due to increased desiccation risk), as a food source parents deliberately deposit embryos in pools containing their offspring to ensure quick metamorphosis.	This paper, Poelman & Dicke 2007
benedicta		Brown *et al.* 2008c
cyanovittata	-	-
defleri	-	Twomey & Brown 2009
fantastica		Brown *et al.* 2008c
flavovittata	Likely territorial, males frequently participate in vocal bouts	this paper
imitator	Extremely territorial, males defend territories using vocal bouts and wrestling.	Brown *et al.* 2008ab, Brown 2009
reticulata		this paper
sirensis	Males territorial, males participate in vocal bouts and wrestling	Von May *et al.* 2008b; J.L. Brown, unpub. data
summersi		Brown *et al.* 2008c
toraro	-	this paper
uakarii		
vanzolinii	Extremely territorial, males defend territories using vocal bouts and wrestling.	Caldwell & de Oliveira 1999
variabilis	Males transported between 1-6 tadpoles. Little to no site fidelity or territoriality. This species exhibits larval parasitism, where males deposit tadpoles in pools containing non-related embryos that are cannibalized when they hatch and fall into the phytotelm.	this paper
ventrimaculata	Males have been observed carrying 1-3 tadpoles at a time.	E. H. Poelman, unpub. data
yavaricola	Likely territorial, males frequently participate in vocal bouts	Perez-Peña *et al.* 2010

Definition and diagnosis. SVL 16–19 mm; black to bronze dorsum; conspicuous dorsolateral stripes absent (weak dorsolateral stripes present in *A. bombetes*); head brightly spotted or uniformly yellow or red with identically colored labial stripe (except in *A. abditus*); white, yellow, orange or red spots in groin (not upper surface of thigh as in *Ranitomeya*) and between axilla and upper surfaces of forearms (sometimes extending to elbow); limbs uniformly dark (occasionally dorsal coloration extending to limbs, i.e., some populations of *A. opisthomelas*); venter black, either uniform (*A. abditus*), with pale to bright spotting (*A. dorisswansonae*, *A. opisthomelas* and *A. tolimensis*), or marbled bluish-white (*A. bombetes*, *A. virolinensis*); LTRF either 2(2)/3 (known in *A. bombetes* and *A. virolinensis*) or 2(2)/3(1) (known in *A. abditus*, *A. opisthomelas* and *A. tolimensis*); larvae with medial gap in papillae on posterior labium (known only in *A. abditus*, *A. bombetes*, *A. opisthomelas, A. virolinensis* and *A. tolimensis*, Table 4); oral disc emarginated. Vocalizations of species in this group characterized as drawn-out buzz or rattle, consisting of notes 0.8–2.3 sec in length, repeated at approximately 6–17 notes per minute (Fig. 8, Table 5)

Ranitomeya **Bauer 1988**

Account authors: J.L. Brown, E. Twomey
Figs. 3, 4, 9–45, Tables 2–7

Type species. *Dendrobates reticulatus* Boulenger, 1884 “1883”

Proposed sister group. *Andinobates* gen. nov.

Definition and diagnosis. Unambiguous synapomorphies include: 5 nuclear and 16 mitochondrial synapomorphies (based upon the dataset used in this study, Fig. 3, Tables 2 and 3); distinctive pale reticulation on limbs and venter present (Fig. 2c-i and Fig. 2h-i). Secondary losses of this pale limb reticulation appear to have occurred in *R. yavaricola* and *R. summersi*, some morphs of *R. fantastica*, *R. imitator* and *R. sirensis*. Other features include: adult SVL less than 21 mm; adults typically brightly colored, often with bright yellow, red, or green dorsal coloration (either uniform, spotted, or striped); dorsolateral stripe, if present, extending to top of thigh (vs. not reaching thigh in *Andinobates*), ventrolateral stripe and oblique lateral stripe present or absent; Distinctive, bright coloration on throat present (usually yellow, orange or red); dorsal skin texture nearly smooth to weakly granular; head narrower than body; teeth absent; vocal slits present in males; finger I greatly reduced and shorter than finger II; finger discs II–IV greatly expanded; in adults disc on finger III at least two times wider than distal end of adjacent phalanx; thenar tubercle conspicuous (commonly vestigial, occasionally absent); toe discs III–V moderately expanded; toe webbing absent; median lingual process absent; larval vent tube dextral; larval oral disc emarginated; larvae without medial gap in papillae on posterior labium (known in all species expect *R. cyanovittata* and *R. ventrimaculata*, Table 4); scansorial; adults use arboreal phytotelmata for reproduction and deposit eggs away from or at edge of water in phytotelmata (Table 6); tadpoles deposited individually, typically by male; small clutches (2–6 eggs, Table 6); vertebrae 2 and 3 unfused (known in *R. amazonica, R. toraro* sp. nov*., R. imitator, R. variabilis, R. vanzolinii, R. fantastica, R. reticulata* and *R. sirensis*).

Distribution. This genus occurs within Amazonian rainforests of Brazil (States: Acre, Amapá, Amazonas, Pará, Rondônia), Bolivia (Department: Pando), Colombia (Departments: Amazonas, Caquetá, Putumayo (tentative), Vaupés), Ecuador (Provinces: Morona-Santiago, Napo, Orellana, Pastaza, Sucumbíos), French Guiana (Arrondissements: Cayenne, Saint-Laurent-du-Maroni), Guyana (District: Potaro-Siparuni) and Peru (Departments[1]: Amazonas, Cusco, Huánuco, Junín, Loreto, Madre de Dios, Pasco, San Martín, Ucayali). Species within this genus occur between sea level and 1600 m, Fig. 9.

Species included (16). *Dendrobates amazonicus* Schulte 1999; *Ranitomeya benedicta* Brown, Twomey, Pepper & Sanchez-Rodriguez 2008; *Ranitomeya cyanovittata* Perez-Peña, Chavez, Twomey & Brown 2010; *Ranitomeya defleri* Twomey & Brown 2009; *Dendrobates fantasticus* Boulenger 1884 “1883”; *Dendrobates flavovittatus* Schulte 1999; *Dendrobates imitator* Schulte 1986 with its junior synonyms *Dendrobates imitator intermedius* Schulte 1999 and *Dendrobates imitator yurimaguensis* Schulte 1999 (Vences & Lötters 2000, Lötters *et al.* 2003

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[1] Since 2009, Peru officially reclassified ‘Departmentos’ as ‘Regiones’. At the time of writing, however, ‘region’ is infrequently used in scientific literature. Here we use Departments as a synonym of Regions.

and this paper); *Dendrobates reticulatus* Boulenger 1884 “1883” with its junior synonym *Dendrobates tinctorius igneus* Melin 1941; *Dendrobates sirensis* Aichinger 1991 with its junior synonyms *Dendrobates biolat* Morales 1992 and *Dendrobates lamasi* Morales 1992 (this paper); *R. summersi* Brown, Twomey, Pepper & Sanchez-Rodriguez 2008; *Ranitomeya toraro* sp. nov. (this paper); *Dendrobates uakarii* Brown, Schulte & Summers 2006; *Dendrobates vanzolinii* Myers 1982; *Dendrobates variabilis* Zimmermann & Zimmermann 1988; *Dendrobates ventrimaculatus* Shreve 1935 with its junior synonym *Dendrobates duellmani* Schulte 1999 (this paper); *Ranitomeya yavaricola* Perez-Peña, Chavez, Twomey & Brown 2010.

Remarks. Our definition of *Ranitomeya* is essentially equal to the definition of Caldwell & Myers (1990) *ventrimaculatus* group. The genus apparently diverged from *Andinobates* approximately 14 mya during the mid-Miocene (Santos *et al.* 2009).

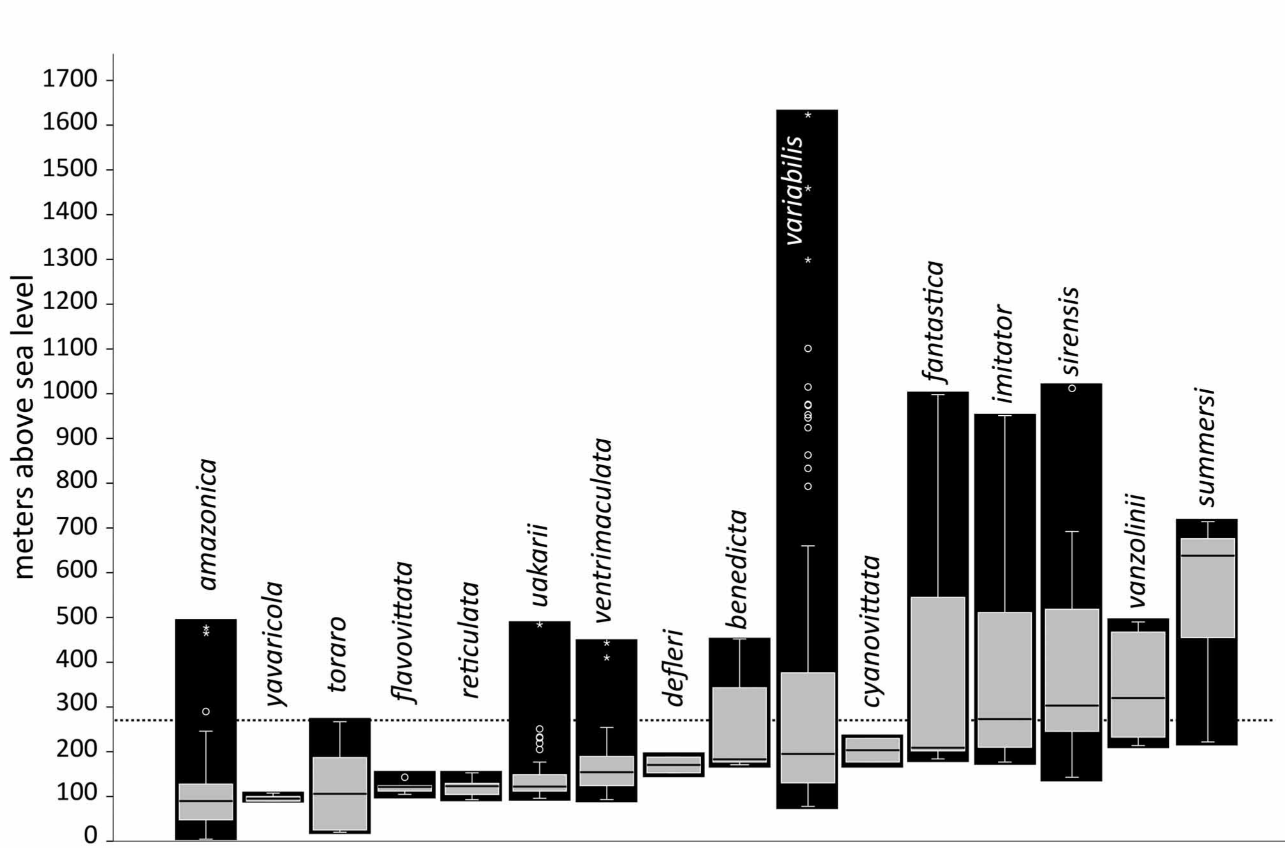

FIGURE 9. Known elevation distributions of *Ranitomeya*. Dotted line is mean for all samples. Dark boxes display the total elevation range of each species, within each contains a corresponding box plot.

Species groups contained within *Ranitomeya*

Ranitomeya defleri species group

Figs. 3, 4, 9, 10–14, Tables 4–7

A monophyletic assemblage of two divergent species: *Ranitomeya defleri* Twomey & Brown 2009 and *R. toraro* sp. nov. (this paper).

Definition and diagnosis. Adult SVL 13–18 mm; black dorsum; largely complete yellow dorsolateral and middorsal stripes present; cream spots near body on upper surfaces of legs and forearms; limbs and venter black with pale to bright blue reticulation forming round black spots on limbs and irregular spots on venter; large intestine entirely pigmented; LTRF either 2(2)/2(1) (*R. toraro* sp. nov.) or 2(2)/3(1) (*R. defleri*), oral disc emarginated (Table 2); larvae gray; eggs dark (Table 6). Vocalizations known only in *R. defleri* and consist of a series of short, insect-like buzzes, notes 0.41–0.62 sec in length, repeated at approximately 27 notes per minute (Table 5).

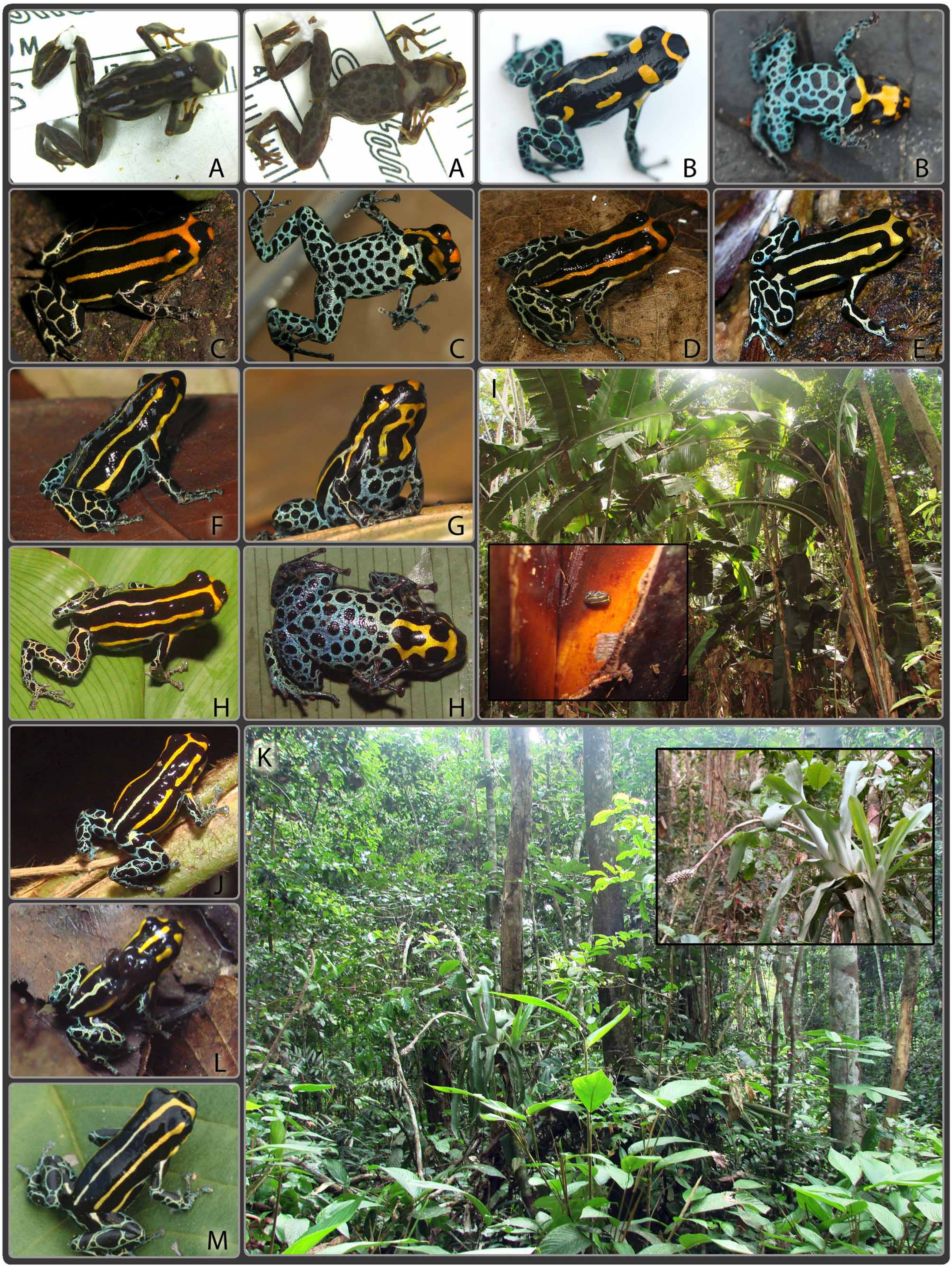

FIGURE 10. ***Ranitomeya* Plate 1.** defleri group: **A–B: *Ranitomeya defleri*** (all from Vaupés, Colombia); A: Holotype at MCZ (Ω); B: near Estación Biológica Caparú (1 Φ). **C–M: *Ranitomeya toraro*** from Brazil; C–D: Careiro da Varzea, Amazonas (A. P. Lima); E: Humaitá, Amazonas (P. I. Simoes); F–G: Cachoiera do Jirau, Rondônia (W. Hödl); H: near Boca do Acre, Amazonas (PRMS and MBS, Ω); I: Host plant of *R. toraro: Phenakospermum guyanense* near Boca do Acre, Acre (MBS); J: near Boca do Acre, Amazonas (PRMS and MBS); K: Habitat of *R. toraro* near Boca do Acre, Acre, inset: *Aechmea* sp. used for tadpole deposition (MBS); L: near Boca do Acre, Amazonas (PRMS and MBS); M: Rio Ituxi, Amazonas (JPC, Ω). (nΦ = number of individual in phylogeny, Ω = population sampled in phylogeny).

FIGURE 11. ***Ranitomeya*** **Plate 2.** <u>*defleri* group:</u> **A–H:** ***Ranitomeya toraro*** (all from Brazil); A-B: Rio Branco, Acre (T. Grant); C-F: Upper Jurua, Acre (unknown). From Colombia: G: Leticia, Amazonas (Jose Manuel Padial, Ω); H: Axil of *Aechmea* sp. with two *R. toraro* embryos, near Boca do Acre, Amazonas, BZ (MBS). **I:** *Adelphobates quinquevittatus*, near Boca do Acre, Amazonas, BZ (PRMS); **J:** *R. uakarii* near Porto Walter, Acre, BZ (JPC, Ω); **K:** Tadpole of *R. toraro* (MBS). (Ω = population sampled in phylogeny).

Ranitomeya toraro Brown, Caldwell, Twomey, Melo-Sampaio & Souza sp. nov.

Account authors: J.L. Brown, J.P. Caldwell, E. Twomey, P.R. Melo-Sampaio, M.B. Souza

Figures 3, 4, 9, 10 (c-m), 11 (a-g, k), 12**,** 13, Table 4–7

Dendrobates quinquevittatus (non Steindachner 1864) – Silverstone 1975 (partim): p. 35 [CAS 85681 collected by F. Baker and W.M. Mannat “Manaos, Brazil” 1911]

Dendrobates ventrimaculatus sensu lato (non Shreve 1935) – Caldwell & Myers 1990 (partim): p. 18, Fig. 11A [MZUSP 63792 and USNM 266119 collected by A. L. Gardner at Cachoeira Nazaré, Brazil, 9 43’S, 61 55”W, on the Rio Jiparaná (= Rio Machado), 1986 (MZUSP specimen not seen by authors)]; Christmann 2004 (partim): p.21, Figs. on p. 21, 99, 153; Brown *et al.* 2006 (partim): p. 49, Table 2, Figs. 1, 2e, 4; Noonan & Wray 2006 (partim): p. 1012, Table 2, Figs. 2, 4, 5.

Ranitomeya ventrimaculata sensu lato (non Shreve 1935) – Grant *et al.* 2006 (partim): p. 171; Twomey & Brown 2008 (partim): p. 129, Fig. 6; 2009: p. 58; Souza 2009 (partim): p. 32; Perez-Peña *et al.* 2010 (partim): p. 18, Fig. 13.

Ranitomeya sp. – Lötters *et al.* 2007: p. 510, Fig. 639; Twomey & Brown 2009: p. 58 as sp. B

Holotype. MPEG 13838, an adult male (Fig. 12) collected by J.P. Caldwell (original field number JPC 15713) on 22 December 1998, in Brazil, Amazonas state, municipality of Castanho, at km 12 on road to Autazes (ca. 40 km south of Manaus), 40 m elevation, 3° 30' 52.24" S, 59° 49' 51.13" W. This individual was hopping along a 2 cm horizontal branch about 25 cm above ground in primary forest.

Paratypes. All from the state of Amazonas, Brazil (Fig. 12). OMNH 37438–37442, MPEG 13839–13842, collected from 20 Dec 1998 to 11 January 1999 by J. P. Caldwell, L. J. Vitt, S. S. Sartorius, A. P. Lima, M. C. Araújo and T. C. Avila-Pires, same locality as holotype. OHMH 36666–36667 and MPEG 13036–13037, collected from 10 February–26 March 1997 by J. Caldwell, L. J. Vitt, S. S. Sartorius, T. C. Avila-Pires and M. C. Araújo, at Scheffer Madeireira on Rio Ituxi, ca. 170 km southwest of Lábrea, 107 m elevation, 8° 28' 45" S, 65° 42' 59" W.

FIGURE 12. ***Ranitomeya toraro*** **sp. nov. type series.** All specimens from two localities in Brazil: Amazonas state, municipality of Castanho, at km 12 on road to Autazes (ca. 40 km south of Manaus) or Scheffer Madeireira on Rio Ituxi, ca. 170 km southwest of Lábrea (labeled with ‡). Top row, from the collections of MPEG (L-R): 13839, 13838 (holotype), 13841, 13840, 13842 and 13037(‡). Bottom row, from the collections of OMNH (L-R): 37441, 37440, 36666 (‡), 37442, 37439, 36667(‡), 37438. Black bar = 20 mm (5 mm increments). Sequenced individuals (number in phylogeny): OMNH 36666 (7), OMNH 37440 (5), OMNH 36667 (6), MPEG 13841 (4)

Etymology. The species name is in reference to the noun "to 'raro," which in the Apurinã language means "frog." This indigenous Amazonian tribe occupies the center of the range of the new species. The specific epithet is used as a noun in apposition.

Definition and diagnosis. Assigned to the genus *Ranitomeya* due to the combination of the following characteristics: Adult SVL 15–17.0 mm, dorsal coloration conspicuous, dorsolateral stripes extend to top of thigh, ventrolateral stripes present, brightly colored throat, distinctive pale reticulation on limbs and venter, dorsal skin smooth, finger I greatly reduced and shorter than finger II, finger discs II–IV greatly expanded, disc of finger 1.7–2.3 times wider than finger width, thenar tubercle conspicuous, toe discs III–V moderately expanded, toe webbing absent, larval vent tube dextral, adults use arboreal phytotelmata for reproduction and deposit eggs above phytotelm, maxillary and premaxillary teeth absent.

Dorsal body and head black with complete yellow middorsal and dorsolateral stripes, extending from vent to rostrum and extending from upper surface of thighs to orbits, respectively. Limbs and venter black with pale to bright blue reticulation forming round black spots on limbs and irregular spots on venter. Chin yellow with large black paired gular spots and a central spot, irregular in some individuals. Tadpole gray, ovoid, with irregular yellow markings present from early in development.

Ranitomeya toraro can be distinguished from all other dendrobatids by its distinctive color pattern. Other species with which it could be confused include *R. amazonica, R. defleri, R. flavovittata, R. sirensis* (and its junior synonyms *R. biolat* and *R. lamasi*), *R. uakarii* and *R. ventrimaculata* (including its junior synonym *R. duellmani*). *Ranitomeya defleri* and *R. flavovittata* have highly variable dorsal markings consisting of yellow dots and elongated spots on a black ground color (versus complete middorsal and dorsolateral stripes in *R. toraro*); further, *R. defleri* has characteristic large yellow blotches behind the eyes. *Ranitomeya flavovittata* typically has a pale conspicuous yellow spot on the upper surface of each thigh (versus absent in *R. toraro*).

Some populations of *Ranitomeya sirensis* have complete, broad, yellow middorsal and dorsolateral stripes. Because of these characters, these morphs are similar in appearance to *Ranitomeya toraro*; however, in *R. toraro* the stripes are thinner and the middorsal stripe widens anteriorly, becoming at least two times wider on the head (versus equal width in *R. sirensis*). Almost all individuals of *R. sirensis* possess a large spot that is the same color as the stripe coloration (typically yellow) in the center of the venter (versus spot absent in *R. toraro*). *Ranitomeya variabilis* and *R. amazonica* are fairly variable species, but the morphs most similar to *R. toraro* have a yellow dorsum with a conspicuous black 'Y' that extends from the rump to the eyelids (versus the appearance of two black stripes due to complete medial stripe that extends to vent in *R. toraro*).

In southwest Brazil, the co-occurring *R. uakarii* appears to be a Müllerian mimic of *R. toraro*, but instead of having bicolored dorsolateral and ventrolateral stripes, all its stripes are completely yellow (see *R. uakarii* account for complete discussion). *Ranitomeya toraro* can be distinguished from the southern morphs of *R. uakarii* by the following characters: absence of a large black spot on the rostrum (versus typically present in *R. uakarii*), absence of a complete labial stripe (versus present in *R. uakarii*), fusing of black nostril spots, creating the appearance of a upside-down 'U' on the tip of the snout (versus absent in *R. uakarii*), single pair of large black gular spots (versus typically two smaller pairs in *R. uakarii*), and a middorsal stripe that is two times wider on the head compared to the sacral region (versus constant width in *R. uakarii*).

Measurements (in mm) of holotype. SVL 15.7; FL 6.9; TL 6.7; KK 12.6; FoL 6.7; HaL 4.4; HL 5.0; HW 5.0; BW 5.5; UEW 2.4; IOD 2.0; IND 1.9; TD 0.9; ED 2.0; DET 0.4; L1F 1.6; L2F 2.4; W3D 0.9; W3F 0.4. For paratype measurements see Table 7.

Description of holotype. Head widest at jaw articulation; head slightly narrower than body. Head width equal to head length; head width 31.8% of SVL. Snout acuminate in lateral view, truncate with slight rounding in dorsal view. Naris directed posterolaterally, 1.6 from tip of snout; internarial distance 2.4, 47.2% of head width. Canthus rostralis rounded, loreal region flat. Eye–naris distance 1.4, 70.0% of horizontal eye diameter. Tympanum slightly oval, posterodorsal margin hidden by depressor muscle, tympanum 45.0% of eye diameter. Tongue ovoid, attached anteriorly; median lingual process absent. Teeth absent. Paired vocal slits small, located near jaw articulation.

Body with three parallel stripes; middorsal stripe bifurcates anterior to eyes, dorsolateral stripe extends above the center of the eye to groin; ventrolateral stripe integrates into ventral reticulate pattern. Skin texture smooth on head and most of dorsum, becoming weakly granular on posterior surface of dorsum and on limbs. Ventral surfaces of body and limbs weakly granular, chin nearly smooth. Forelimbs slender, hand relatively large, 27.8% of SVL. Finger I considerably shorter than finger II when fingers appressed; finger III > II > IV > I. Discs on fingers II, III and IV greatly expanded; disc on finger I small, rounded. No webbing or lateral fringes on hand. Width of disc on finger III 2.3 times width of adjacent phalanx. Outer metacarpal tubercle (= palmar tubercle) large, round, unpigmented; inner metacarpal tubercle (= thenar tubercle) oval, located at base of finger I. Unpigmented proximal subarticular tubercles present at bases of fingers II, III and IV; on finger I tubercle is halfway to tip of digit. Smaller, distal subarticular tubercles present only on fingers III and IV, tubercle diffuse on finger IV. Tubercles raised in lateral view. Dorsal scutes present on all digits.

Length of legs moderate; heels of appessed legs reach level of eyes. Femur and tibia nearly equal in length; tibia 97.3% of femur; knee–knee distance 80.1% of SVL. Relative lengths of appressed toes, IV > III > V > II > I. Toe I short with rounded disc; toes II, IV and V with moderately expanded discs. Unpigmented outer metatarsal tubercle round, raised; unpigmented inner metatarsal tubercle oval, located at base of toe I. Unpigmented outer metatarsal tubercle located laterally at base of fifth metatarsal; unpigmented inner metatarsal tubercle located medially near base of toe I. Weakly defined tarsal keel extends from inner metatarsal tubercle for about one-third length of tarsus; tarsal tubercle absent. Two subarticular tubercles present on toes III and V, one on toes I and II. Three subarticular tubercles on Toe IV, the basal tubercle weakly defined. Toes lack webbing and lateral fringes.

Variation. Based on the 14 specimens in the type series, SVL (in mm) of adult males averaged 15.1 ± 0.2 (14.8–15.7; n = 9), adult females 16.4 ± 0.3 (16.2–16.7; n = 2), females thus slightly larger (1.3) larger than males. SVL (in mm) of juvenile females averaged 12.2 ± 0.9 (10.3–13.1; n = 3).

The striping pattern among these 14 specimens was remarkably consistent with only minor deviations. Five of the 14 individuals had a slight break in the middorsal stripe; one of these specimens had three breaks and a horizontal stripe connecting the middorsal and left dorsolateral stripe. Only one specimen had a break in either dorsolateral stripe. Specimens from the Autazes locality (n = 10) differed slightly from the Ituxi specimens (n = 4). Those from the Ituxi locality had breaks in the bifurcation of the middorsal stripe, two with breaks on both sides, and two others with breaks only on the left side. No Autazes specimens had breaks in the bifurcation of the middorsal stripe. The dorsolateral stripes in the Autazes specimens were complete (extended below eye to side of body) in two specimens, including the holotype, broken below the eye on both sides in five specimens, and on one side only in three specimens. All Ituxi specimens had breaks below the eye on both sides. Also see variation in Figs. 10 (c-m) and 11 (a-g, k).

TABLE 7. Measurements of the type series of *Ranitomeya toraro*. Individual ID: 1= OMNH 3666; 2= OMNH 36667; 3= OMNH 37438; 4=OMNH 37439; 5= OMNH 37440; 6 =OMNH 37441; 7=OMNH 37442; 8=MPEG 13036; 9=MPEG 13037; 10= MPEG 13838; 11=MPEG 13839; 12=MPEG 13840; 13=MPEG 13841, 14=MPEG 13842. All measurements are in mm.

ID	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Mean (max- min)
SVL	16.2	15.1	13.1	14.9	14.8	16.7	15.6	10.3	15.2	15.47	14.9	13.1	14.8	15.3	14.9 (16.7–13.1)
FL	7.2	7.0	6.0	6.8	8.1	7.0	7.3	4.7	7.3	6.9	5.9	5.5	7.1	7.1	6.8 (8.1–5.5)
TL	6.8	6.4	6.0	6.6	7.2	7.0	7.0	4.5	6.9	6.7	5.9	5.6	6.9	6.5	6.6 (7.2–5.6)
KK	13.6	13.0	11.0	13.0	14.2	13.6	13.3	---	13.3	12.6	12.1	10.9	14.0	12.6	12.9 (14.2–10.9)
FoL	6.5	6.1	5.4	6.2	6.1	6.6	6.3	3.9	6.4	6.7	5.1	5.7	6.0	6.0	6.1 (6.7–5.1)
HaL	4.2	4.2	3.7	4.2	4.2	4.5	4.3	2.7	4.3	4.4	4.2	3.7	4.1	4.2	4.2 (4.6–3.7)
HL	5.5	4.7	4.5	4.4	5.0	5.5	5.4	3.9	4.9	5.0	4.7	4.2	4.8	4.7	4.9 (5.5–4.2)
HW	5.3	5.1	4.2	4.7	5.0	5.0	5.1	3.8	4.9	5.0	4.7	4.4	4.9	4.9	4.9 (5.3–4.2)
BW	5.5	5.4	4.6	5.0	5.3	6.0	5.3	4.0	5.2	5.5	5.4	5.4	5.0	5.0	5.3 (6.0–4.6)
UEW	2.4	2.6	2.3	2.1	2.2	2.7	2.3	1.7	2.3	2.4	2.4	2.0	2.4	2.3	2.4 (2.7–2.0)
IOD	2.1	2.0	2.0	2.2	2.0	2.1	2.3	1.8	2.4	2.0	2.1	1.9	2.3	2.0	2.1 (2.4–1.9)
IND	2.2	2.1	1.9	2.2	2.1	2.1	2.1	1.8	2.3	1.9	2.0	2.0	2.3	2.1	2.1 (2.3–1.9)
TD	0.9	0.9	0.7	0.8	0.9	0.9	0.8	0.6	0.7	0.9	0.8	0.8	0.9	1.0	0.8 (1.0–0.7)
ED	2.3	2.2	2.0	1.6	2.0	2.6	2.1	1.5	2.2	2.0	1.9	1.7	2.0	1.9	2.0 (2.6–1.6)
DET	0.4	0.6	0.3	0.4	0.4	0.4	0.4	0.4	0.3	0.4	0.3	0.3	0.4	0.4	0.4 (0.6–0.3)
L1F	1.7	1.6	1.3	1.3	1.7	1.4	1.3	1.2	1.4	1.6	1.4	1.3	1.6	1.4	1.5 (1.7–1.3)
L2F	2.4	2.3	2.0	2.4	2.3	2.4	2.2	1.9	2.1	2.4	2.4	2.0	2.3	2.3	2.3 (2.4–2.0)
W3D	0.9	0.8	0.7	0.7	0.9	0.7	0.7	0.4	0.8	0.9	0.8	0.8	0.7	0.7	0.8 (0.9–0.7)
W3F	0.4	0.4	0.3	0.3	0.4	0.3	0.3	0.3	0.3	0.4	0.4	0.3	0.3	0.4	0.4 (0.4–0.3)
SEX	F	M	JF	M	M	F	M	JF	M	M	M	JF	M	M	9M, 2F, 3JF

Color in life. Ituxi specimens: ground color of dorsum black with three longitudinal stripes; dorsolateral stripes are iridescent yellow; middorsal stripe light yellow or light blue on back, becoming deep yellow on head. Middorsal stripe bifurcates on head (incomplete in some specimens) and extends anterior to eye not fusing with labial stripe, dorsolateral stripe extends above the center of the eye (in some speciments posterior to eye) to groin, ventrolateral stipe near axilia is light blue or greenish blue, then yellow in groin. Stripe expands on proximal upper arm to form a triangular light yellow spot. Small yellow rostral spot on tip of snout. Arms, legs and ventral surfaces with blue reticulate pattern on black ground color, forming large black round or elongate spots. Iris black. Specimens from Autazes similar, although some specimens have a light yellow reticulate pattern on the legs and venter.

Color in preservative. Dorsum dark gray with three whitish but distinct longitudinal stripes on body and head. Middorsal stripe bifurcates on head anterior to eye and extends below eye alongside to groin. Large central whitish spot on tip of snout. Reticulate pattern distinct, in shades of gray, on upper limbs, sides and all ventral surfaces except chin. Chin with central irregular whitish spot that connects to reticulate pattern on chest.

Tadpole. Five back-riding tadpoles were available for description. Three were taken from OMNH 36667 on 13 February and two were taken from MPEG 13037 on 26 March. Both nurse frogs were males and taken from the same locality; therefore, the five tadpoles are described together. All measurements (mm) are means ± SE (range in parentheses).

All tadpoles in stage 25; no external gills, not yet feeding, intestine with some yolk remaining. Snout rounded in dorsal and lateral profile; body depressed. Total length 9.5 ± 0.07 (9.3–9.6); body length 3.4 ± 0.04 (3.2–3.5); tail length 6.1 ± 0.05, 64.2% of total length. Body width 2.5 ± 0.1 (2.1–2.6); body depth 1.8 ± 0.09 (1.6–2.1); body depth 72% of body width. Eye well developed; naris small; distance from naris to anterior edge of eye 0.4 ± 0.02 (0.3–0.5). Eye positioned dorsally on head, directed dorsolaterally. Spiracle sinistral; vent tube dextral.

Tip of tail bluntly rounded. Tail muscle height at base of tail 0.9 ± 0.04 (0.8–1.0); tail muscle width at base of tail 0.9 ± 0.03 (0.8–1.0); maximum tail height 1.4 ± 0.03 (1.3–1.5). Dorsal fin slightly higher than ventral fin.

Oral disc ventral, emarginate; transverse width 0.9 ± 0.02 (0.8–0.9), 36% of body width. Single row of small papillae present laterally and ventrally; dorsal gap where papillae absent. The three tadpoles from OMNH 36667 have only A-1 developed on upper labium; P-1 on lower labium with narrow medial gap; P-2 short. The two tadpoles from MPEG 13037 have A-2 developed in addition to A-1. A-2 composed of two small segments with a large medial gap. LTRF for latter two tadpoles 2(2)/2(1), additional posterior row may develop in older tadpoles.

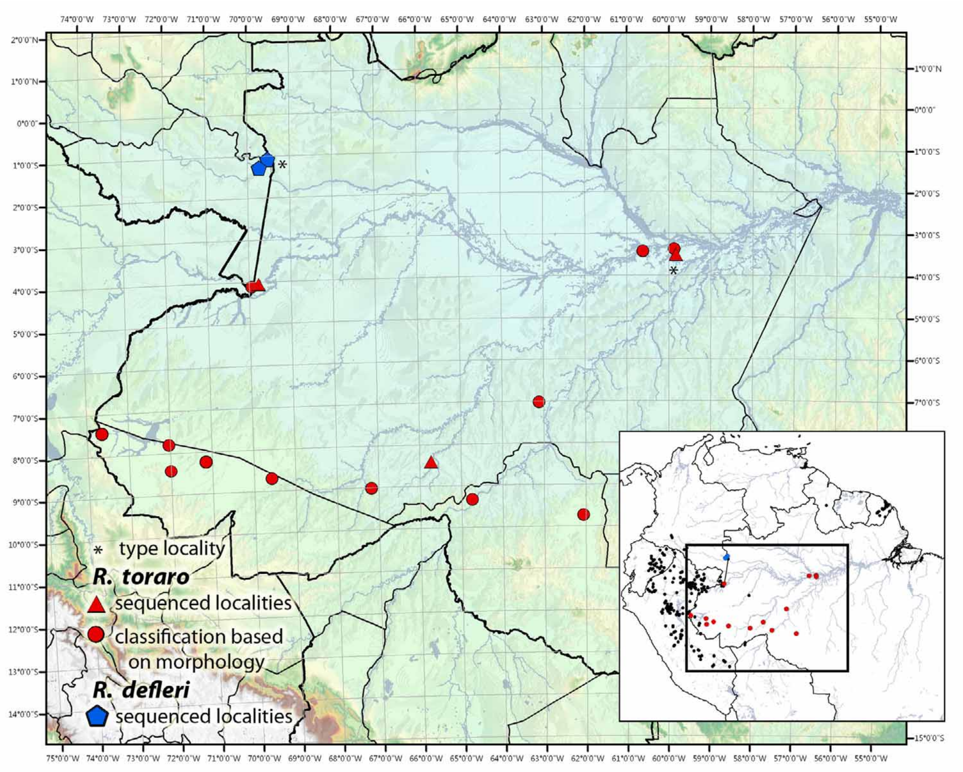

FIGURE 13. Known distribution of the *defleri* group. The inset map displays the geographic extent of distributions (black circles = all other *Ranitomeya*).

Color in preservative. Dorsum light yellow-brown with minute brown flecks. Skin opaque, gut reddish-brown. Tail musculature yellow-brown with tiny brown evenly spaced flecks; tail fins transparent with tiny brown evenly spaced flecks.

Vocalizations. Unknown.

Distribution and natural history. *Ranitomeya toraro* occurs in southwestern Brazil and the southeastern tip of Colombia, where it is known from 12 localities (Fig. 13; genetic data are from three localities). This species has been observed in the Brazilian states of Amazonas, Acre and Rondônia and the Colombian department of Amazonas. It likely occurs widely throughout the Madeira, upper Juruá and upper Purus river drainages, although further sampling is needed to determine the extent of its distribution.

Individuals from all localities have been found in undisturbed "terra firme" primary forest or old-growth secondary forest in Amazonia. These forests are not subject to flooding during the rainy season. At three localities (Boca do Acre, Autazes, Ituxi), undisturbed forests were characterized by large rainforest trees, such as Brazil nut trees (*Bertholletia excelsa*). Canopy height varied from 20 to 35 meters. The understory was open to relatively dense.

These frogs were relatively uncommon at all sites surveyed. At the Rio Ituxi site, only five frogs were observed in two months of fieldwork. Eleven individuals were found in 24 days at the Autazes site, and nine individuals were found in six days at the Boca do Acre site. At the Rio Ituxi site, frogs were found only in terra firme forest, even though extensive work was done in flooded forests along the river. Of the five frogs observed, two were in leaf litter and three were an average of 35 cm above ground on a leaf, a fallen branch and a log. At the Autazes site, two frogs were found in undisturbed primary forest and nine were found in old second-growth forest. Three were in leaf litter and eight were above ground (average, 80 cm) on leaves (two), logs (three), *Heliconia* leaves (two) and a dead palm frond (one).

To date, tadpole development sites have been found only at the Boca do Acre site. Forests at the Autazes and Ituxi sites had relatively few obvious types of phytotelmata that could serve as tadpole habitats, although *Heliconia* stands were present at the Autazes site. Four frogs found transporting tadpoles on their backs had one, two, three and three tadpoles, suggesting that males frequently carry more than one tadpole at a time. Two egg clutches were found at the Boca do Acre site, one with two eggs 5 cm about the waterline of a bromeliad, *Aechmea* cf. *bromeliifolia* and another with a single egg in the axil of the bananeira-brava plant (Strelitziaceae: *Phenakospermum guyanense*). Five tadpoles were found in bromeliad tanks and 20 were found in axils of *P. guyanense*; these tadpoles were always found occurring in separate tanks or axils, indicating that cannibalism may occur.

Notes. Unlike many species of *Ranitomeya, R. toraro* displays remarkably little morphological variation across its expansive geographic range. Although this species is sister to *R. defleri*, the two species display distinct morphological differences and deep genetic divergence. These differences are maintained even when examining *R. toraro* from Leticia, CO, which is the site where the two species come in closest contact (to our knowledge). Thus, it is unlikely that the morphological and genetic differences we observe between the two species are products of isolation-by-distance.

Conservation status. Following the IUCN Red List categories and criteria (IUCN 2010), we tentatively suggest listing this species as Least Concern (LC). The total geographic extent of this species exceeds 800,000 km^2 and much of the forests in the Madeira, upper Juruá and upper Purus drainages remain intact. However, given dramatic deforestation rates in Brazil, significant habitat loss in the near future could endanger this species.

Ranitomeya defleri Twomey & Brown 2009

Account author: J.L. Brown
Figs. 3, 4, 9–11, 13, 14
Tables 1, 4–6

Dendrobates quinquevittatus (non Steindachner 1864) – Silverstone 1975 (partim): p. 20, Fig. 14, pattern F
Ranitomeya defleri Twomey & Brown 2009: p. 1, Figs. 1–6 [MCZ 28061 (holotype) collected by Isadore Cabrera at "Rio Apaporis, Colombia", 1952]
Dendrobates defleri – Santos *et al.* 2009, by implication

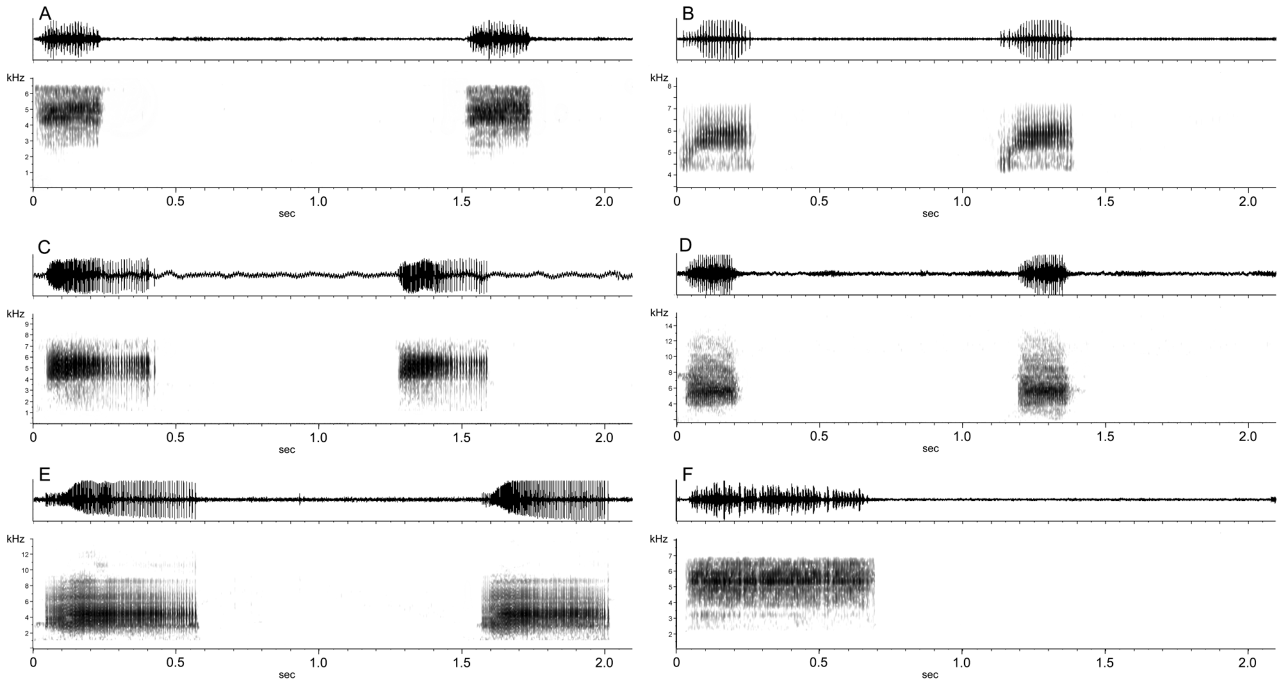

FIGURE 14. Advertisement calls of *Ranitomeya* species in the *variabilis* group and *defleri* group. A. *Ranitomeya amazonica* from 23 km S Iquitos, Loreto, Peru (type locality), recorded at 26° C; **B.** *Ranitomeya amazonica* from French Guiana, unknown temperature (call courtesy Erik Poelman); **C.** *Ranitomeya variabilis* from Cainarachi valley, San Martín, Peru, recorded at 22° C. **D.** *Ranitomeya variabilis* from Cerro Yupatí, Amazonas, Colombia, recorded at 27° C; **E.** *Ranitomeya variabilis* from Saposoa, San Martín, Peru, recorded at 24.5 C; **F.** *Ranitomeya defleri* from Rio Apaporis, Vaupés, Colombia, recorded at 26° C.

Background information. No new information is available on this species. For a summary of current knowledge on this species see Twomey & Brown (2009).

Distribution. This species is known to occur in two localities in the Amazonian rainforests of Vaupés and Amazonas departments, Colombia, though it likely also occurs in Amazonas, Brazil (Fig. 13).

Ranitomeya reticulata species group

Figs. 3, 4, 9, 15–18
Tables 1, 4–6

A monophyletic assemblage of six species: *Ranitomeya reticulata* Boulenger 1884 "1883" with its junior synonym *R. ignea* Melin 1941; *R. fantastica* Boulenger, 1884 "1883"; *R. ventrimaculata* Shreve 1935; *R. uakarii* Brown, Schulte & Summers 2006; *R. summersi* Brown, Twomey, Pepper & Sanchez-Rodriguez 2008 and *R. benedicta* Brown, Twomey, Pepper, & Sanchez-Rodriguez 2008.

Definition and diagnosis. Medium to large adult SVL (17–21 mm); black dorsum; typically orange to red dorsal patterning; LTRF 2(2)/3, oral disc emarginate; large intestine entirely pigmented; eggs dark; promiscuous mating system, male parental care; grayish tadpoles and embryos, females produce between 2–5 eggs per mating. Vocalizations consist of a series of very short buzz-like notes (0.1–0.5 sec in length) given in rapid succession (104–200 notes per minute) (Fig. 18).

Ranitomeya benedicta Brown, Twomey, Pepper and Sanchez-Rodriguez 2008

Account authors: J.L. Brown, E. Twomey, M. Pepper
Figs. 3, 4, 9, 15 (a–d), 18, 19
Tables 1, 4–6

Dendrobates quinquevittatus (non Steindachner 1864) – Silverstone 1975 (partim): p. 33, Fig. 14 (drawing), patterns K, L [USNM 127933, 127197, 127198 from "Orellana, Domo Santa Clara, Loreto, Peru", 1947]
Dendrobates fantasticus (non Boulenger, 1884 "1883") – Schulte 1999 (partim): p.57, Fig. 5, patterns K, L; Lima *et al.* 2006: p. 21, Fig. B
Ranitomeya benedicta Brown, Twomey, Pepper and Sanchez-Rodriguez 2008: p. 3, Figs. 1, 3, 5, 11 [MUSM 26957 (holotype) collected by Mark Pepper and Evan Twomey from near Shucushuyacu, Loreto, Peru, 2006]; – von May *et al.* 2008a: p. 395, Appendix 2
Dendrobates benedictus – Santos *et al.* 2009, by implication

Background information. For a summary of current knowledge on this species see Brown *et al.* 2008c.

Distribution. This species occurs within the Amazonian rainforests of San Martín and Loreto, Peru (Fig. 19).

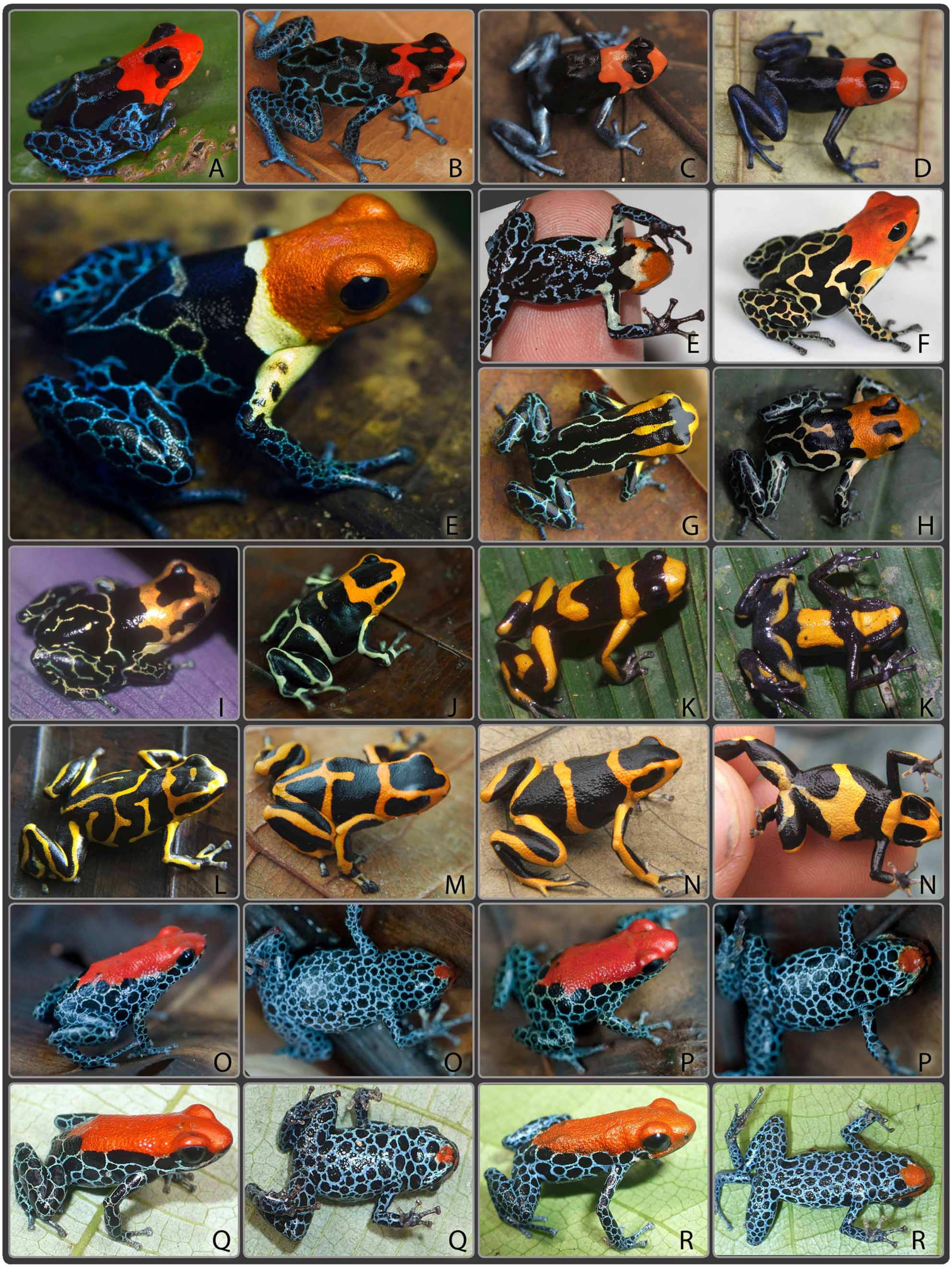

FIGURE 15. ***Ranitomeya*** **Plate 3.** reticulata group: **A–D: *Ranitomeya benedicta*** (all from Peru); A–B: Shucushuyacu, Loreto (1Φ); C-D: Pampa Hermosa, Loreto. **E–L: *Ranitomeya fantastica*** (all from Peru); E: Yurimaguas, Loreto; F: near Yumbatos, San Martin; G: Pongo de Cainarachi, San Martin (Ω); H: Cainarachi Valley, San Martin (Ω); I: San Antonio, San Martin (KS); J: Tarapoto, San Martin (Ω); K: Santa María de Nieva, Loreto (K.-H. Jungfer, 1Φ); L: Lower Huallaga Canyon, San Martin (Ω). **M & N: *Ranitomeya summersi*** (all from San Martin, Peru); M: Chazuta (3Φ); N: Sauce (Ω). **O–R: *Ranitomeya reticulata*** (all from Loreto, Peru); O-P: Iquitos (Ω); Q: Puerto Almendras (PPP); R: Upper Rio Itaya (PPP). (nΦ= number of individual in phylogeny, Ω = population sampled in phylogeny).

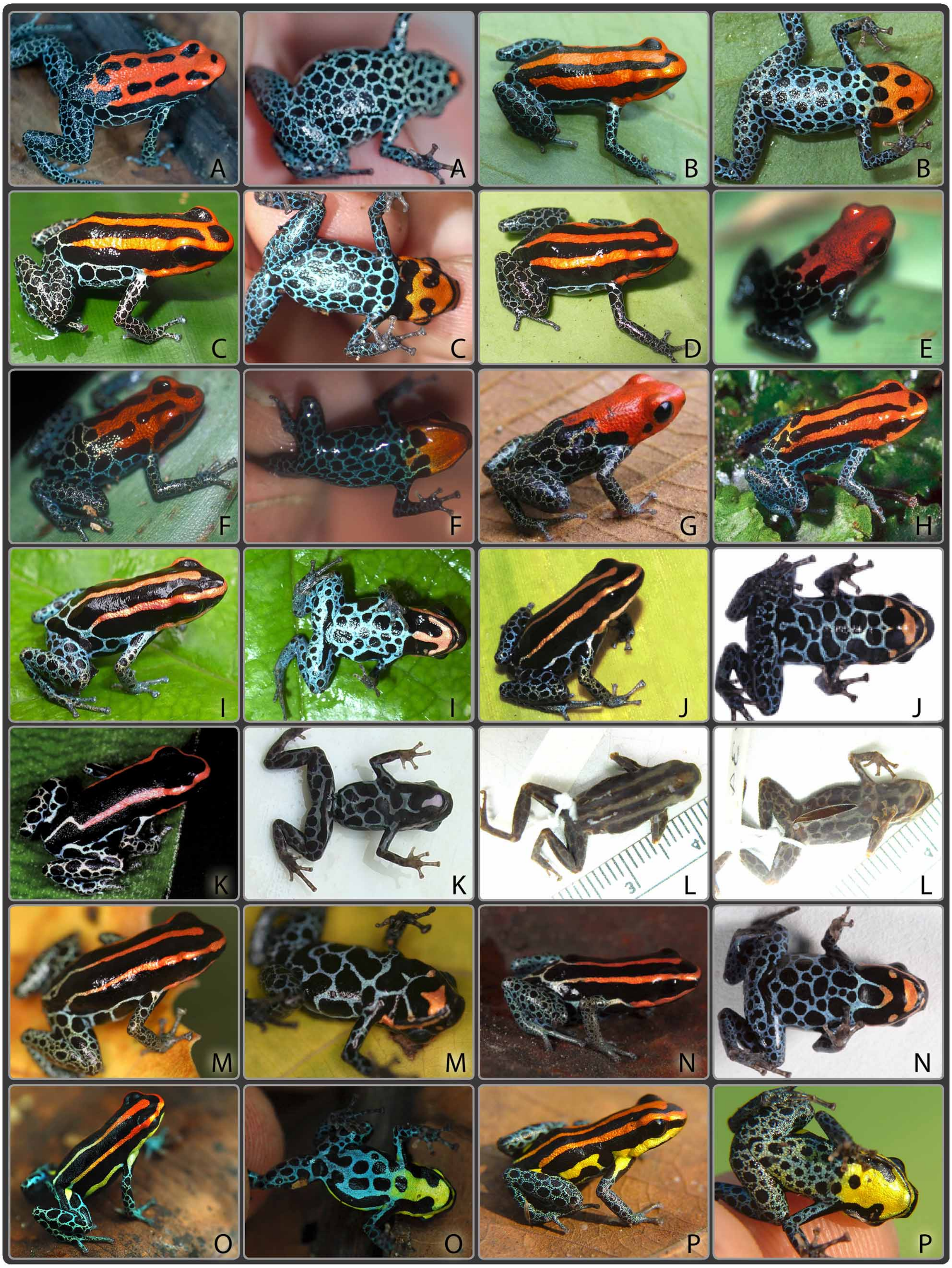

FIGURE 16. ***Ranitomeya*** **Plate 4.** reticulata group: **A–G: *Ranitomeya reticulata*** (all from Loreto, Peru); A: Lower Rio Itaya (Ω); B–D: Upper Itaya Drainage; E-F: Rio Sucusari (KS); G: 30 km west of Pevas (MSR). **H–M: *Ranitomeya ventrimaculata*:** H: Kapawi, Pastaza, EC (L. Coloma, 7Φ); I: Upper Curaray Drainage, Loreto, PE (PPP); J: Yasuní, Orellana, EC **(**A. Blasco Z., Ω); K: central Rio Nanay (M. Callegari, 6Φ); L: Holotype at MCZ, Sarayacu, Pastaza, Ecuador ; M: Yasuní, Orellana, EC (J. Yeager, Ω); N: Yasuní, Orellana, EC (S. Ron, Ω). **O & P: *Ranitomeya uakarii*** (all from Loreto, Peru): O: Tamshiyacu village (8Φ) P: Quebrada Blanco (12Φ). (nΦ = number of individual in phylogeny;Ω = population sampled in phylogeny).

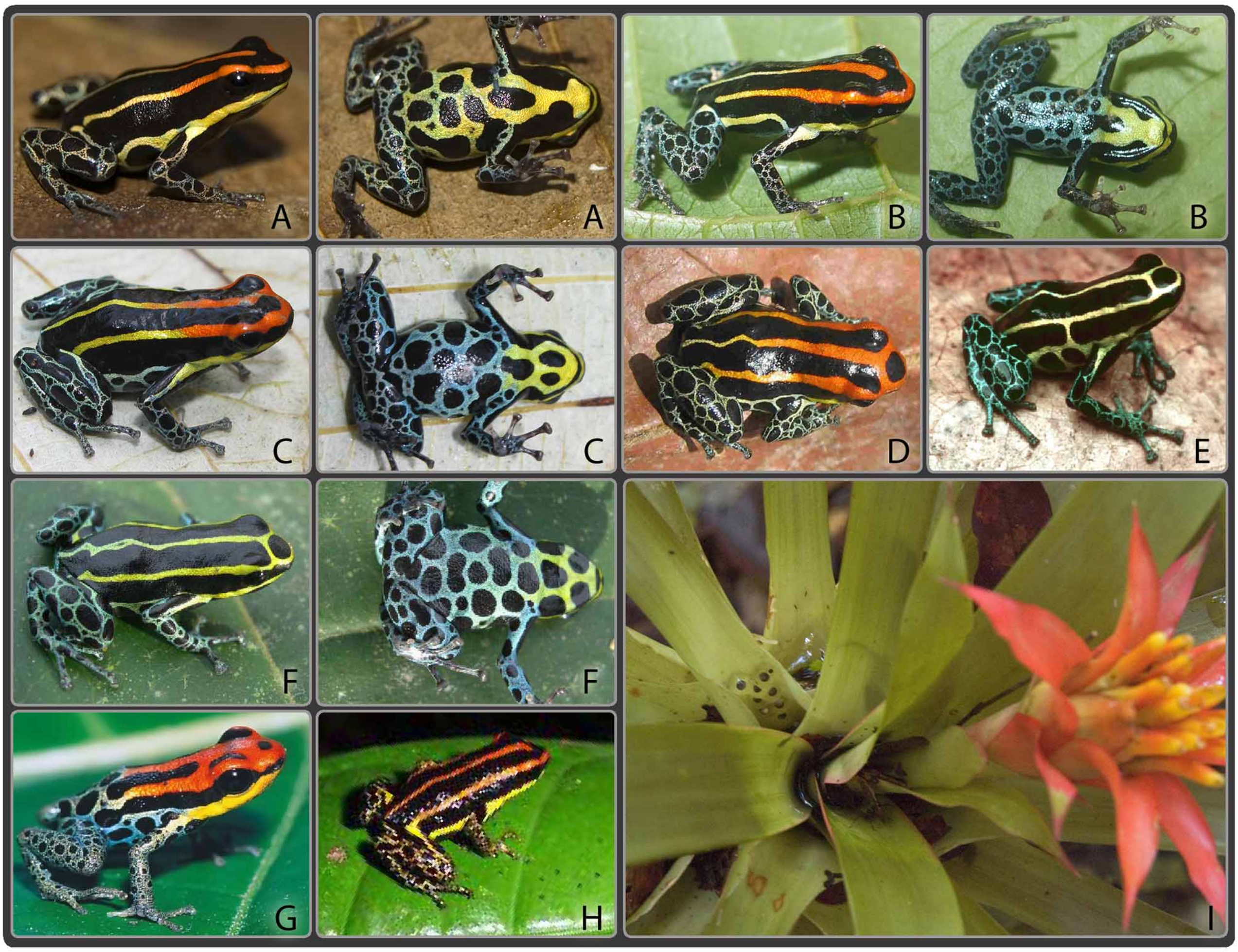

FIGURE 17. ***Ranitomeya*** **Plate 5.** reticulata group**: A–I:** ***Ranitomeya uakarii***: A: Central Rio Yavari, Loreto, Peru (PPP); B: Quebrada Blanco, Loreto, Peru (PPP, Ω); C: Rio Boncuya, Loreto, Peru (G. Gagliardi); D: Tournavista, Huánuco (A. Toebe); E: Porto Walter, Acre, Brazil (JPC); F: Rio Los Amigos, Madre de Dios, Peru (RVM); G: *R. uakarii* sp. aff. Caquetá, Colombia (J. M. Rengifo); H: *R. uakarii* sp. aff. Iwokrama, Guyana (unknown photographer); I: *Guzmania* bromeliad with *R. uakarii* embryos near Tamshiyacu village, Loreto, Peru. (Ω = population sampled in phylogeny).

Ranitomeya fantastica (Boulenger 1884 "1883")

Account authors: J.L. Brown, E. Twomey
Figs. 3, 4, 9, 15 (e–l), 18, 20
Tables 1–6

Dendrobates fantasticus Boulenger 1884 "1883": p. 635, Plate 57, drawing 3 [NHML 1947.2.15.1–4 (four syntypes) collected by Paul Hahnel from "Yurimaguas, Huallaga River, Peru"]; – Myers 1982: p. 1; Kneller 1983: p. 148; Divossen 1999: p. 58, 2002: p. 20; Schulte 1999 (partim): p. 57, Fig. 5, pattern I, L, M Cordillera Oriental "Alto Cainarachi", Cordillera Oriental "Achinamisa", Huallaga River "Reticulated Hybrid?" morphs, (I, L, M, reprinted from Silverstone, 1975); Symula *et al.* 2001 (partim): p. 2415, Fig. 1 photo E, Fig. 3 (phylogenetic tree/drawing); Symula *et al.* 2003 (partim): p. 452, Table 1, Fig. 3 (phylogenetic tree/drawing); Christmann 2004: p. 6, Figs. on p. 37, 159; Santos *et al.* 2009, by implication

Dendrobates quinquevittatus (non Steindachner 1864) – Silverstone 1975 (partim): p. 33, Fig. 14 (drawing), patterns I, L, M

Ranitomeya fantastica – Bauer 1988: p. 1; Grant *et al.* 2006: p. 171, Fig. 76; Lötters *et al.* 2007 (partim): p. 472, Figs. 588, 590; Brown *et al.* 2008a: p. 1154; 2008b: p. 5, Fig. 1; 2008c: p. 2, Figs. 1, 3, 5, 8–10; von May *et al.* 2008a: p. 394, Appendix 1

Background information. For a summary of current knowledge on this species see Brown *et al.* (2008c), with the exception of the following comments. Recently, E. Twomey rediscovered a population of *R. fantastica* that exactly matched Boulenger's description (identical to 3 of 4 types, Fig 15e) less than 20 km from Boulenger's stated type locality. Two other populations of *R. fantastica* are known to occasionally lack black crown markings (near Varadero, Loreto and near Yumbatos, San Martin), however both populations bear subtle differences and occur further from the presumed type locality (ca. 40 km NW and 55 km SW, respectively).

In 2008, Karl-Heinz Jungfer discovered a new population of this species in the Cordillera Campanquis near the Pongo de Manseriche, Loreto, Peru. Given its unique morphology and apparently disjunct distribution, we originally suspected that these frogs might represent an undescribed species. However, after performing phylogenetic analyses on sequences collected from these individuals, there is little phylogenetic support for this hypothesis and they appear to simply represent a northern population of *R. fantastica*. Ironically, the discovery of this population (which is morphologically similar in appearance to *R. summersi*), further supports the classification of *R. summersi* as a separate species from *R. fantastica*. Based on our phylogeny, a population of *R. fantastica* that occurs less than 30 km from a population of *R. summersi* is most closely related to a population of *R. fantastica* from Pongo de Manseriche. These two populations of *R. fantastica* are separated by more than 250 km and several mountain ranges, versus less than 30 km and relatively contiguous habitat. This relationship could also be attributed to incomplete lineage sorting and should be further investigated.

The phylogenetic topology of *R. fantastica*, *R. summersi* and *R. benedicta* differs from that published in Brown *et al.* (2008c). In this study, the lower Huallaga populations of *R. fantastica* are sister to *R. summersi*, which form a clade that is sister to *R. benedicta*; this entire clade is sister to the rest of the members of *R. fantastica*. In Brown *et al.* (2008c), *R. summersi* was sister to *R. fantastica* (in which, *R. fantastica* consisted of two main clades, one containing individuals from the lower Huallaga and an individual from Tarapoto and all individuals from lower Huallaga sister to all other *R. fantastica*) and both species were sister to *R. benedicta*. To clarify these differences, we performed reciprocal topology tests (using Shimodaira-Hasegawa tests, Table 3); each study's topology was tested on both datasets (note: samples not included in both analyses were left as they were in the unconstrained topology as much as possible). When using the current dataset, which contains fewer base pairs than Brown *et al.* (2008c), we found no statistical differences in either topologies (p = 0.491) suggesting they are equally probable. The differences in tree length (under Parsimony) were 1. However when using the dataset from Brown *et al.* (2008c), the Shimodaira–Hasegawa test rejected the topology observed in this study (p = 0.012), supporting the specific relationships observed in Brown *et al.* (2008c), with individuals from lower Huallaga being members of *R. fantastica*). The difference in tree lengths (via Parsimony) between these two tree topologies was 13. Thus, despite the topology of our phylogeny, we maintain that *R. benedicta* is sister to a clade containing the sister species *R. fantastica* and *R. summersi*.

Even though these results support the specific status of the lower Huallaga individuals as *R. fantastica* (Brown *et al.* 2008c; Fig. 15), this population's phylogenetic status (and specific status) is not entirely clear. In other unpublished analyses (based on different datasets), these populations were observed sister to *R. summersi* (as in this study), and based on morphology we cannot reject this possible relationship (that these populations are members of *R. summersi*). To clarify this, additional morphological and sequence data are necessary, using both mitochondrial and nuclear genes, and molecular data should be analyzed using coalescent-based phylogenies.

Distribution. This species is known to occur within the departments of Amazonas, Loreto and San Martín, Peru (Fig. 20).

Ranitomeya reticulata Boulenger, 1884 "1883"

Account authors: J.L. Brown, E. Twomey, S. Lötters, P. Perez-Peña
Figs. 3, 4, 9, 15 (o–r), 16 (a–g), 18, 21
Tables 1, 4–6

Dendrobates reticulatus Boulenger, 1884 "1883": p. 635, Plate 57, drawing 2 [NHML 1947.2.15.5–12 (eight syntypes) collected by Paul Hahnel from "Yurimaguas, Huallaga River, Peru"]; – Myers & Daly 1980: p. 20; Zimmermann & Zimmermann 1984: p. p. 35, 1985; Almendariz 1987: p. 77; Hermann 1988: p. 78; Wiltenmuth & Nishikawa 1994: p. 57; Divossen 1999: p. 58, 2000: p. 20; Rodriguez & Duellman 1994: p. 16; Lötters *et al.* 2003: p. 1909; Christmann 2004: p. 6, Figs. on p. 87, 92, 96; Santos *et al.* 2009, by implication

Dendrobates tinctorius igneus Melin, 1941: p. 66, Fig. 37A–B [MHNG 19.1.1925, 20.1.1925 (two syntypes) from "Rio Itaya (near Iquitos), Perú", collected in 1925]

Dendrobates quinquevittatus (non Steindachner 1864) – Silverstone 1975 (partim): p. 33, Fig. 14 A–C; Lescure & Bechter 1982: p. 26

Ranitomeya reticulata—Bauer 1988: p. 1; Grant *et al.* 2006: p. 171; Lötters *et al.* 2007: p. 489, Figs. 619, 620; von May *et al.* 2008a: p. 394, Appendix 1; Werner *et al.* 2010, 2011: p. 16, Figs. 1–3

Ranitomeya ignea—Grant *et al.* 2006: p. 171

Dendrobates igneus—Santos *et al.* 2009, by implication

Background information. *Ranitomeya reticulata* shares, with *R. fantastica*, the distinction of being the first species of *Ranitomeya* to be described (Boulenger 1884 "1883"). This species is also the type species of the genus *Ranitomeya* (Bauer 1988; for discussion see Grant *et al.* 2006). In the last 30 years, little controversy has surrounded the validity of this species. For a comparison of *R. reticulata* to *R. ventrimaculata,* see the *R. ventrimaculata* account.

Tadpole. The description is based on a single live tadpole from Yanamono, Loreto, Peru. Mouthparts were verified in another tadpole from the same locality. The tadpole was feeding on detritus.

Tadpole in stage 30; no external gills. Body ovoid in dorsal view, wider near vent. Total length 16.6; body length 9.8; tail length 6.8, tail length 41% of total length. Body width 5.1; body depth 4.0, 78% of body width. Eye well-developed; naris small; distance from naris to anterior edge of eye 0.7. Eye positioned dorsally on head, directed dorsolaterally. Spiracle well developed; vent tube dextral.

Tip of tail bluntly rounded. Tail muscle height at base of tail 2.5; tail muscle width at base of tail 2.3; maximum tail height 4.1. Dorsal fin same height as ventral fin.

Oral disc ventral, emarginate; transverse width 2.4, 14% of body width. Single row of small papillae present laterally and ventrally; wide dorsal gap where papillae absent. LTRF 2(2)/3(1) with A-1 developed on upper labium, A-2 with wide medial gap (30% of total width); P-1 on lower labium with narrow medial gap; P-2 equal in width to P-1; P-3 80% width of P-1.

In life, head and body gray; mouthparts visible from above. Abdomen mostly transparent; intestinal coils black, heart visible. Tail musculature uniform gray, dorsal and ventral fins opaque gray.

Natural history. Some authors have observed this species engaging in biparental care and maternal egg provisioning in captivity (Zimmermann & Zimmermann 1984; Christmann 2004), such as has been observed in the wild in *R. imitator* and *R. vanzolinii* (Caldwell 1997, Caldwell & de Oliveira 1999, Brown *et al.* 2010). These behaviors have never been confirmed in the field in *R. reticulata*, despite considerable attention by researchers (Divossen 1999, 2000; Werner *et al.* 2011). In these studies, the authors observed a species with male-only parental care and a polygamous mating system. Lastly, other members of the *reticulata* group (where parental care behaviour is known) demonstrate male-only parental care and biparental care is limited to some members of the *vanzolinii* group (Summers & McKeon 2004; Lötters *et al.* 2007). The phylogenetic placement of this species, sister to other male parental care species, cannot exclude the possibility of the independent evolution of this trait; however, it is not likely, given that biparental care/maternal provisioning is only known to have evolved twice in the family Dendrobatidae (Summers & McKeon 2004).

Taxonomic notes. In 1941, Melin described *Dendrobates tinctorius igneus*. Little information is published on this putative taxon, possibly because of a lack of credence in its validity (see Silverstone 1975). Schulte (1999) regarded it as a junior synonym of *R. reticulata*, and stated that it was a morph that maintained juvenile coloration. Grant *et al.* (2006) elevated this subspecies to specific status as *Ranitomeya ignea*, without comment or justification. After examining the holotype, Lötters & Vences (2000) suggested this species may be conspecific with either *amazonica* and/or *reticulata* (both sensu this paper). However, based on our (J.L. Brown, E. Twomey, unpub. data) observations on Puente Itaya frogs (the type localiy of *ignea*), we are confident the frogs described by Melin are referable to *reticulata* and not *amazonica*. The holotype (NHMG 512) possesses dorsolateral and middorsal stripes (partially broken) that extend about three-fourths of the SVL (14.9 mm), a characteristic common in striped *R. reticulata*. In contrast, in *R. amazonica* the middorsal stripe typically terminates between the shoulders (i.e., about one-fourth of the SVL). Lastly, we observed several populations of *R. reticulata* along the Iquitos–Nauta road, especially near Puente Itaya, that possess black dorsal markings similar to the holotype of *ignea* (which forms a dashed 'U'). As a conclusion, we place *Dendrobates tinctorius igneus* Melin, 1941 as a junior synonym of *Ranitomeya reticulata* (Boulenger, 1884 "1883").

Distribution. This species in known to occur within the Amazonian rainforests of Peru (Loreto Department) and Ecuador (Pastaza Province), Fig. 21.

Conservation status. Following the IUCN Red List categories and criteria (IUCN 2010), we tentatively suggest listing this species as Near Threatened (NT). Although the distribution of this species is estimated to be around 20,000 km^2, much deforestation has occurred along Río Amazonas. Further, Iquitos, a very large city, occupies the center of its distribution.

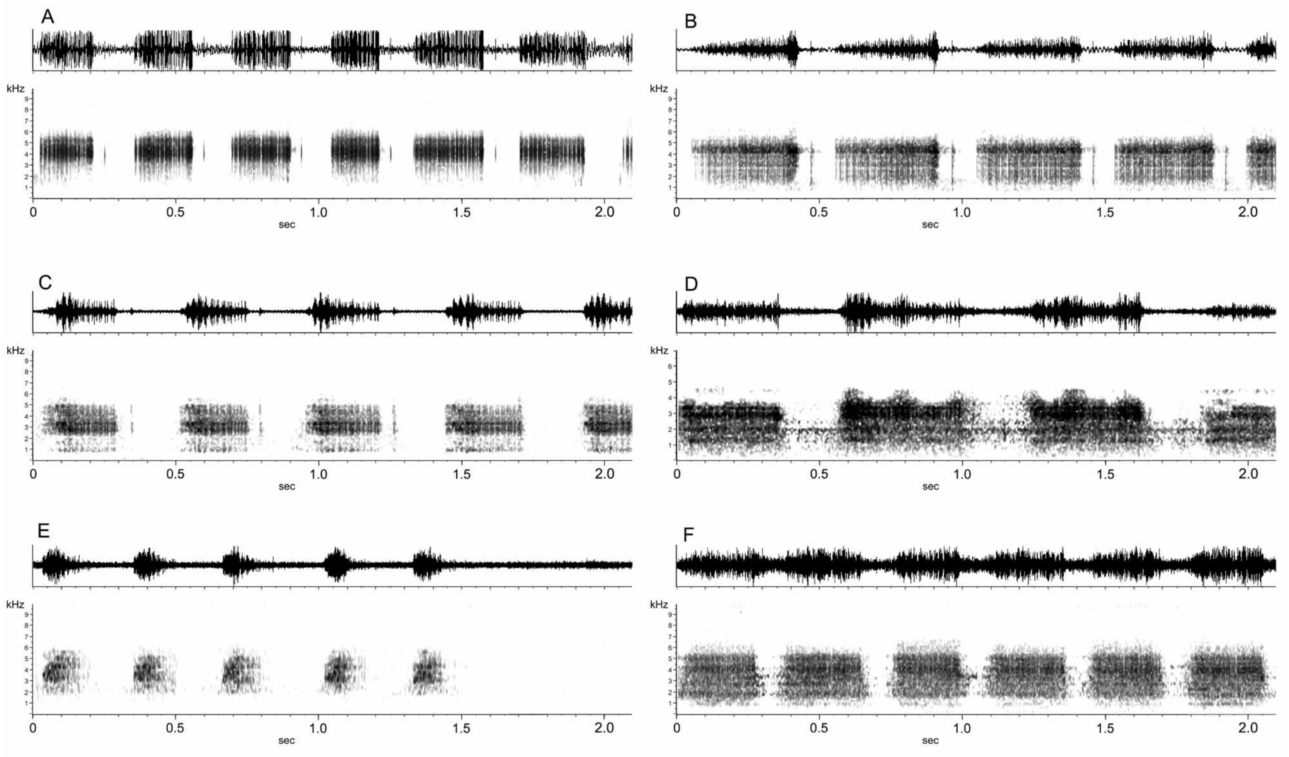

FIGURE 18. Advertisement calls of *Ranitomeya* species in the *fantastica* group. A. *Ranitomeya reticulata* from Iquitos, Loreto, Peru, recorded at 29° C; **B**. *Ranitomeya ventrimaculata*, unknown locality or temperature; **C.** *Ranitomeya fantastica* from Cainarachi valley, San Martín, Peru, recorded at 24° C; **D.** *Ranitomeya summersi* from Sauce, San Martín, Peru, recorded in captivity at 24.5° C; **E.** *Ranitomeya benedicta* from Shucushuyacu, Loreto, Peru, recorded in captivity at 26.5° C; **F.** *Ranitomeya uakarii* from Rio Tahuayo, Loreto, Peru, recorded in captivity at 26° C.

Ranitomeya summersi Brown, Twomey, Pepper & Sanchez-Rodriguez 2008

Account authors: J.L. Brown, E. Twomey, M. Pepper

Figs. 3, 4, 9, 15 (m, n), 18, 19

Tables 1, 4–6

Dendrobates quinquevittatus (non Steindachner, 1864)—Silverstone 1975 (partim): p. 33, Fig. 14 (drawing), patterns G, H

Dendrobates fantasticus (non Boulenger, 1884 "1883")—Schulte 1999 (partim): p. 57, Fig. 5 pattern G, H, Cordillera Oriental "West flank" and Cordillera Azul "North spur"; Symula *et al.* 2001 (partim): p. 2415, Fig. 1 photo E, Fig. 3 (phylogenetic tree/drawing); 2003 (partim): p. 458, Table 1 (*D. fantasticus*, Sauce), Fig. 3 (phylogenetic tree/drawing; *D. fantasticus*, Sauce); Christmann 2004: p. 32, Figs. on p. 32

Ranitomeya fantastica (non Boulenger, 1884 "1883")—Grant *et al.* 2006 (partim): p. 171; Lötters *et al.* 2007 (partim): p. 473, Fig. 592

Ranitomeya summersi Brown, Twomey, Pepper & Sanchez-Rodriguez, 2008: p. 9, Figs. 1, 5, 6, 10. [MUSM 26994 (holotype) collected by Jason L. Brown and Evan Twomey near the town of Sauce, San Martín, Perú];—von May *et al.* 2008a: p. 396, Appendix 2

Dendrobates summersi—Santos *et al.* 2009, by implication

Background information. For a summary of knowledge on this species see Brown *et al.* (2008c). An individual from near Chazuta (the locality of some of the paratypes) was included in this study's phylogeny. The results support the classification of this population based on morphology as *R. summersi* (Brown *et al.* 2008c). See *R. fantastica* account for discussion of this study's phylogenetic results and the results of Brown *et al.* (2008c).

Distribution. This species in known to occur within a small area of San Martín, Peru (Fig. 19).

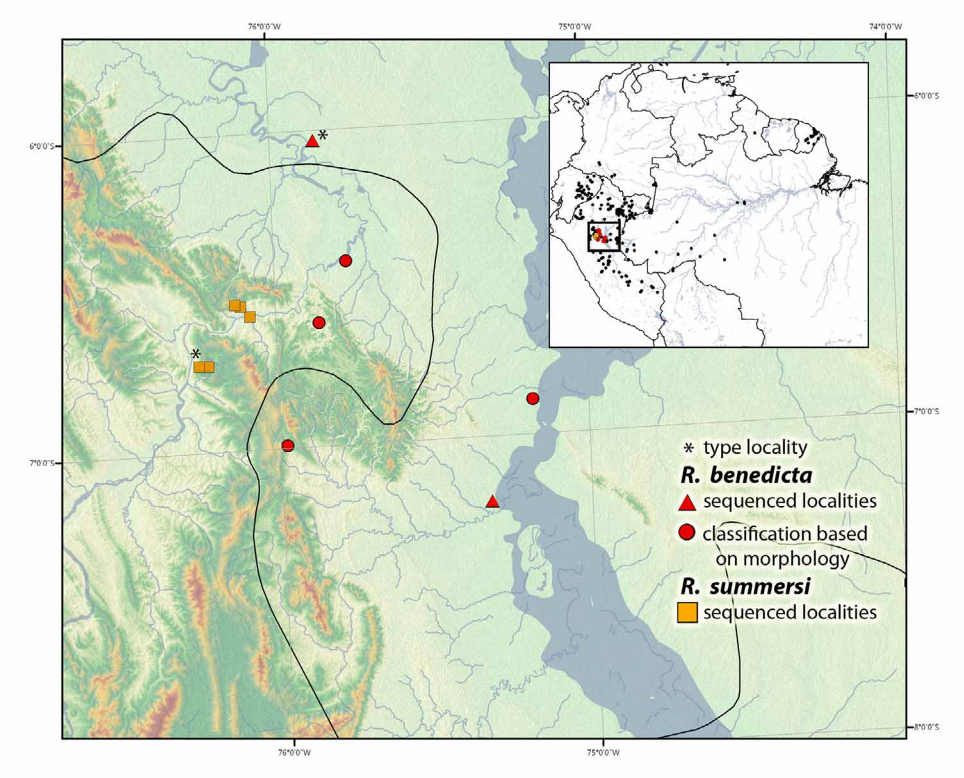

FIGURE 19. Known distribution of *Ranitomeya benedicta* and *R. summersi*. The inset map displays the geographic extent of distributions (black circles = all other *Ranitomeya*).

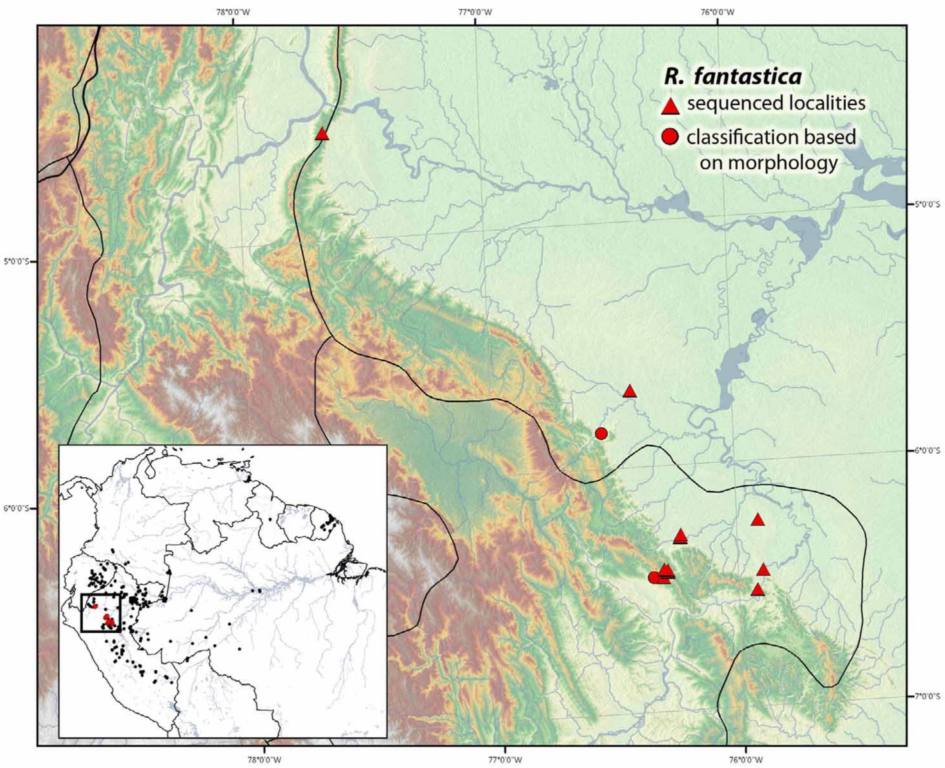

FIGURE 20. Known distribution of *Ranitomeya fantastica*. The inset map displays the geographic extent of distributions (black circles = all other *Ranitomeya*).

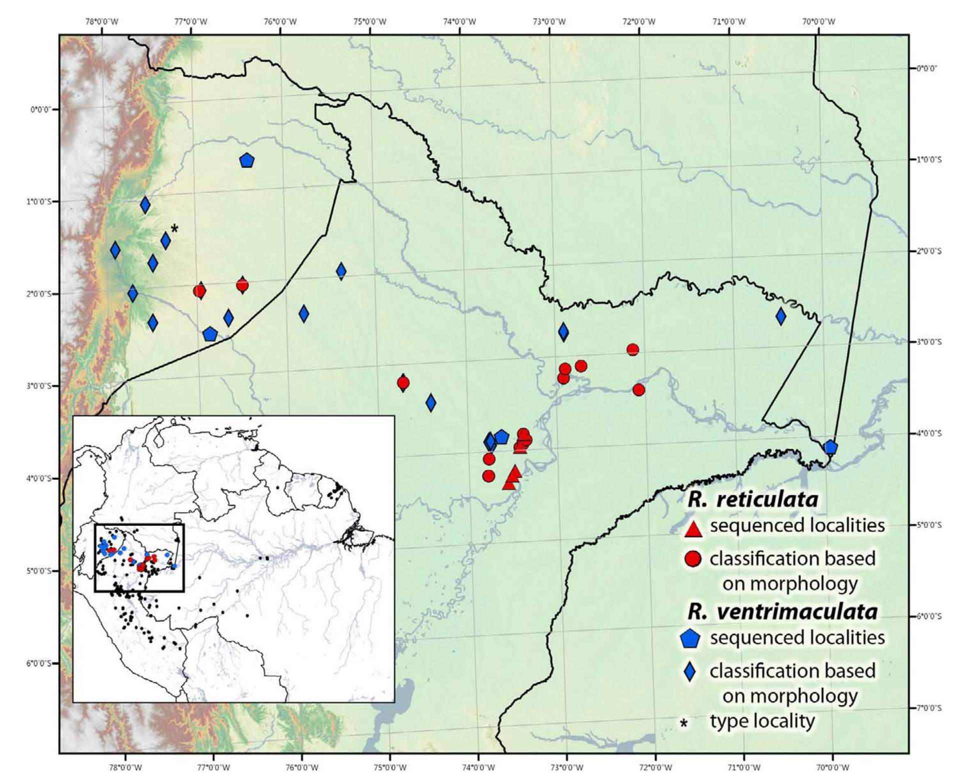

FIGURE 21. Known distribution of *Ranitomeya reticulata* and *R. ventrimaculata*. The inset map displays the geographic extent of distributions (black circles = all other *Ranitomeya*).

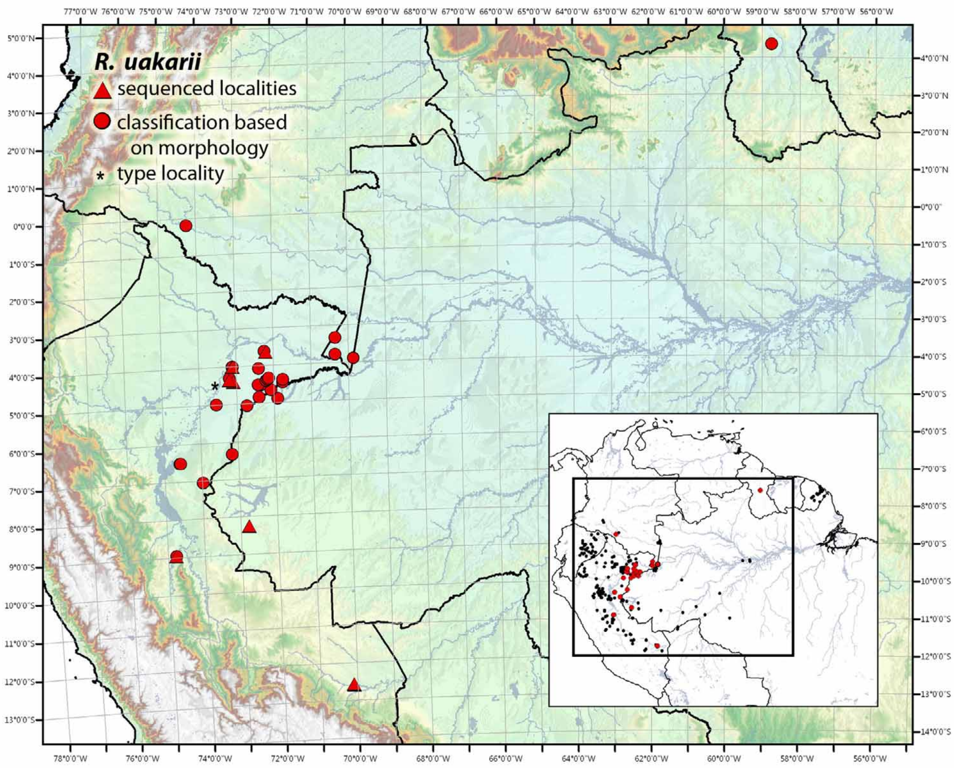

FIGURE 22. Known distribution of *Ranitomeya uakarii*. The inset map displays the geographic extent of distributions (black circles = all other *Ranitomeya*).

Ranitomeya uakarii Brown, Schulte & Summers 2006

Account authors: J.L. Brown, E. Twomey, R. von May, J.P. Caldwell, P.R. Melo-Sampaio, M.B. Souza
Figs. 3, 4, 9, 16 (o, p), 17(a–h), 18, 22
Tables 1, 4–6

Dendrobates quinquevittatus (non Steindachner 1864)—Silverstone 1975 (partim): p. 33

Dendrobates ventrimaculatus (non Shreve 1935)—Rodriguez & Knell 2003 (partim): p. 148; Christmann 2004 (partim): p. 19, Figs. on p. 19, 97, 154; Brown *et al.* 2006 (partim): p. 45, Table 2, Figs. 1, 4; Roberts *et al.* 2006a (partim): p. 382, Table 1, Fig. 4

Dendrobates duellmani (non Schulte 1999)—Roberts *et al.* 2006a (partim): p. 377, Table 1, Figs. 1, 4.

Dendrobates uakarii Brown, Schulte & Summers 2006: p.47, Figs. 1–4, Table 1, 2 [MUSM 23246 (holotype) collected by Mario Callegari upstream Quebrada Blanco near the Tamshiyacu–Tahuayo Reserve, Department Loreto, Peru, 2004];—Santos *et al.* 2009, by implication

Ranitomeya uakarii—Grant *et al.* 2006, by implication; Lötters *et al.* 2007: p. 494, Fig. 624; von May *et al.* 2008a: p. 396, Appendix 2; Perez-Peña *et al.* 2010: p. 2, Figs. 8, 13

Ranitomeya cf. *reticulata* (non Boulenger, 1884 “1883”)—Lötters *et al.* 2007: p. 493, Fig. 623.

Ranitomeya cf. *uakarii*—Lötters *et al.* 2007: p. 495, Fig. 625

Ranitomeya ventrimaculata (non Shreve 1935)—Perez-Peña *et al.* 2010 (partim): p. 18, Fig. 13

Background information. Prior to the formal description of this species as *R. uakarii*, it was considered a morph of *R. ventrimaculata* sensu this paper (see below). The type series consists of five individuals collected from just outside Tamshiyacu–Tahuayo reserve. Since this description, we have learned of additional populations of *uakarii*-like frogs from numerous localities throughout the Amazon basin. Molecular phylogenetic analyses indicate that these populations represent several morphs not discussed in the original description, making it necessary to redefine *R. uakarii.*

Definition and diagnosis. Assigned to the genus *Ranitomeya* due to the combination of the following characters: Size small (adults < 17.5 mm SVL), dorsal coloration conspicuous, dorsolateral stripes extend to top of thigh, ventrolateral stripes present, brightly colored throat, distinctive pale reticulation on limbs and venter, dorsal skin smooth, finger I greatly reduced and shorter than finger II, finger discs II–IV greatly expanded, disc of finger 2–2.5 times wider than finger width, thenar tubercle conspicuous, toe disc III–V moderately expanded, toe webbing absent, larval vent tube dextral, adults use arboreal phytotelmata for reproduction and deposit eggs above the waterline in phytotelm, maxillary and premaxillary teeth absent. Tadpole gray, ovoid, with irregular markings present from early in development. Three morphs of this species are currently known: (**i**) the Nominotypical morph (Figs. 16o–p, 17a–c, h), (**ii**) the Toraro morph (Fig. 17e**,** f) and (**iii**) the Tri-Country morph (Fig. 17g). The limbs and venters of all morphs are reticulated in blue to greenish blue on black, forming black spots.

(i) The Nominotypical morph has a dorsum with paired red or reddish-orange dorsolateral stripes (thin or thick) that extend from the tip of the snout, where they form a U-shape, to the groin. A single middorsal stripe starts on the top of the head and terminates above the vent. This stripe may occasionally form a ‘Y’ on the head, connecting with the dorsolateral stripes to create a black spot on top of snout. A yellow labial stripe continues to form a spot on the upper forearm. A yellow, irregular ventrolateral stripe is present. Venter is reticulated blue or greenish blue on black. Chin is yellow with paired black spots. This morph occurs throughout the lowlands east of Río Ucayali and southeast of Río Amazonas in Peru (Loreto and possibly Ucayali Departments) and has been observed in central Peru along Río Pachitea (Huánuco Department). A population of frogs similar in appearance has been discovered in Guyana (District: Potaro-Siparuni, Fig. 17h). Due to the seemingly widespread distribution of *R. uakarii*, we provisionally consider the Guyana population as *R. uakarii*.

(ii) The Toraro morph is so named because of its strong resemblance to *R. toraro* sp. nov. (in fact, these two species were long thought to be conspecific and may in fact be Müllerian mimics, see mimicry section). It has thin yellow dorsolateral and oblique lateral stripes. A similar middorsal stripe begins at the top of the head and terminates above the vent. The stripe typically divides into a ‘Y’ on the head (between the orbits) connecting with both dorsolateral stripes. The ventrolateral stripes often form irregular connections to the dorsolateral stripes. This morph is infrequently encountered, though it can be locally abundant (e.g., near Porto Walter, Brazil). This morph occurs within the lowland forests of southwestern Brazil (States: Acre, Amazonas), in southeastern Peru (Department: Madre de Dios) and possibly into northwestern Bolivia (Department: Pando).

(iii) In the Tri-Country morph, both the dorsolateral and middorsal stripes blend with the limb and flank reticulation in the middle of the dorsum (between the axilla and groin, gradually changing from red to blue). The black space between the dorsolateral and middorsal stripe typically creates the appearance of a black 'U' with the bottom near the snout (occasionally this 'U' is broken and the red nose spot fuses with the red middorsal stripe). The upper lip has a short yellow stripe that terminates on the upper surface of the forearms. This morph lacks a distinct oblique lateral stripe. This morph has not been genetically sampled, thus its classification should be considered provisional. This rare morph is known to occur in southeastern Colombia (Departments: Amazonas and Caquetá) near the three-country corner shared between Peru, Colombia and Brazil. Thus, we would not be surprised if this morph were discovered in nearby Brazil or Peru.

The Nominotypical morph is similar in appearance to *Ranitomeya amazonica*, *R. ventrimaculata* (sensu this paper) and some morphs of *R. reticulata*. *Ranitomeya amazonica* typically possesses a conspicuous black 'Y' which starts mid-dorsum and terminates at the snout (some morphs of *R. ventrimaculata* appear similar to this, possessing a broken 'U', giving the appearance of a black 'Y', but they typically have complete to largely complete middorsal stripes). Individuals of *R. uakarii* with red dorsolateral stripes typically have yellow ventrolateral stripes (versus typically absent in *R. ventrimaculata* and *R. reticulata*, or, if present, the ventral and limb reticulation are the same color).

The Toraro morph can be distinguished from its apparent mimic, *R. toraro*, by the following characters: presence of a large black spot on the rostrum (typically absent in *R. toraro*), presence of a complete labial stripe (absent in *R. toraro*), non-fused black nostril spots (nostril spots fused in *R. toraro*, creating the appearance of a upside down 'U' on the tip of the snout), typically two smaller pairs of black gular spots (single pair of large spots in *R. toraro*), and a middorsal stripe that is constant width (middorsal stripe two times wider on the head compared to the sacral region in *R. toraro*). Often the ventrolateral and dorsolateral stripes are connected by small irregular stripes, middorsally.

The Tri-Country morph is similar in appearance to *R. reticulata* and *R. ventrimaculata* sensu this paper but possesses a yellow labial stripe (versus red in *R. reticulata* and pinkish-red in *R. ventrimaculata*).

Tadpole. The description is based on a single live tadpole from Río Tahuayo, Loreto, Peru. Mouthparts were verified in two other tadpoles of *R. uakarii* from Quebrada Blanco, Loreto and Tournavista, Huánuco. The tadpole was feeding on detritus.

Tadpole in stage 29, no external gills. Body ovoid in dorsal view, wider near vent. Total length 16.5; body length 6.3; tail length 10.2, 62% of total length. Body width 4.6; body depth 3.7, 80% of body width. Eyes well developed; naris small, distance from naris to anterior edge of eye 0.6. Eye positioned dorsally on head, directed dorsolaterally. Spiracle well developed; vent tube dextral.

Tip of tail bluntly rounded. Tail muscle height at base of tail 1.8; tail muscle width at base of tail 1.6; maximum tail height 2.5. Dorsal fin slightly higher than ventral fin.

Oral disc ventral, emarginate; transverse width 1.6, 35 % of body width. Single row of small papillae present laterally and ventrally; dorsal gap where papillae absent. LTRF 2(2)/3(1) with A-1 developed on upper labium, A-2 with wide medial gap (one-third total width of tooth row); P-1 on lower labium with narrow medial gap; P-2 equal width of P-1; P-3, 75% width of P-1.

Color in life. Head gray, mouthparts visible from above. Body gray, color evenly distributed; abdomen mostly transparent, intestinal coils black, heart visible. Tail musculature uniform gray, dorsal and ventral fins opaque gray.

Distribution. This species occurs in Amazonian rainforests of Brazil (States: Acre, Amazonas), possibly into Bolivia (Department: Pando), Colombia (Departments: Amazonas, Caquetá), Guyana (Potaro-Siparuni) and Peru (Departments: Huánuco, Loreto, Madre de Dios and possibly Ucayali), Figure 22.

Conservation status. Following the IUCN Red List categories and criteria (IUCN 2010), we suggest listing this species as Least Concern (LC). It exhibits a large geographical range and occurs within several protected areas.

Taxonomic remarks. This species warrants further study and could possibly represent a species complex given the geographically distinct morphs. Under the current phylogeny we find little support for this arrangement and the nominotypical and Toraro morph are not reciprocally monophyletic.

Ranitomeya ventrimaculata Shreve 1935

Account authors: J.L. Brown, E. Twomey, E.H. Poelman
Figs. 3, 4, 9, 16 (h–n), 18, 21
Tables 1, 4–6

Dendrobates minutus ventrimaculatus Shreve 1935: p. 213 [MCZ 19734 (holotype) collected by O. C. Felton from "Sarayacu, Ecuador" 1933]

Dendrobates quinquevittatus (non Steindachner 1864)—Silverstone 1975 (partim): p. 33; Almendariz 1987 (partim): p. 77; Lötters 1987 (partim) p. 72, Fig. 1

Dendrobates ventrimaculatus—Daly *et al.* 1987 (partim): p. 1025; Rodriguez & Duellman 1994 (partim): p. 17, Plate 2d; Caldwell & Myers 1990 (partim): p. 1; Santos *et al.* 2009, by implication

Dendrobates duellmani Schulte, 1999: p. 69 [NHMK 231832 (holotype, wrongly given as NHMK 221832 in the original description and corrected by Lötters & Vences 2000: p. 252), unspecified collector from "San Jacinto, 2 km, nahe der ekuadadorianischen Grenze, Loreto, Peru," restricted to "Südöstliche Umgebung vom Ölcamp San Jacinto (bei 2°18'42.8" S, 75°51'57.9" W), circa 180 m NN, östlich des Rio Tigre, Departamento Loreto, Peru" by Lötters & Vences 2000: p. 252];—Lötters & Vences 2000: p. 252; Santos *et al.* 2003: p. 12794, Fig. 1; Cisneros-Heredia 2003; Christmann 2004: p. 8, Figs. on p. 16, 103, 104; Darst & Cannatella 2005: p. 60, Fig. 1; Brown *et al.* 2006: p. 45, Table 2, Figs. 1, 2; Roberts *et al.* 2006a (partim): p. 377, Table 1, Figs. 1, 4; Santos *et al.* 2009, by implication

Dendrobates sp. G—Santos *et al.* 2003: p. 12794, Fig. 1; Darst & Cannatella 2005: p. 60, Fig. 1

Ranitomeya aff. *uakarii*—Lötters *et al.* 2007: p. 496, Fig. 626

Ranitomeya duellmani—Grant *et al.* 2006: p. 171; Lötters *et al.* 2007: p. 470, Fig. 587: Venegas & von May 2010: p. 282; von May & Mueses-Cisneros 2011: p. 306.

Background information. This species was originally described by Shreve (1935) as a subspecies of *Dendrobates minutus*. Silverstone (1975) considered it a junior synonym of *Dendrobates quinquevittatus*. In 1982, Myers wrote that "New material, as well as closer attention to morphological details and evidence of sympatry, convinces me that *Dendrobates quinquevittatus* Steindachner, sensu Silverstone is a composite of five or more species of distinctively colored frogs." Interestingly, almost a decade later Caldwell & Myers (1990) would point out that none of those species were in fact *D. quinquevittatus* sensu stricto.

In 1999, Schulte described *Dendrobates duellmani* from northern Peru. Its description promptly sparked criticism from Lötters & Vences (2000), primarily because most of the description was based on a photograph of a single live frog (from Rodriguez & Duellman 1994), which is traceable as NMHK 231832, and the use of other unorthodox "specimens" including a postal stamp issued by the Ecuadorian government. Nevertheless, due to unique morphology, Lötters & Vences (2000) agreed that *duellmani* was a valid species. In 2006, Grant *et al.* placed this species in the genus *Ranitomeya* within the *ventrimaculata* group. That same year, Roberts *et al.* (2006a) demonstrated that *duellmani* was polyphyletic, with one individual (the population closest to the type locality) nested within a clade of *reticulatus* and another individual that was sister to a species referred to as *ventrimaculatus* (the latter now considered to be *Ranitomeya uakarii*, see account in this paper).

Recently, the plea of Caldwell & Myers (1990) that taxonomists proceed with caution when dealing with the systematics of this group was further justified. After reading Shreve's description of *Dendrobates minutus ventrimaculata* and examining the type material, J.L. Brown was surprised to learn that most of the specimens, including the holotype, were actually identical to *R. duellmani*. It is not clear exactly when the "unofficial" definition of *R. ventrimaculata* changed to *R. variabilis* sensu this paper; however, shortly after the description of *R. duellmani*, this "definition" became absolute in the scientific literature. One cause for this change was likely due to the presumption that Schulte (1999) considered the type specimens of *R. ventrimaculata* when describing *duellmani*. The situation was further exacerbated by an abundance of observations of the more widely distributed species: *variabilis* and *amazonica* sensu this paper, which at that time were also being called *ventrimaculata*. Due to the clarity of Shreve's definition (see excerpt below) and morphology of the type specimens, we herein formally consider *Ranitomeya ventrimaculata* to be senior synonym of the junior synonym *Ranitomeya duellmani*. For classification of species considered to be *R. ventrimaculata* from 1987 to 2010, see the *R. variabilis* and *R. amazonica* accounts.

> *Black above, three prominent, longitudinal, grayish lines extending from the head almost the entire length of the back, the outermost starting about the posterior border of the upper eyelid, the median about on a level with the anterior border of the upper eyelid (in the paratypes* [and type] *these dorsal lines are often rather pinkish). Fifteen of the paratypes have substantially the same dorsal markings as the type; ten* [now considered to be *R. variabilis*] *show an alternative set of dorsal markings. In these the median dorsal line is much shortened and sends out a pair of branches on the head (sometimes one of the pair is missing)…*[and] *the outermost lines* [i.e., the oblique and dorsolateral lines] *are often joined by a transverse line at their posterior ends* [commonly observed in *R. variabilis* but not *R. ventrimaculata* sensu stricto]…
>
> B. Shreve 1935, p. 214

Definition and diagnosis. Assigned to the genus *Ranitomeya* due to the combination of the following characters: adults small, SVL < 18.0 mm, dorsal coloration conspicuous, dorsolateral stripes extending to top of thigh, brightly colored throat, distinctive pale reticulation on limbs and venter, dorsal skin smooth, finger I greatly reduced and shorter than finger II, finger discs II–IV greatly expanded, disc of finger two times wider than finger width, thenar tubercle conspicuous, toe discs III–V moderately expanded, toe webbing absent, larval vent tube dextral, maxillary and premaxillary teeth absent.

This species possesses thin pink to reddish-pink middorsal and dorsolateral stripes. Dorsolateral stripes typically extend from the groin, pass through the eyes and fuse at the tip of the snout. Middorsal stripe starts between the eyes and typically terminates above the vent. Ventrolateral and oblique lateral stripes absent. In most populations, both the dorsolateral and middorsal stripes blend with the limb and flank reticulation in the middle of the dorsum (between the axilla and groin, gradually changing from red to blue). The black space between the dorsolateral and middorsal stripe typically creates the appearance of a black ‘U’ with the bottom near the snout (occasionally this ‘U’ is broken and the red nose spot fuses with red medial stripe). Labial stripe, identically colored as dorsal stripes, terminates at the upper surface of the forearms. Venter, flanks and limbs are finely reticulated in blue-gray to gray on black; the throat coloration varies from being entirely pinkish to pinkish only at the tip (with the remaining throat being predominantly black). Some populations near Río Nanay, ca. 40 km west of Iquitos, Loreto, and on Río Momón near Iquitos lack a middorsal stripe and possess pinkish to plum dorsolateral stripes.

This species is similar in appearance to *Ranitomeya amazonica*, *R. uakarii* and some morphs of *R. reticulata*. *Ranitomeya amazonica* typically possesses a conspicuous black ‘Y’ that starts mid-dorsum and terminates at the snout (some morphs of *R. ventrimaculata* appear similar to this, possessing a broken ‘U,’ giving the appearance of black ‘Y;’ however, they typically have a complete to largely complete middorsal stripe). *Ranitomeya uakarii* individuals with red dorsolateral stripes typically have yellow oblique lateral stripes (typically absent in *R. ventrimaculata*, or, if present, they are the same coloration as ventral and limb reticulation). Some preserved specimens lose their red dorsal coloration, and can appear identical to some morphs *R. uakarii*. The latter generally possess distinct gular spots that do not connect, giving the appearance of an hourglass on the throat (versus fused gular spots, possessing light coloration- in life pinkish- only at the anterior edge of the throat in *R. ventrimaculata*). Certain morphs of *R. reticulata* (and almost all juveniles of this taxon) possess a similar black ‘U,’ although it is typically broken rather than a complete stripe. The middorsal stripe is broad, blending with incomplete dorsolateral stripes that terminate near the mid-dorsum (Fig. 16a, f). The Río Nanay/Río Momón populations are distinct; no other *Ranitomeya* lacks a middorsal stripe while possessing pinkish dorsolateral stripes (Fig. 16k).

Natural history. Individuals of this species were found in undisturbed primary forest with deep leaf litter and low to moderately dense understory vegetation. In Napo province, Ecuador, we observed 1 to 3 individuals per day, suggesting that these frogs occur in low densities. Most frogs were observed foraging on leaf litter, occasionally climbing on tree trunks up to a meter above the forest floor. At localities where they were observed, bromeliads were not abundant on the forest floor (in many cases absent), but large bromeliads were present in the canopy. On several occasions we found vocalizing males, and males carrying 2 or 3 tadpoles on the forest floor. These observations suggest that the species has male parental care and egg clutches may be deposited in the leaf litter. However, to date, we have not been able to locate egg clutches or where males deposit their tadpoles.

Ranitomeya variabilis, *R. reticulata*, *R. uakarii*, *Allobates zaparo*, *Ameerega bilinguis* and *A. parvula* co-occur with *R. ventrimaculata*.

Vocalizations. The call of this species consists of a rapid buzz, notes 0.32–0.38 sec in length, repeated at approximately 124 notes per minute. Interestingly, in both *R. ventrimaculata* and its sister species *R. reticulata,* pulse rates are remarkably high compared to other members in their species group. Within a note, we found that individual ‘pulses’ are actually composed of triplets or quadruplets, a character that was not found in other members of the *reticulata* species group. This difference may be related to the quality of the recording (being able to detect such fine note structure in high quality recordings) rather than physiological differences in call production between species.

Distribution. This species occurs in Amazonian rainforests of Colombia (Amazonas Department), Ecuador (Provinces: Napo, Orellana, Pastaza, Sucumbíos) and Peru (Loreto Department), Fig. 21.

Conservation status. Following the IUCN Red List categories and criteria (IUCN 2010), we tentatively suggest listing this species as Least Concern (LC).

Taxonomic remarks. Over the past decade, mostly unpublished discussion has questioned the legitimacy of this species. Some have suggested that *R. ventrimaculata* is a morph of *R. reticulata* with the retention of juvenile coloration (paedomorphy; Roberts *et al.* 2006a). We remain skeptical of classifying these species as distinct because the potential distributions of both *R. reticulata* and *R. ventrimaculata* overlap considerably, something that is rare among closely related species. Further, in some areas it is impossible to distinguish them from each other, e.g., an individual from Kapawi, Ecuador is genetically classified as *R. ventrimaculata*, however is identical in coloration and pattern to some populations *R. reticulata* (possessing broad-bright red dorsal stripes versus thin-pinkish dorsal stripes observed in all other *R. ventrimaculata*). However, because our phylogenetic results support two reciprocally monophyletic clades (Fig. 3b) that are mostly consistent with the morphological differences ascribed to each species, we suggest they remain distinct until more data are available.

Ranitomeya vanzolinii species group

Figs. 3, 4, 9, 23–29
Tables 1, 4–6

A monophyletic assemblage of six species: *Ranitomeya vanzolinii* Myers 1982; *R. sirensis* Aichinger 1991 with its junior synonyms *R. biolat* Morales 1992 and *R. lamasi* Morales 1992; *R. imitator* Schulte 1986 with its junior synonyms *R. imitator intermedius* Schulte 1999 and *R. imitator yurimaguensis* Schulte 1999; *R. flavovittata* Schulte 1999; *R. yavaricola* Perez-Peña, Chavez, Twomey & Brown 2010 and *R. cyanovittata* Perez-Peña, Chavez, Twomey & Brown 2010.

Definition and diagnosis. Medium to large adult SVL (17–21 mm); black dorsum; highly variable morphology; LTRF 2(2)/3(1), oral disc emarginated; large intestine unpigmented; larvae whitish to gray; eggs cream; territoriality present in males; promiscuous (known in *R. sirensis*) or monogamous mating system (known in *R. vanzolinii* and *R. imitator*), male parental care (observed in *R. sirensis*) or biparental (observed in *R. vanzolinii* and *R. imitator*); females produce between 2–4 eggs per mating. The advertisement call of species in this group consists of a loud trill, highly tonal, with notes 0.4–1.1 sec in length, repeated at 2–14 notes per minute (Fig. 28).

Ranitomeya cyanovittata Perez-Peña, Chavez, Brown & Twomey 2010

Account author: J.L. Brown
Figs. 3, 4, 9, 23 (a, b), 29
Tables 1, 4–6

Ranitomeya cyanovittata Perez-Peña, Chavez, Brown & Twomey 2010: p. 12, Figs. 8, 10 [CORBIDI 02266 (holotype) collected by Diego Vasquez in the Río Blanco Basin near Zona Reservada Sierra Del Divisor, Departamento Loreto, Peru, September 2008]

Background information. For a summary of current knowledge on this species see Perez-Peña *et al.* 2010. Our phylogenetic results place this species in the *vanzolinii* group, sister species to *R. yavaricola*.

Distribution. This species occurs within Amazonian rainforests of Peru (Departments: Loreto, possibly Ucayali) and possibly Brazil (States: Acre, Amazonas), Fig. 29.

FIGURE 23. ***Ranitomeya*** **Plate 6.** vanzolinii group: **A & B:** ***Ranitomeya cyanovittata***: Sierra del Divisor, Ucayali, Peru (G. Knell and D. Vasquez, 1:Ω,2: 1Φ). **C & D:** ***Ranitomeya yavaricola*** (all from Loreto, Peru): C: Rio Blanco (G. Knell); D: Lago Preto (PPP, Ω). **E–I:** ***Ranitomeya flavovittata*** (all from Quebrada Blanco, Loreto, Peru (Photo credits: JLB, ET and PPP, Ω). **J–K:** ***Ranitomeya vanzolinii*** Atalaya, Ucayali, Peru (J. Yeager). **L–V:** ***Ranitomeya imitator*** (All from San Martin, Peru): L–O: Upper Canarachi Valley (‡); P–Q: Tarapoto (‡); R: Shapaja (‡); S: Chumia (‡) and T–V: Chazuta (Ω). (nΦ = number of individual in phylogeny, Ω = population sampled in phylogeny, ‡ = genetically sampled, but not included in our phylogeny).

FIGURE 24. ***Ranitomeya*** **Plate 7.** vanzolinii group: **A–Y:** ***Ranitomeya imitator*** (all from San Martin, Peru unless noted): A-B: Chazuta (Ω); C: Central Huallaga Canyon (‡); D-H: Callanayacu (‡); I-J: Lower Huallaga Canyon (‡); K-Q: Pongo de Cainarachi (Ω); R-S: Balsapuerto, Loreto (‡); T–V: Varadero, Loreto (‡) and W–Y: Curiyacu (‡). (Ω = population sampled in phylogeny, ‡ = genetically sampled, but not included in our phylogeny).

FIGURE 25. ***Ranitomeya*** **Plate 8.** *vanzolinii* group: **A–I: *Ranitomeya imitator*** Curiyacu, San Martin, Peru (‡). **J–T: *Ranitomeya sirensis*** (all from Peru unless noted): J-L: CICRA Station, Madre de Dios (Rio Los Amigos, Ω); M: near Rio Branco, Acre, Brazil (PRMS); N & O: Central Rio Urubamba, Cusco (G. Chavez); P & Q: Tingo Maria, Huánuco (ET, Ω); R: Bamboo forest, *R. sirensis* often uses the phytotelmata within bamboo for tadpole deposition, Tingo Maria, Huánuco (ET); S: Aguaytía, Ucayali; T: Codo del Pozuzo, Huánuco (20Φ). (nΦ = number of individual in phylogeny, Ω = population sampled in phylogeny, ‡ = genetically sampled, but not included in our phylogeny).

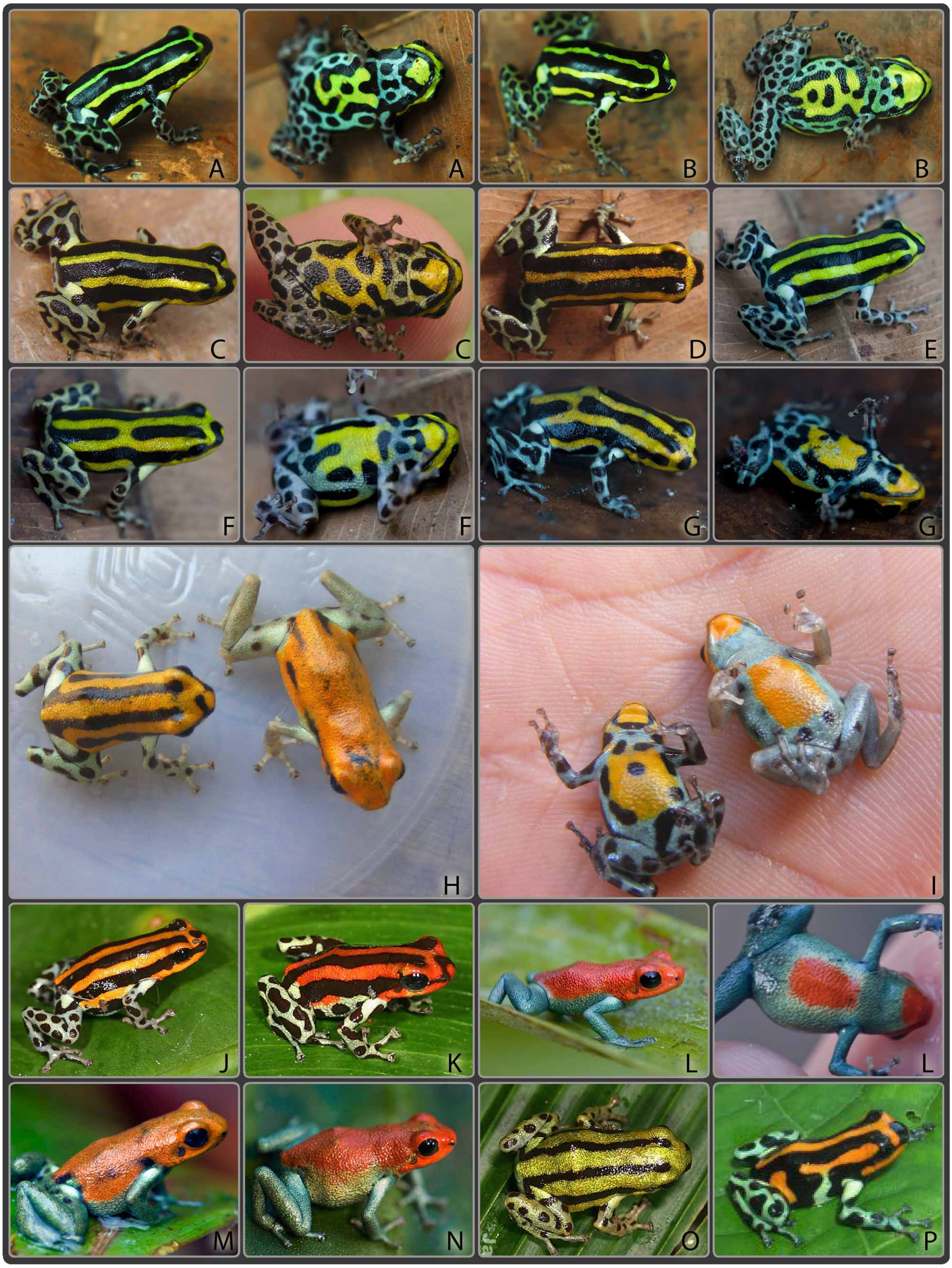

FIGURE 26. ***Ranitomeya* Plate 9.** vanzolinii group: **A–P: *Ranitomeya sirensis*** (all from Peru): A–G: Puerto Inca, Huánuco (JLB and ET, Ω); H & I: Breeding pair of *R. sirensis* found in the type locality between the lowland and highland populations, Cordillera El Sira, Huánuco (MSR); J & K: Rio Pachitea, Huánuco (J. Stenicka); L–N: Cordillera El Sira, Huánuco (B. Wilson and JLB, 10-11Φ); O: Rio Pachitea, Huánuco (J. Stenicka, 17Φ); P: Yanayacu Maquia, Ucayali. (nΦ = number of individual in phylogeny Ω = population sampled in phylogeny).

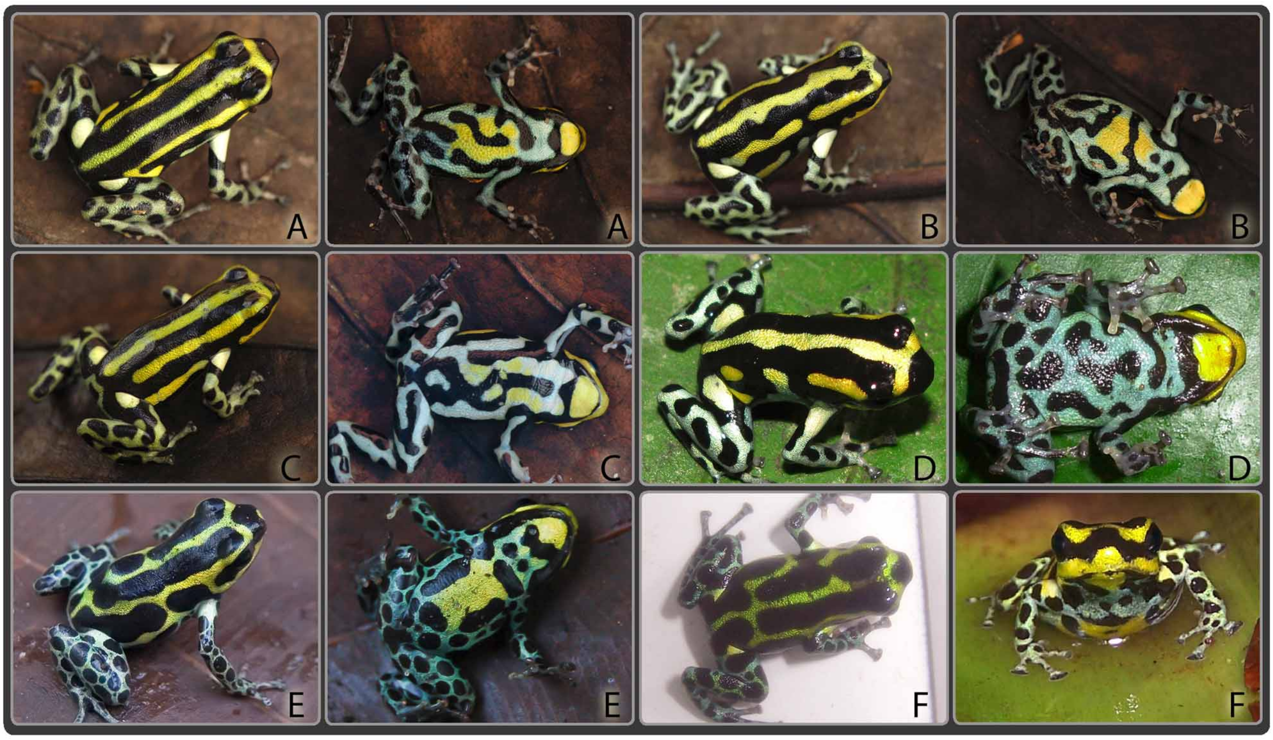

FIGURE 27. ***Ranitomeya*** **Plate 10.** *vanzolinii* group: **A–F:** ***Ranitomeya sirensis*** (all from Peru): A–D: near Contamana, Loreto (JLB and G. Gagliardi, 1-3Φ); E: uncertain locality, likely Iscozacin, Junin (7 Φ); F: Estación Biológica Paujil, Junin (L. Schulte). (nΦ = number of individual in phylogeny).

Ranitomeya flavovittata Schulte 1999

Account authors: E. Twomey, J.L. Brown, P. Perez-Peña
Figs. 3, 4, 9, 23 (e–i), 29
Tables 1, 4–6

Dendrobates flavovittatus Schulte 1999: p.80 [CRS BD 10H (holotype) from "Boca des Río Tahuayo, Nordufer, 120 m NN" = mouth of Río Tahuayo, north shore, 120 m.a.s.l, collected by Rainer Schulte];—Lötters & Vences 2000: p. 252; Brown *et al.* 2006: p. 46, Fig. 1; Roberts *et al.* 2006a: p. 378, Table 1, Figs. 2, 4; Santos *et al.* 2009, by implication

Ranitomeya flavovittata—Grant *et al.* 2006: p.171; Lötters *et al.* 2007: p. 47, Figs. 595, 596; Twomey & Brown 2008: p. 129, Table 3, Fig. 6, 2009: p. 50; von May *et al.* 2008a: p. 395, Appendix 2; Perez-Peña *et al.* 2010: p. 2, Figs. 7, 8, 13

Background information. This species was described from a single juvenile reared in the laboratory of INIBICO (Instituto de Investigación Biológica de las Cordilleras Orientales, Tarapoto, Peru). Schulte (1999) suggested that this species was closely related to *Adelphobates quinquevittatus* and *A. castaneoticus*, primarily on the basis of larval morphology. Schulte (1999) described the call as follows: "a short, harsh trill-call, this call type is unprecedented in Peru and forms a new call group" [translated from German]. Although the description was lacking in some aspects (particularly with regard to intraspecific variation), Lötters & Vences (2000), in a severe critique of Schulte (1999), nevertheless agreed on the validity of *R. flavovittata*. Roberts *et al.* (2006a) published the first genetic data for this species, supporting its validity, and found it to be nested within the *vanzolinii* group as the sister taxon to *R. vanzolinii*.

Morphologically, *R. flavovittata* strongly resembles *R. yavaricola*, although the latter lacks black markings on the legs. Each of the traits appears to be fixed within each species, respectively (Perez-Peña *et al.* 2010).

Tadpole. The description is based on a single tadpole in stage 26 from Río Tahuayo, Loreto, Peru. Tadpole in stage 26. Body ovoid in dorsal view, wider near vent. Total length 17 mm; body length 7.3; tail length 9.7, 57% of total length. Body width 6.9; body depth 5.4, 78% of body width. Eye well developed; naris small; distance from naris to anterior edge of eye 1.8. Eye positioned dorsally on head, directed dorsolaterally. Spiracle well developed; vent tube dextral.

Tip of tail bluntly rounded. Tail muscle height at base of tail 2.7; tail muscle width at base of tail 1.7; maximum tail height 3.9. Dorsal fin slightly higher than ventral fin.

Oral disc ventral, emarginate; transverse width 1.9, 28% of body width. Single row of small papillae present laterally and ventrally; dorsal gap where papillae absent. LTRF 2(2)/3(1) with A-1 developed on upper labium, A-2 with wide medial gap (one-third total width of oral disc); P-1 on lower labium with narrow medial gap; P-3 80% width P-1; P-2 equal to width P-1.

Color in life. Head whitish, mouthparts visible from above. Abdomen whitish, mostly transparent, intestinal coils tan, heart visible. Tail musculature uniform tan, dorsal and ventral fins semi-transparent, white.

Natural history. Almost nothing has been published on the natural history of this species. Schulte (1999) mentioned that he found two white eggs in a small bromeliad (*Guzmania* sp.) 1.2 m from the ground. Based on our own observations, this species appears to have similar life-history traits as other members of the *vanzolinii* group. We have witnessed adults (presumably males) carrying single tadpoles in the vicinity of *Guzmania* bromeliads. We also encountered one courting pair in the axils of a species of palm. Near Rio Yavari-Mirin, we encountered a single tadpole within a bromeliad attached to a liana 1.5 meters above the ground. Males call regularly throughout the day. It is still unknown whether this species displays biparental care like its closest relatives *R. vanzolinii* and *R. imitator* (Caldwell & de Oliveira 1999; Brown *et al.* 2010). However, anecdotal data from terrarium observations reveal that tadpoles of this species engage in “begging” behavior similar to the behavior displayed by *R. imitator* and *R. vanzolinii* when begging for food eggs (Chris Miller, pers. comm.). Therefore, this species may also have biparental care, although further study is required.

Vocalizations. The call of *R. flavovittata* is a stereotypical *vanzolinii* species group call: loud trill, notes 0.8-1.1 sec in length, repeated at roughly 2 notes per minute (Fig. 28, Table 5). We disagree with Schulte’s assertion that this species has an unusual call which should be considered a new call group. At the time of this species’ description in 1999, the calls of several species of the *vanzolinii* species group frogs were known and the call of *R. flavovittata* fits into that call type.

Distribution. The type locality is described as ‘mouth of Río Tahuayo, north shore.’ Although this leaves some ambiguity as to the precise location (Río Tahuayo flows into the Amazon on a north–south axis, therefore the two ‘shores’ are better described as east or west), we can assume that the type locality is south of the Amazon. Since 2004 we have documented several other localities for this species, all of which are in the Tamshiyacu–Tahuayo region, except for two records: one from Río Yavari and another further south from nearby Genaro Herrera (Fig. 29, Giuseppe Gagliardi, pers. comm). Based on extensive field work within this region (mainly by P. Perez-Peña), it appears that *R. flavovittata* has a highly restricted range, although areas south of Río Yavari remain under-studied. Several *flavovittata*-like frogs have been observed in Brazil near Reserva Extrativista do Alto Juruá and Parque Nacional da Serra do Divisor; however, it remains undetermined whether these frogs represent populations of *R. flavovittata* or *R. vanzolinii*. Surveys of these populations are central to clarifying the alpha-taxonomic status of this species.

This species occurs within Amazonian rainforests of Peru (Departments: Loreto, possibly in Ucayali) and possibly within Brazil (States: Acre, Amazonas).

Conservation status. The IUCN Red List of Threatened Species considers this species as Data Deficient (DD) on the basis of the unverified taxonomic status and the ambiguous type locality. This species is now known from 6 localities in the Tamshiyacu–Tahuayo region of northern Peru and its taxonomic status appears to be valid. We recommend listing this species as Least Concern (LC), applying IUCN Red List categories and criteria (IUCN 2010) since it is locally abundant and occurs in habitat that is largely unaffected by humans.

Taxonomic remarks. As in previous studies (e.g., Roberts *et al.* 2006a, Twomey & Brown 2008), our results support the arrangement of *R. flavovittata* as sister species to *R. vanzolinii*. However, our expanded dataset (which includes five *R. flavovittata* as opposed to a single individual in previous studies) raises some uncertainty as to the taxonomic status of this species. In our current phylogeny, *R. flavovittata* is paraphyletic with respect to *R. vanzolinii*. Still, *R. vanzolinii* and *R. flavovittata* are morphologically distinct and therefore we maintain the current taxonomy here until more data can be collected, particularly from intermediate geographical regions (as mentioned above). Regardless of the aforementioned taxonomic issues, introgressive hybridization appears to have occurred between this species and other members of the *vanzolini* group; we collected an individual of *R. sirensis* (Panguana morph from Contamana) whose mtDNA was most closely related to *R. flavovittata* (suggesting historic hybridization between a female *R. flavovittata* and a male *R. sirensis*, Fig. 3b).

If *R. flavovittata* is determined to be a separate species from *R. vanzolinii*, the observed phylogenetic topology could be attributed to historic introgression between the ancestors of *R. flavovittata* and *R. vanzolinii*. However, until additional populations of *R. vanzolinii* are surveyed, these questions cannot be addressed. For additional information see the *R. vanzolinii* account.

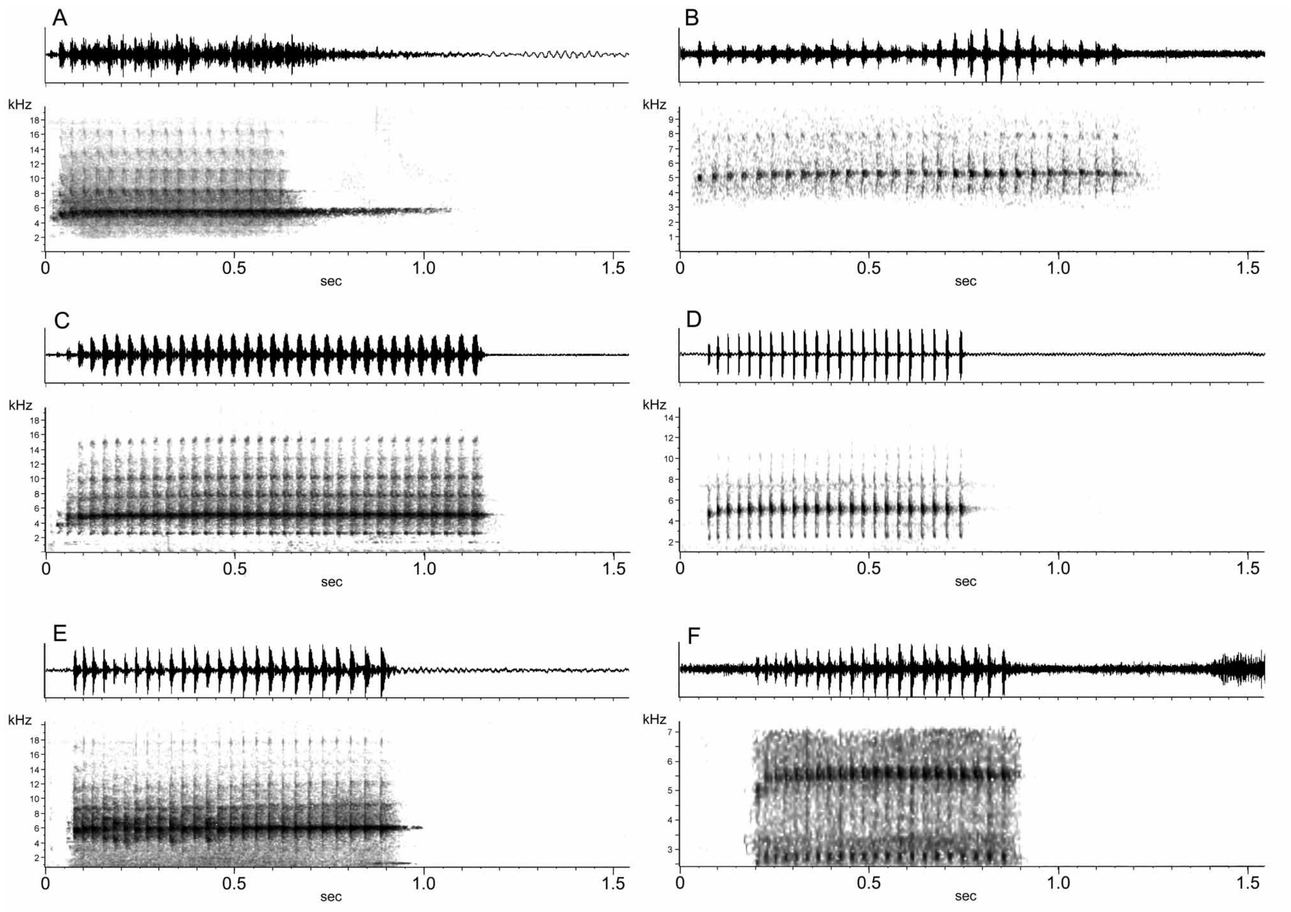

FIGURE 28. Advertisement calls of *Ranitomeya* species in the *vanzolinii* group. A. *Ranitomeya vanzolinii* from Pongo de Mainique, Cuzco, Peru, recorded in captivity at 26° C; **B.** *Ranitomeya sirensis* from Ishanga near Tocache, San Martín, Peru, recorded at 25.5° C; **C.** *Ranitomeya imitator* from Varadero, Loreto, Peru, recorded at 23.5° C; **D.** *Ranitomeya imitator* from Cainarachi valley, San Martín, Peru, recorded at 22 C; **E.** *Ranitomeya flavovittata* from Rio Tahuayo, Loreto, Peru, recorded in captivity at 25° C; **F.** *Ranitomeya yavaricola* from Lago Preto, Loreto, Peru, recorded at 24° C (call courtesy Pedro Pérez-Peña).

Ranitomeya imitator Schulte 1986

Account authors: J.L. Brown, E. Twomey
Figs. 3, 4, 9, 23 (l–v), 24 (a–y), 25 (a–i), 28, 30
Tables 1, 4–6

Dendrobates quinquevittatus (non Steindachner 1864)—Silverstone 1975 (partim): p. 35; Zimmermann and Zimmermann 1984 (partim): p. 35; 1988 (partim): p. 132

Dendrobates ventrimaculatus (non Shreve 1935)—Caldwell & Myers 1990 (partim): p. 18, Fig. 11

Dendrobates imitator Schulte 1986: p. 11, Figs. 1–10 [MUSM BATR 10501 (holotype) collected by Rainer Schulte at km 33, near the village of San Jose, Carretera Tarapoto–Yurimaguas, San Martín, Peru];—Caldwell & Myers 1990: p. 17, Fig. 11c; Divossen 1999: p. 59; Symula *et al.* 2001: p. 2145, 2003: p. 452, Table 1, Figs. 1–6; Christmann 2004: p. 6, Figs. on

p. 26, 27, 123–125; Brown *et al.* 2008a: p. 1140, Table 1, Fig. 1, 2008b: p. 1, Table 1, Figs. 1–3, 2009b: p. 478, Table 1–4, Fig. 3, 2009c: p. 148; Santos *et al.* 2009, by implication

Dendrobates imitator imitator—Schulte 1999: p. 93 Figs. PB-015, PB-016; Lötters & Vences 2000: p. 253; Lötters *et al.* 2003: p. 1905; Christmann 2004: p. 142, Figs. on p. 142, 143

Dendrobates imitator intermedius Schulte 1999: p. 95, Figs. ZB-009, PB-037, PB-034, PB-036, PB-029, PB- 040, PB-031 [CRS BD 27 (holotype) collected by Rainer Schulte at "Huallaga Canyon, Department San Martín, Perú, 200 m NN."];—Lötters & Vences 2000: p. 252; Christmann 2004: p. 30, Figs. on p. 30, 127, 128

Dendrobates imitator yurimaguensis Schulte 1999: p. 104, Figs. DB-056, PB-051, PB-035, PB-039 [CRS BD 41 (holotype) collected by Rainer Schulte on "Carretera Yurimaguas–Tarapoto, Alto Amazonas, Río Paranapura Drainage"];—Christmann 2004: p. 28, Figs. on p. 28, 29.

Ranitomeya imitator—Bauer 1988: p.1; Grant *et al.* 2006: p. 171; Lötters *et al.* 2007: p. 478, Figs. 597–609; Brown *et al.* 2008c: p. 9; 2009a: p. 1877, Table 1, 2010: p. 436, Figs. 1, 2, 4, 5; von May *et al.* 2008a: p. 396, Appendix 2

Ranitomeya intermedia—Grant *et al.* 2006: p. 171; von May *et al.* 2008a: p. 396, Appendix 2

Dendrobates intermedius—Santos *et al.* 2009, by implication

Background information. Few poison frogs have received as much attention from the public and the scientific community as *R. imitator*. Initial studies were focused on this species' validity and its mimetic relationship with *R. variabilis* and *R. summersi*, each sensu this paper, e.g., Schulte (1986), Symula *et al.* (2001, 2003). Recently, this species has been the focus of several studies regarding the evolution of parental care, mate choice and the evolution of Müllerian mimicry (e.g., Brown *et al.* 2008ab, 2009b, 2010).

This species was discovered in the late 1980s by Rainer Schulte (1986). After naming the species in 1986, Schulte (1999) further subdivided it into three subspecies, *R. imitator imitator*, *R. imitator yurimaguensis* and *R. imitator intermedius* (described below as three color morphs). These names posed various taxonomic problems (see Lötters & Vences 2000) and immediately after their publication, the name *imitator yurimaguensis* was formally synonymized with the nominotypical form by Lötters & Vences (2000). However, *imitator intermedius* tentatively remained. Grant *et al.* (2006) elevated the status of *imitator intermedius* to full species (as *R. intermedia),* but provided no justification for this taxonomic arrangement.

Ranitomeya imitator has been the subject of several phylogenetic and population genetic studies and has been densely sampled throughout its known range (Symula *et al.* 2001, 2003; E. Twomey & J.L. Brown, unpub. data). In addition, researchers have collected a considerable amount of acoustic, morphological and behavioral data on most populations of this species (E. Twomey, J.L. Brown & J. Yeager, unpub. data). None of the data from these studies indicate that *R. imitator* is a species complex or adequately justifies the use of subspecies. In particular, recent population genetic studies have demonstrated that most color morphs are not reciprocally monophyletic, or even genetically distinct. Furthermore, within many populations different color morphs are known to coexist. To maintain the use of subspecies (and the resulting classification of *R. intermedia*) is misleading, ignoring considerable variation within and between most populations. Because of these reasons, we consider *R. intermedia* to be a junior synonym of *R. imitator.*

Definition and diagnosis. Assigned to the genus *Ranitomeya* due to the combination of the following characters: adult SVL < 20.0 mm, dorsal coloration conspicuous, dorsolateral stripes, when present, extend to top of thighs, brightly colored throat, distinctive pale reticulation on limbs and venter (absent in some populations), dorsal skin smooth, finger I greatly reduced and shorter than finger II, finger discs II–IV greatly expanded, disc of finger two times wider than finger width, thenar tubercle conspicuous, toe discs III–V moderately expanded, toe webbing absent, larval vent tube dextral, adults use phytotelmata for reproduction and deposit eggs away from phytotelm, maxillary and premaxillary teeth absent. Vocal slits present in males.

Rantiomeya imitator is one of the most polymorphic poison frog species and a Müllerian mimic throughout most of its range, making identification of this taxon difficult. Furthermore, it possesses no single diagnostic morphological character that is consistent for all morphs. Three primary morphs exist: **(i)** Striped morph (Fig. 24b–g, i–v), **(ii)** Spotted morph (Fig. 23l–v, 24a, h) and **(iii)** Banded morph (Figs. 24w–y, 25a–i). Although these three morphs predominate many populations do not exactly fit any of them (e.g., Fig. 24b, c, x, y). To thoroughly describe the morphs of a species that possesses such an immense variation undervalues complicated intrapopulation and interpopulation variation. Thus, the color morphs described below should be interpreted 'loosely' and in the context that they do not always represent a population or common ancestry.

(i) The Striped morph has a black dorsum with three thin yellow longitudinal stripes extending the length of the body. The presence of two paired spots on the nostrils creates the appearance of a yellow 'cross' anterior to the eyes (occasionally spots fuse to make a black "U," Fig. 24o). Flanks are black and usually have a single yellow ventrolateral stripe that runs from the axilla to the groin. Legs, forelimbs and venter are black with fine light green to blue reticulation. The striped morph occurs throughout the lowlands northeast of the Cordillera Escalera, extending eastward, across the Río Huallaga, into the Pampas del Sacramento. It occurs as far north as Varadero (Department Loreto) but not reaching Río Marañón, and as far south as the northern Cordillera Azul, San Martín, Peru.

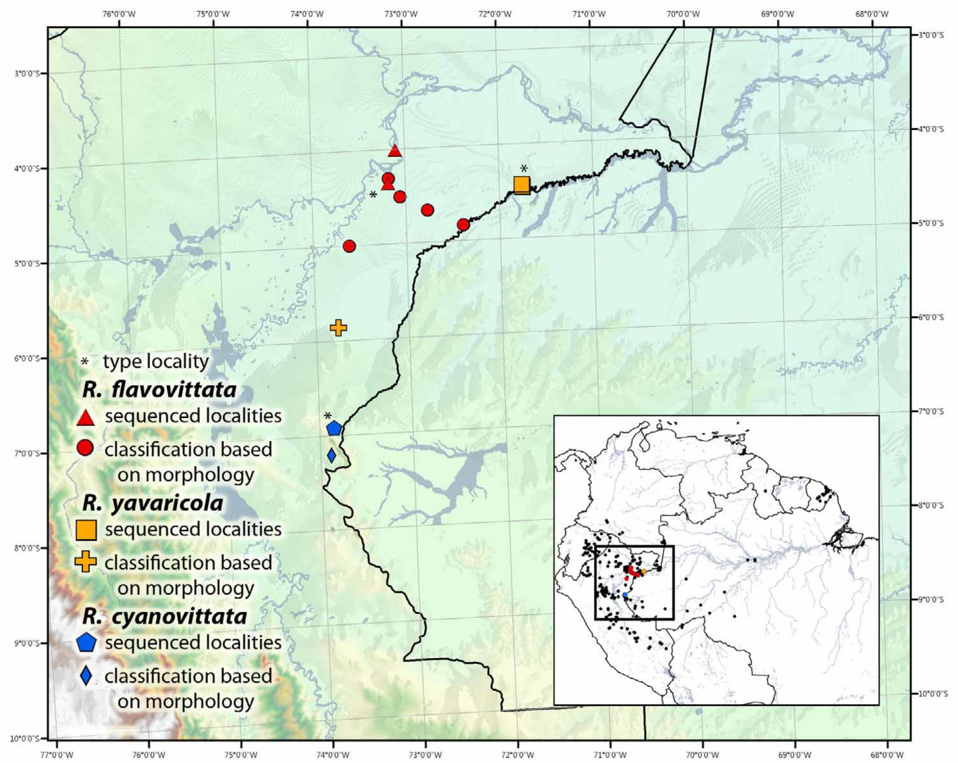

FIGURE 29. Known distribution of *Ranitomeya flavovittata*, *R. yavaricola* and *R. cyanonvittata*. The inset map displays the geographic extent of distributions (black circles = all other *Ranitomeya*).

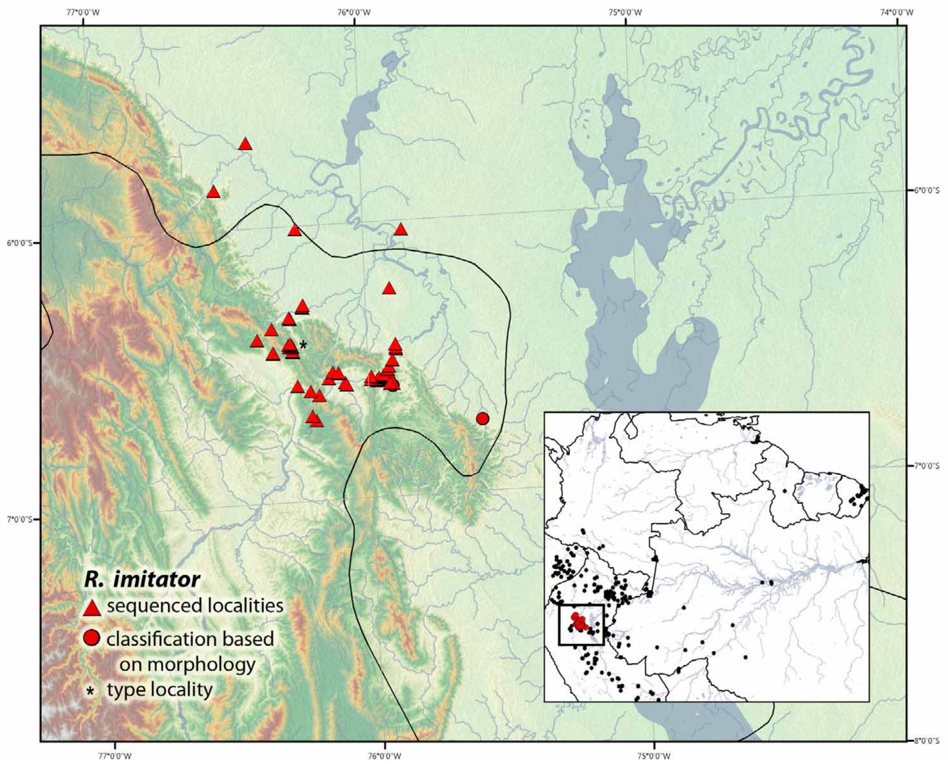

FIGURE 30. Known distribution of *Ranitomeya imitator*. The inset map displays the geographic extent of distributions (black circles = all other *Ranitomeya*).

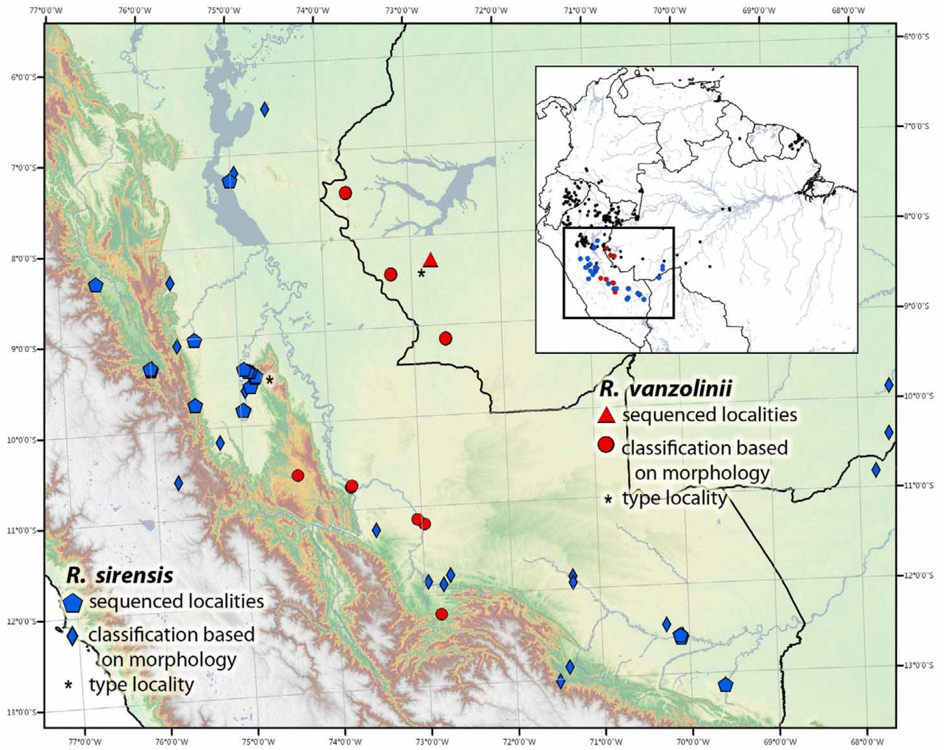

FIGURE 31. Known distribution of *Ranitomeya sirensis* and *R. vanzolinii*. The inset map displays the geographic extent of distributions (black circles = all other *Ranitomeya*).

(ii) The Spotted morph has a dorsal ground color of orange, golden yellow, or green. The dorsum has small to medium black spots that occasionally fuse, resembling irregular stripes. This morph typically possesses paired black spots on the nostrils (occasionally these spots are fused and resemble a 'U'). Legs, forelimbs and venter are the same as the Striped morph, but can also be finely to coarsely reticulate in the colors of teal to gold. This morph is montane and occurs throughout the Cordillera Escalera as far north as Balsapuerto, Loreto, Peru and as far south as Chazuta, San Martín, Peru.

(iii) The Banded morph is the most variable; however, the majority of individuals possess a black dorsum with symmetrical orange (occasionally yellow) bands (occasionally possessing a complete or partial vertebral stripe). This morph is found throughout the central Huallaga canyon, San Martín, Peru.

Ranitomeya imitator is a Müllerian mimic of *R. summersi* (banded morph) and *R. variabilis* (spotted and striped morphs, see discussion). *Ranitomeya imitator* can be distinguished from these species by its loud, trill-like call (compared to faint buzz-calls in the model species) which is audible from over 5 meters. It can be distinguished from *R. variabilis* by the presence of black paired nostril nose spots (single spot in *R. variabilis*). *Ranitomeya imitator* can usually be distinguished from *R. summersi* by the presence of a black ovoid head spot (versus pentagonal in *R. summersi*) and the absence of paired black gular spots (present in *R. summersi*). This species, particularly the Striped morph, is also similar in morphology to some morphs of *R. sirensis*, although *R. imitator* lacks a yellow ventral patch and white axillary and inguinal spots typical of most forms of *R. sirensis*.

Tadpole. The description is based on a stage 26 tadpole from Cainarachi Valley, San José, San Martín, Peru. Body ovoid in dorsal view, wider near vent. Total length 17.5; body length 6.7; tail length 10.8, 62% of total length. Body width 3.7; body depth 2.2, 60% of body width. Eye well developed; naris small; distance from naris to anterior edge of eye 1.6. Eye positioned dorsally on head, directed dorsolaterally. Spiracle well developed; vent tube dextral.

Tip of tail bluntly rounded. Tail muscle height at base of tail 1.7; tail muscle width at base of tail 0.9; maximum tail height 1.9. Dorsal fin slightly higher than ventral fin.

Oral disc ventral, weakly emarginate; transverse width 1.4, 38% of body width. Single row of small papillae present laterally and ventrally; dorsal gap where papillae absent. LTRF 2(2)/3(1) with A-1 developed on upper labium, A-2 with wide medial gap (one third total width of A-2); P-1 on lower labium with narrow medial gap; P-3, 55% width P-1; P-2 equal in width P-1.

Color in preservative. Head whitish, mouthparts visible from above. Whitish abdomen, mostly transparent, intestinal coils black. Tail musculature uniform tan, dorsal and ventral fins opaque white.

Natural history. This species is a Müllerian mimic of several congeneric species throughout its range (see discussion). *Ranitomeya imitator* exhibits a seasonal monogamous mating system and biparental care. After one to two embryos hatch, the male carries the tadpoles on its back and deposits each individually in a phytotelm. Both parents then return weekly and the female deposits trophic eggs after being stimulated by the male. The tadpoles are continually fed until metamorphosis. For details and discussion of these behaviors and their evolution, and the natural history of this species see Brown *et al.* (2008a, b, 2009b, 2010).

Vocalizations. The call of *R. imitator* is stereotypical for members of the *vanzolinii* group. It is a loud trill, notes 0.44–1.07 sec in length, repeated at 7–11 notes per minute. Despite major morphological differences between populations, acoustic divergence between populations appears to be minimal (E. Twomey, unpub. data).

Distribution. This species occurs within Amazonian rainforests of Peru (Departments: Loreto and San Martín), Fig. 30.

Conservation status. Following the IUCN Red List categories and criteria (IUCN 2010), we tentatively suggest listing this species as Least Concern (LC). Its distribution is estimated to be around 10,000 km^2. Because of the pet market demand and extreme morphological variation over a small geographic area, some color morphs maybe vulnerable.

Ranitomeya sirensis Aichinger 1991

Account authors: J.L. Brown, E. Twomey, M. Pepper, M. Sanchez-Rodriguez, P.R. Melo-Sampaio, M.B. Souza
Figs. 3, 4, 9, 25 (j–t), 26 (a–p), 27 (a–f), 28, 31
Tables 1–6

Dendrobates quinquevittatus (non Steindachner 1864)—Silverstone 1975: p. 35 (partim) [Huánuco, Tingo Maria (CAS 85147, 85150; USNM 1666904-06)]; Meede 1980: p. 39

Dendrobates ventrimaculatus (non Shreve 1935)—Caldwell & Myers 1990 (partim): p. 19, Fig. 12 [USNM 268841–268844 collected by Reginald B. Cocroft at Tambopata, Madre de Dios, Peru]

Dendrobates sirensis Aichinger 1991: p. 1, Fig. 1–3, Table 1[NHMW 31892 (holotype) collected by Manfred Aichinger in the Serrania de Sira, Río Llullapichis drainage, Huánuco, Peru, 1987];—Schulte 1999: p. 135, Fig. DB-075; Santos *et al.* 2009, by implication

Dendrobates biolat Morales 1992; p. 195, Table 2, 3, Figs. 3–5 [MUSM 7143 (holotype) collected by Victor R. Morales at the Reserva de la Biosfera del Manu, Madre de Dios, Perú, 1987]; – Duellman & Thomas 1996; Schulte 1999: p. 121, Fig. DB-071; De La Riva *et al.* 2000: p. 3; Doan & Arriaga 2002: p. 108; Lötters *et al.* 2003: p. 1908; Christmann 2004: p. 6, Figs. on p. 37, 159; Medina-Müller 2006: p. 1; Roberts *et al.* 2006a: p. 381, Table 1, Figs. 1, 4; Brown *et al.* 2008a: p. 5, Fig. 1; Santos *et al.* 2009, by implication

Dendrobates lamasi Morales 1992; p. 191, Fig. 1, 2, 5 Table 1, 2 [MUSM 1461 (holotype) collected by Victor R. Morales at Bosque Castilla, northwest of Iscozacín, Huanacabamba, Pasco, Peru, 1986];—Schulte 1999: p. 115, Figs. PB-050, PB-018; Lötters *et al.* 2003: p. 1909; Symula *et al.* 2003: p. 453, Table 1, Figs. 2–6; Christmann 2004: p. 6, Figs. on p. 34, 35, 129–132, 148–149, 155–157; Roberts *et al.* 2006a: p. 381, Table 1, Fig. 4; Santos *et al.* 2009, by implication

Ranitomeya biolat—Grant *et al.* 2006: p. 171, Fig. 76; Lötters *et al.* 2007: p. 466, Figs. 582–586; Maldonado *et al.* 2007: p. 14, Fig. 1; von May *et al.* 2008a: p. 395, Appendix 2, 2008b: p. 66, Table 1, Fig. 1; Waldram 2008: p. 232, Fig. 1-2; Melo-Sampaio & Souza 2009: p. 447

Ranitomeya lamasi—Grant *et al.* 2006: p. 171, Fig. 76; Lötters *et al.* 2007: p. 484, Figs. 610–618; von May *et al.* 2008a: p. 396, Appendix 2

Ranitomeya sirensis—Grant *et al.* 2006: p. 171; Lötters *et al.* 2007: p. 513, Figs. 614–642; von May *et al.* 2008a: p. 394, Appendix 1

Background information. This species was described in 1991 (as *Dendrobates sirensis*) on the basis of four specimens collected in the 1970s and 1980s from the western slope of the northern Cordillera El Sira (also known as the Serranía de Sira). This site was the focus of several scientific investigations during the 1960s and 1970s, including one herpetological survey conducted in 1973 (Duellman and Toft 1979). Surprisingly, this survey did not encounter any *Ranitomeya* species and it was not until 1976 that this species was first collected, found in elfin forest at 1,560 m elevation by Werner Hanagarth. Later, in the mid 1980s, Manfred Aichinger led a herpetological survey in the Sira which lasted over a year. During this survey, only five individuals were encountered, two of which escaped after capture.

Recent efforts have been made to sample this interesting species. Not only was this species described from a remote and isolated mountain range, but morphologically it seemed quite distinct from other *Ranitomeya* species, lacking the limb reticulation typical of this genus. In 2005, M. Pepper and M. Sanchez-Rodriguez led an expedition to the Sira in an attempt to find *R. sirensis*. They were able to reach one of Aichinger's camps but were unable to locate any *R. sirensis*. In 2007, Pepper and Sanchez-Rodriguez returned to the Sira with J.L. Brown and E. Twomey and were lucky enough to find two adult *R. sirensis* less than 4 kilometers from the type locality at an elevation of 442 m (an elevation much lower than previously known for this species—it remains questionable whether this species occurs at elevations > 1400 m, as stated in the original description). This discovery occurred while returning to the camp after searching higher elevation forests less than 1 km from the type locality. The two frogs perfectly matched the original description (pictured in Fig. 26l, n) and were wedged deep within the axil of a *Xanthosoma* plant on an abandoned hunting camp.

Later that year J.L. Brown sequenced samples collected from toe-clips of these individuals and was surprised to find the sequences nested within a clade of *Ranitomeya lamasi*, described by Morales (1992), from Panguana. This clade was part of a larger clade composed of other *R. lamasi* and *R. biolat*, also described by Morales (1992). Not satisfied with the knowledge gained from this expedition, Pepper and Sanchez-Rodriguez returned again in 2008 to further clarify the status of this species. When previously in the Sira, the researchers ignored the abundant calls of *R. lamasi* and did not pursue these individuals. However, in light of the close relationship between *lamasi* and *sirensis* based on sequence data, the 2008 team pursued all individuals with *lamasi*-like calls. After several days the team had collected several courting pairs and solitary individuals. Two of the pairs were partaking in "hybridization" events between *R. lamasi* and *R. sirensis*. The first observation consisted of a male *R. sirensis* (SVL 17.3 mm) courting a female *R. lamasi* (SVL 15.6 mm, Fig. 26h). After being captured, the pair was held overnight in a plastic bottle (prior to being released) and they bred. The eggs were fertilized and began to develop. The second observation was of a male *R. lamasi* courting an intermediate female (likely a mix of the two nominal species: it had coloration like *R. sirensis* with SVL 16.1 mm, though more orange with faint broken black stripes and ventral spotting, Fig. 26m). Lastly a lone individual with intermediate morphology (as described above) was observed. These data suggest that these interactions are not atypical at the site where we observed these two nominal species. In fact, only the two individuals sequenced lacked any dark pigmentation (of the five frogs with morphologies similar to *R. sirensis*). There is the possibility that the two *R. sirensis* individuals sequenced were also "hybrids" and both were descendants of parents that had undergone maternal introgression (from *R. lamasi*) and the two represent natural species. However, given the frequency of hybridization, similar call and the shared ventral spot, we consider it highly likely that *sirensis* and *lamasi* represent one species.

In 2007, J.L. Brown spent four days in southern Peru at the CICRA research station located at the confluence of the Río Los Amigos and Río Madre de Dios. There he and R. von May, who had been conducting field work in this site for years, observed a thriving population of *R. biolat* that occupied primarily (though not exclusively) a large bamboo forest. Individuals in this population used the abundant phytotelmata within the bamboo internodes for tadpole rearing. Not surprisingly, the species used other phytotelmata, at CIRCA research station they found tadpoles in tree holes and in a mature floodplain forest in the Tambopata National Reserve, R. von May observed ten tadpoles in fallen bracts of *Iriartea deltoidea* (one of the most common large palms in western Amazonia). At both localties adults we observed calling outside of the bamboo forests (see Natural History). This behavior was similar to *R. lamasi* (i.e., from near Tingo Maria).

At the CICRA research station and Tambopota National Reserve, R. von May and J.L. Brown encountered individuals that were identical in pattern to lowland populations of *R. lamasi*, which lacked the characteristic cross on the rostrum (i.e. Fig. 25k). After sequencing several individuals of *R. biolat*, J.L. Brown found that several individuals were nested within a larger clade containing other *R. lamasi* (Fig. 3).

To reconcile the monophyly of either species (*R. biolat* and *R. sirensis*), so that each was a distinct and valid species, numerous populations of *R. lamasi* would have to be elevated to specific status. In recent years, gene trees have not been congruent with species trees in some studies (particularly mitochondrial gene trees, as used here; see Brown & Twomey 2009 for more info); however, in this case, we have no evidence to suggest that these two species are not simply morphs of a widespread, highly variable species. Within *Ranitomeya lamasi* sensu Morales (1992), several populations possess unique morphologies (i.e., Fig. 27e, 27k, now classified as morphs 2, 3 and 5 below). Of those sampled in our phylogeny, none of them are reciprocally monophyletic with respect to other morphs (including *R. biolat* and *R. sirensis*). Thus, using molecular phylogenetics, behavioral, morphological and acoustic characters, we considered *R. biolat* and *R. lamasi* to be junior synonyms of *R. sirensis*. It seems ironic that the junior synonyms of this species have been subjects of considerable scientific study, though they now bear the name of what once was one of the rarest and most enigmatic poison frogs.

Definition and diagnosis. Assigned to the genus *Ranitomeya* due to the combination of the following characters: adult SVL< 20.0 mm, dorsal coloration conspicuous, dorsolateral stripes extend to top of thighs, brightly colored throat, distinctive pale reticulation on limbs and venter, dorsal skin smooth, finger I greatly reduced and shorter than finger II, finger discs II–IV greatly expanded, disc of finger 2–2.4 times wider than finger width, thenar tubercle conspicuous, toe discs III–V moderately expanded, toe webbing absent, larval vent tube dextral, maxillary and premaxillary teeth absent. Adults use phytotelmata for reproduction and deposit eggs above phytotelm. Tadpole light gray, ovoid, with irregular markings present late in development. Five principal morphs of this species currently are known: (**i**) the Sira morph (Fig. 26l–n), (**ii**) the Lamasi morph (Fig. 27e–f), (**iii**) the Divisoria morph (Fig. 25p–s), (**iv**) the Biolat morph (Fig. 25j–o) and (**v**) the Panguana morph (Figs. 25t, 26a–g, j,k, o, p, 27a–d). All possess a large, brightly-colored ventral spot (typically yellow) on a bluish to greenish ground color (a possible synapomorphy shared with *R. vanzolinii* and occasionally *R. flavovittata*).

(**i**) The Sira morph is an amelanistic morph (lacking any black pigmentation). This morph has a solid red to orange-red dorsum and metallic, sage-green limbs and ventral coloration. The throat and center of the belly each have a large spot, identically colored as dorsum. This is the nominotypical morph for the species and is only known to occur within the Cordillera El Sira, Huánuco, Peru.

(**ii**) The Lamasi morph possesses irregular and broken yellow to yellow-green dorsolateral, ventrolateral and middorsal stripes that often connect to each other irregularly. Venter and limbs are green to blue-green and coarsely reticulated. Most individuals possess bright white to cream spots on the upper surface of the upper thighs, near the groin and upper surface of the forearms, near the axilla. All other morphs have blue to blue-gray reticulation/spotting on venter and limbs on a black ground color. Further, they all possess largely complete middorsal, dorsolateral and ventrolateral stripes. This morph in only known to occur within the lowlands and mid-elevation forests of the Departments Pasco and Huánuco, Peru.

(**iii**) The Divisoria morph has very broad bright yellow dorsolateral stripes (fusing entirely with oblique lateral stripes) and an identically colored, but thinner middorsal stripe. The middorsal stripe fuses with the labial stripe (anterior to the orbits), creating the appearance of a short 'Y' or 'T.' The middorsal stripe is incomplete (though see below); the stripe breaks in the center of the dorsum, and the black ground coloration between the middorsal and dorsolateral stripes creates a large black "X" that covers most of the dorsum (occasionally this morph is referred to as the 'X' morph). Other Divisoria populations are identical in all regards; however, they possess a complete middorsal stripe. The black nostril spots fuse on the rostrum, creating the appearance of an upside-down 'U' on the tip of the snout. The venter and limbs are typically light blue to sky blue, giving the appearance of being evenly stippled in identically sized large black spots. This morph is only known to occur within the east versant of the Divisoria range of the southern Cordillera Azul near Aguaytia, Department Ucayali, Peru.

(**iv**) The Biolat morph has thin yellow dorsolateral, middorsal and ventrolateral stripes. A middorsal stripe extends to the tip of the snout, creating the appearance of a crucifix that crosses anterior to orbits. Often the middorsal stripe is slightly darker, appearing yellow-green. The ventrer and limbs are typically blue-green to light gray and can be finely reticulated or evenly stippled in identically sized black spots. This morph occurs predominantly in the lowlands of southern Peru (mostly known from the Department of Madre de Dios and occasionally observed in the Department of Cusco), southwestern Brazil (State: Acre) and northern Bolivia (Department: Pando) where it is typically found in bamboo forests (Maldonado & Reichle 2007; Melo-Sampaio & Barbosa 2009; von May *et al.* 2009a).

(**v**) The Panguana morph is one of the most variable and widespread morphs. The ventral spot, chin, dorsolateral, ventrolateral and middorsal stripes range from bright red, orange, or green to bright or dull yellow. The middorsal stripe fuses with the labial stripe anterior to the orbits, creating the appearance of a short 'Y' or 'T.' The black nostril spots typically fuse on the rostrum, creating the appearance of an upside down 'U' on the tip of the snout. Most individuals possess large bright white to cream spots on the dorsal surfaces of the limbs at the groin and axilla. The venter and limb coloration is typically bluish green to metallic green to light gray. The limbs and venter can be finely reticulated or have the appearance being evenly stippled in identically sized black spots. This morph occurs within the humid cloud forests and lowland rainforests of Departments Huánuco, Pasco, Junín, Ucayali, southwestern Loreto and southern San Martín.

Morphs 2–5 are similar in appearance to *R. amazonica, R. toraro* sp. nov., *R. variabilis, R. ventrimaculata* and *R. imitator*; however, all these species lack a large, brightly colored belly spot. No other species of *Ranitomeya* is easily confused with the Sira morph.

Natural history. Recently, von May *et al.* (2008b) published a detailed description the tadpole of *R. sirensis* (as *Ranitomeya biolat*). Our observations of other populations match this description, based on observations on tadpoles of *R. sirensis* (the Panguana morph) from Puerto Inca and Contamana.

In that same publication, von May also noted that this species exhibited male-only parental care. This is supported by other observations, i.e., the lack of observations of trophic eggs, which are commonly observed in pools containing *R. imitator* and *R. vanzolinii* larvae (Brown *et al.* 2008b; Caldwell & de Oliveira 1999). Typically the tadpoles of *R. sirensis* consumed soft-bodied mosquito larvae (*Trichoprosopon digittatum* and *Culex* sp.) and occasionally consumed predaceous mosquito larvae in the genus *Toxorhynchites* (von May *et al.* 2009a, b). This species also has considerably larger home ranges than other biparental care species (mean 150 ± 184 m^2 versus 31.50 ± 23.05 m^2 in *R. vanzolinii* and 10.9 ± 14.31 m^2 in *R. imitator*; Waldram 2008, Brown *et al.* 2009b). However, this comparison is not entirely legitimate because Waldram (2008) used a coarse (and unconventional method) to measure space use, sampling data at a spatial resolution of 25 m^2, a resolution that frequently exceeds the territory sizes of biparental care species and is almost equal to many male-parental care species (Pröhl 2005; Brown *et al.* 2009b, Werner *et al.* 2011). In Tambopata, *R. sirensis* individuals were observed on average in six grid cells (150 m^2/25 m^2 = 6). Because of this, it is fair to assume the home ranges for this species are large (even if the individuals only occurred in a small portion of each grid), and are much larger than those observed for any biparental care species. *Ranitomeya sirensis* has larger clutches than other biparental care species (3.3 versus 1.6 in *R. imitator* with biparental care and 3.6 in *R. variabilis,* a male-only parental care species; Brown *et al.* 2009b).

Waldram (2008) suspected that tadpole oophagy was an important food source but never observed egg feeding or trophic eggs after six months of observation. Further, von May *et al.* (2009a, b) studied this species for 12 months and never observed egg feeding or the presence of unfertilized trophic eggs (which are typically deposited singly or in pairs below the surface of the water). In Tambopata, von May observed the tadpoles of *R. sirensis* cannibalize the tadpoles of *Allobates femoralis*, *Ameerega trivittata*, as well as on mosquito larvae, whenever they co-occurred in the same phytotelm. Because Waldram (2008) did not report whether tadpoles were consuming eggs or newly hatched tadpoles, it is difficult to determine if this species actually consumes embryos, as do, for example, Ecuadorian *R. variabilis* (Summers 1999) and French Guianan *R. amazonica* (Poelman & Dicke 2007).

Vocalizations. Based on extensive field observations and a small handful of recordings, the call of *R. sirensis* is a typical *vanzolinii*-group call. The call is a loud trill, with notes 0.9–2.2 sec in length, repeated at 6–14 notes per minute. Although we have recordings from only a few localities, we have heard calls of this species at every locality included in our phylogeny (including the type locality) and these calls all appear to be very similar.

Distribution. This species occurs in Amazonian rainforests of Bolivia (Department: Pando), Brazil (State: Acre) and Peru (Departments: Cusco, Huánuco, Junín, Loreto, Madre de Dios, Pasco, San Martín, Ucayali), Fig. 31.

Conservation status. Following the IUCN Red List categories and criteria (IUCN 2010), we tentatively suggest listing this species as Least Concern (LC). Due to the small range of some morphs, e.g., the Sira morph, they may require additional protection.

Ranitomeya vanzolinii **Myers 1982**

Account authors: J.P. Caldwell, J.L. Brown, E. Twomey, P.R. Melo-Sampaio, M.B. Souza
Figs. 3, 4, 9, 23 (j, k), 28, 31
Tables 1, 4–6

Dendrobates quinquevittatus (non Steindachner, 1864)—Silverstone 1975 (partim): p. 33, Fig. 12 (drawing), pattern D and 14 (drawing), pattern E

Dendrobates vanzolinii Myers 1982: p. 9, Fig. 4, Table 1 [MZUSP 51597 collected by Paulo E. Vanzolini and Miguel Petrere at Pórto Walter on Rio Juruá, Acre, Brazil];—Vanzolini 1986; Caldwell & Myers 1990: p. 4; Caldwell 1997: p. 211, Fig. 1; Moreira *et al.* 1997; Caldwell & de Oliveira 1999: p. 565, Table 1–2, Figs. 1–3; Schulte 1999: p. 110, Fig. DB-032, DB-38; Symula *et al.* 2003: p. 452, Table 1, Figs. 1, 3–6; Christmann 2004: p. 6, Figs. on p. 36. 158; Pröhl 2005: p. 358, Table 1; Roberts *et al.* 2006a: p. 379, Table 1, Figs. 1, 4; Santos *et al.* 2009, by implication

Ranitomeya vanzolinii—Bauer 1988: p. 1; Grant *et al.* 2006: p. 171, Fig. 76; Lötters *et al.* 2007: p. 497, Figs. 498–629; von May *et al.* 2008a: p. 396, Appendix 2; Souza 2009: p. 31.

Background information. A population of *R. vanzolinii* from near Porto Walter, State of Acre, Brazil was the focus of intensive behavioral study (Caldwell 1997; Caldwell & de Oliveira 1999) and included in several phylogenetic studies (Symula *et al.* 2003; Grant *et al.* 2006). Little information has been published on other populations of this species. Some confusion exists regarding the taxonomic status of *R. flavovittata*, the sister species to *R. vanzolinii* (see *R. flavovittata* account for more details).

Tadpole. A total of seven tadpoles of *Ranitomeya vanzolinii* were collected from Porto Walter, Acre, Brazil, from 4–17 April 1996. A tadpole in Stage 38 (OMNH 36057) was chosen for a complete description. All seven tadpoles were used to examine variation. These tadpoles ranged from stages 26 to 40, although not all stages were represented in the sample.

Description of OMNH 36057. Total length 27.8; body length 8.9; tail length 18.9, tail length 67.9% total length. Body depressed, maximum width 6.1, maximum depth 4.4. Snout broadly rounded in dorsal view, rounded in lateral view. Nares small, directed anterolaterally, 0.9 from tip of snout; internarial distance 1.6, interorbital distance 1.5. Distance from naris to anterior edge of eye 1.0, eye width, 1.4. Eyes dorsal, directed dorsolaterally.

Spiracle sinistral, short, 1.0, forming small tube free only on outer margin, opening directed posterodorsally 5.7 from tip of snout. Spiracle located 63.8% of body length from tip of snout, just below horizontal midline of body. Vent tube dextral, 0.5 in length.

Caudal musculature depth at body–tail junction 3.0; depth of musculature nearly uniform until it begins tapering at posterior one-third of tail. Upper fin originates 1.1 behind tail–body junction, upper fin at midtail 1.0, slightly deeper than lower fin at midtail, 0.8. Tail tip rounded, notochord ends 0.8 from end tail.

Oral disc emarginate, located ventrally, not visible from above. Transverse width oral disc 2.4, 38.9% of body width. Lower labium free from body wall. Short, conical papillae present on entire margin of posterior labium and laterally on anterior labium; most of anterior labium free of papillae. Papillae mostly in single row, double in few places. Lower jaw sheath broadly V-shaped, deeper than upper jaw sheath. Transverse width upper jaw sheath 1.1, 44.5% transverse width oral disc. Both upper and lower jaw sheaths with finely serrated cutting edges, serrations becoming smaller on proximal lateral processes of upper sheath, absent on ends of lateral processes.

Labial tooth row formula 2(2)/3(1). Labial tooth row A-1 complete, 1.5; A-2 with medial gap, 0.9, right half A-2 length, 0.3, 20.0% of A-1. P-1 with medial gap, 0.1; right half P-1 length, 0.5, 44.6% of P-2; P-2 and P-3 equal in length, 1.1.

Variation. The two smallest tadpoles, stages 26 and 27, averaged 15.1 ± 1.2 total length. Four tadpoles in stages 34 to 38 averaged 24.8 ± 1.2 total length (range, 22.1–27.8). The single tadpole in early metamorphosis at stage 40 was 24.7; in this specimen tooth rows were becoming irregular, the spiracle opening is beginning to close, and the vent tube is partially absorbed.

Tail length as a percentage of total length averaged 62.8 ± 0.01 (range, 60.7–67.9). In the two smallest tadpoles, the upper fin originated at the tail–body junction, whereas in the five largest tadpoles, the fin was low at the tail–body junction, but began to increase in height at an average of 1.4 ± 0.2 (range, 1.0–1.8) behind the tail–body junction. Height of the upper and lower fins was nearly equal in the two smaller tadpoles (upper, 0.40 and 0.45; lower, 0.70 in both individuals). Height of the upper fin was slightly greater in the five larger tadpoles (upper, 1.12 ± 0.10, range 0.90–1.46; lower, 1.01 ± 0.10, range, 0.80–1.38). Tail musculature depth at the tail–body junction was 2.5 ± 0.2 (range, 2.1–2.9) in the five largest tadpoles.

Transverse width as a percentage of body width in the seven tadpoles averaged 39.4 ± 0.01 (range, 35.7–45.6). Transverse width of the upper jaw sheath as a percentage of the transverse width of the oral disc averaged 49.7 ± 0.01 (range, 44.5–55.6). A-2 gap is larger than the P-1 gap. Average percentage of the width of the A-2 gap compared to the total width of A-2 is 49.4 ± 0.04 (range, 37.1–60.5). Average percentage of the width of the P-1 gap compared to the total width of P-1 is 17.8 ± 0.04 (range, 8.3–33.6). P-2 and P-3 are nearly identical in length in 5 tadpoles in which both were normal and well-developed. In the smallest tadpole, P-3 was shorter than P-2 but may not have been fully developed. P-3 was deformed in one other tadpole; the ends of P-3 curved upward and fused with P-2.

Color in life (based on tadpole observed in a small treehole, later transferred to open-air laboratory). Body dark gray, tail musculature lighter gray, fins opaque light gray. Eye black. First observed 3 March, tadpole nearing metamorphosis by 21 March and had developed small light yellow spots on dorsum.

Color in preservative. Dorsum of body grayish brown. Venter opaque, intestinal coils dark grayish brown, some organs seen through venter light yellow. Tail musculature light yellow-brown. Back legs grayish brown. Fins translucent. Eyes black.

Natural history. *Ranitomeya vanzolinii* exhibits biparental care and likely, as observed in *R. imitator*, a monogamous mating system (Caldwell & de Oliveira 1999). After one to two embryos hatch, the male carries the tadpoles on its back and deposits each individually in a phytotelm. Paired males and females remain together in small territories. Males call sporadically each day, and, on average, the female mate responds to his calls every 4.8 days. The male guides the female to their tadpole, they undergo some courtship behavior, and the female deposits two (usually) unfertilized trophic eggs, which the tadpole immediately consumes. The tadpoles are continually fed until metamorphosis. For a more detailed discussion of these behaviors and their evolution see Caldwell (1997) and Caldwell & de Oliveira (1999).

In the Reserva Extrativista do Alto Juruá (REAJ) and Parque Nacional da Serra do Divisor (PNSD) of Brazil, this species is frequently observed in primary forests during the rainy season, mainly in areas abundant in bamboo (*Guadua* sp.), bromeliads, and other phytotelmata (i.e. tree holes; Souza 2009). Adults frequently climb and jump on leaves, stems, and trunks of herbaceous vegetation up to 4 meters in height. In REAJ and PNSD this species uses bamboo internodes, the leaf axils of bromeliads, and other phytotelmata for tadpole deposition (Souza 2009). In forests near Porto Walter, this species uses primarily cavities in small saplings and woody vines for tadpole deposition (Caldwell & de Oliveira 1999).

Vocalizations. Like other members of this species group, the call of *R. vanzolinii* is a loud trill (Fig. 28). Vocalization of *Ranitomeya vanzolinii* was studied at Porto Walter, Acre, Brazil, using two methods: recordings of males analyzed with Raven 1.3 (Cornell Laboratory of Ornithology, Ithaca, New York), and timing of vocalizations recorded during focal observations of males engaged in distinct behaviors. Focal observations were also made of vocalizing frogs defending territories.

Vocalizations of 9 individuals of *R. vanzolinii* were recorded with a Sony WMD-6 tape recorder. Temperatures at the time of recording ranged from 24.0–27.2° C. The number of calls analyzed from these recordings per individual varied from 2 to 10 (mean 6.8 calls/individual); calls were averaged within each individual, then across individuals to obtain means for each call variable. The call of *R. vanzolinii* is a short trill audible from > 5m. Mean number of calls per minute and call duration varied depending on the individual's behavior (see below; Caldwell & de Oliveira, 1999). Mean number of pulses per call was 16.8 ± 1.7 (range, 8.6–23.8), and number of pulses per second was 31.3 ± 0.8 (range, 27.9–33.6). Dominant frequency ranged from 5162–5412 Hz ($n = 7$). Some calls revealed four harmonics; the lowest ranged from 2444–2745 Hz ($n = 5$).

During focal observations of males engaging in three behaviors, time of vocalization (to the second) was recorded using a stopwatch. The number of calls per minute as a measure of call rate was obtained during the following behaviors: 1) calling when no female was present; 2) calling when guiding a female to a tadpole rearing chamber; and 3) calling when inside a tadpole rearing chamber with a female. At times when calling from inside a tadpole rearing chamber (i.e., tiny vinehole or treehole), the calls given were much shorter and had only a few pulses, giving the call a drawn-out "creeking" sound. When calling alone, males vocalized at a rate of 3.41 ± 0.25 calls per minute (range, 0–11; $n = 6$). When calling while guiding a female, males called at a rate of 8.05 ± 0.32 (range, 0–17; $n = 8$), and when calling while inside a rearing chamber with a female, males vocalized at a rate of 3.13 ± 0.23 (range, 0–16; $n = 7$). Thus, males called more intensely when guiding a female to a rearing chamber than when calling alone (Mann-Whitney U-test, $p < 0.001$), or when they were undergoing courtship behavior with a female inside a cavity (Mann-Whitney U-test, $p < 0.001$). Call rate did not differ when males were alone compared to being in a rearing chamber with a female (Mann-Whitney U-test, $p = 0.11$). Call duration also varied depending on the male's behavior. When alone, call duration averaged 0.721 ± 0.08 sec (range, 0.642–0.799; $n = 2$), when guiding a female 0.378 ± 0.12 (range, 0.256–0.500; $n = 2$), and when in a tadpole rearing chamber with a female 0.566 ± 0.09 (range, 0.291–0.844; $n = 5$). Thus, when guiding a female, shorter calls were given at a faster rate.

Territories were maintained using vocal bouts in which two resident males in adjacent territories established posts about 2 m apart and alternated calls (Caldwell and de Oliveira, 1999). In one such encounter in which the timing of vocalizations was recorded for 5 minutes, the bout (defined as number of sequential call given by a male before the other male called was 1.23 ± 0.63 calls (range, 1–5 calls). Calls were alternated between the two frogs 74 times during the 5-minute observation period.

Distribution. *Ranitomeya vanzolinii* is a widespread species occurring from premontane cloud forest (approximately 1300 m elevation) in southern Peru, eastward to lowland rainforests in Brazil. This species is frequently observed on the east versant of Cordillera El Sira (where it has been subjected to frequent collection from smugglers for the pet trade) and in western Brazil in the vicinity of Porto Walter, Acre state. The distribution of this species appears to overlap with other members of the *vanzolinii* group, i.e., *R. sirensis* in the south of Peru and possibly *R. cyanovittata* in far eastern central Peru. However to date, there are no localities where two species within the *vanzolinii* group have been registered. This species occurs in Amazonian rainforests of Brazil (States: Acre and possibly Amazonas) and Peru (Departments: Cusco, Pasco, Ucayali), Fig. 31.

Ranitomeya yavaricola **Perez-Peña, Chavez, Brown & Twomey 2010**

Account author: J.L. Brown
Figs. 3, 4, 9, 23 (c, d), 29.
Tables 1, 4–6

Ranitomeya yavaricola Perez-Peña, Chavez, Brown & Twomey 2010: p. 4, Figs. 2–5, 11 [MZUNAP-01-520 (holotype) collected by Pedro Perez-Peña near Lago Preto, 17 km W of Estiron de Ecuador, Provincia Ramon Castilla, Departamento Loreto, Perú, 2009]

Background information. For a summary of current information this species see Perez-Peña *et al.* 2010. Our phylogenetic results (referenced in Perez-Peña *et al.* 2010 as unpub. data) place this species in the *vanzolinii* group, sister to *R. cyanovittata*.

Distribution. This species is known from Amazonian rainforests of Peru in the Rio Yavari region (Department: Loreto) and may also occur in Brazil (States: Amazonas). Fig 29.

Ranitomeya variabilis **species group**

Figs. 3, 4, 9, 14, 32–37
Tables 1, 4–6

A monophyletic assemblage of two species: *Ranitomeya variabilis* Zimmermann & Zimmermann 1988 and *R. amazonica* Schulte 1999.

Definition and diagnosis. Medium to large adult size (SVL 14–21 mm); two prevalent dorsal patterns: large ovoid black spots on greenish dorsum or complete yellow to red dorsolateral stripes, middorsal stripe and oblique lateral stripes (note that occasionally these species possess ventrolateral stripes, or an intermediate between oblique lateral and ventrolateral stripes, suggesting this trait is a continuous character); large intestine of larvae entirely pigmented; LTRF 2(2)/3(1), oral disc emarginated; larvae gray, tadpoles cannibalistic on embryos and other tadpoles; eggs gray; neither males nor females territorial; promiscuous mating system with male parental care; females produce between 2–6 eggs per mating. Advertisement calls consist of short, regularly spaced buzz calls, notes 0.16–0.44 sec in length, repeated at 24–70 notes per minute (Fig. 14).

Ranitomeya amazonica **Schulte 1999**

Account authors: E. Twomey, J.L. Brown, M. Pepper, M. Sanchez-Rodriguez
Figs. 3, 4, 9, 14, 34 (l–q), 35 (a–q), 36
Tables 1, 4–6, 8

Dendrobates quinquevittatus (non Steindachner 1864)—Silverstone 1975: p. 35 (partim) [French Guiana specimens from Crique Ipoucin, Approuague drainage (LACM 42309); Camopi (MHNP 50-08); Saut Maripa, Fluve Oyapock (MHNP 50-09; LG 73); Crique Gabrielle, Mahury drainage (LG 701); Mont Galbao (LG1422)]; Lescure & Bechter 1982: p. 26; Ávila-Pires & Hoogmoed 1997

Dendrobates ventrimaculatus (non Shreve 1935)—Daly *et al.* 1987: p. 1025 (partim) [specimens from Mishana, Río Nanay drainage, Loreto, Peru]; Kok 2000: p. 19; Estupinan *et al.* 2001: Lescure & Marty 2001; Fig. 3; Brown *et al.* 2006 (partim): p. 55, Table 2, Fig. 1; Christmann 2004: p. 6, Figs. on p. 23, 24, 42, 110, 112, 113; Roberts *et al.* 2006a (partim): p. 381, Table 1, Fig. 3; Noonan & Wray 2006 (partim): p. 1009, Tables 1–2, Figs. 1, 4–5; Poelman & Dicke 2007: p. 217; 2008: p. 271

Dendrobates amazonicus Schulte 1999: p. 32, Figs. DB-047, PB-045, DB-073, [CRS BD 3 P (holotype) collected by Rainer Schulte at "Bosque UNAP, Iquitos (PERU), ca. 130 m NN." = Allpahuayo-Mishana National Reserve near Iquitos, Loreto, Peru, ca. 130 m.a.s.l];—Lötters & Vences 2000: p. 250; Symula *et al.* 2003: p. 453, Table 1; Christmann 2004: p. 17, Figs. on p. 17, 18, 20, 22, 42, 89, 90, 93, 94; Brown *et al.* 2006: p. 55, Table 2, Fig. 1; Santos *et al.* 2009, by implication

Ranitomeya amazonica—Grant *et al.* 2006: p. 171, Fig. 76; Lötters *et al.* 2007: p. 463, Figs. 579–581

Ranitomeya ventrimaculata (non Shreve, 1935)—Grant *et al.* 2006 (partim): p. 171, Fig. 76; Lötters *et al.* 2007 (partim): p. 504, Fig. 635; Perez-Peña *et al.* 2010 (partim): p. 18, Fig. 13

Background information. Specimens of this species have been known at least as early as 1975 from material collected from several localities in French Guiana, when Silverstone (1975) referred to them as *Dendrobates quinquevittatus*. In the same paper, he mentioned a number of specimens from the Iquitos region, although from his drawings and descriptions all these apparently belong to what is currently referred to as *Ranitomeya reticulata*. Later, Myers (1982), after having worked with John W. Daly in Allpahuayo–Mishana near Iquitos, suggested that two species of small *Dendrobates* were present in the area (both of which had been referred to as *quinquevittatus* in Silverstone 1975). One of these was *Dendrobates reticulatus* Boulenger 1884 "1883"; however, for the second species, he continued to apply the name *Dendrobates quinquevittatus*. Caldwell & Myers (1990) began using the name *D. ventrimaculatus* to refer populations of *Dendrobates quinquevittatus* sensu Silverstone after the redescription of *D. quinquevittatus* sensu stricto (now *Adelphobates quinquevittatus*), including the Allpahuayo–Mishana frogs. Schulte (1999) described the Allpahuayo-Mishana as a new species, *D. amazonicus*, primarily on the basis of its advertisement call, which was said to be shorter and more highly pulsed than that of *D. ventrimaculatus*. Schulte also included populations from French Guiana in the definition of *amazonicus* on the basis of call similarities. This description was criticized by Lötters & Vences (2000), who focused on two issues: **(i)** the calls of both *ventrimaculatus* and *amazonicus* were not described on the basis of quantitative data; and **(ii)** the name *amazonicus* was considered a possible junior synonym of *D. igneus* Melin 1941, described from the same general area. We have dealt with the name *D. igneus* and concluded that it is a junior synonym of *R. reticulata* (see account).

Studies using genetic data (e.g., Symula *et al.* 2001; Roberts *et al.* 2006a; Brown *et al.* 2006; Noonan & Wray 2006; Twomey & Brown 2008) supported Schulte's (1999) conclusion that *amazonicus* was a taxon separate from what was called *ventrimaculatus* at that time (now considered *R. variabilis*). Furthermore, putative populations of *amazonicus* from near Iquitos appeared to be closely related to individuals from French Guiana, further confirming Schulte's (1999) arrangement. Still, the taxonomic status of *amazonicus* remained dubious because it rendered *ventrimaculatus* paraphyletic, yet at the same time there was speculation that *ventrimaculatus* may actually include several species, so no taxonomic actions dealing with *amazonicus* were made.

One of the main purposes of this monograph is to clarify the taxonomic status of *R. ventrimaculata* sensu Caldwell & Myers (1990), while simultaneously assessing the validity of *R. amazonica*. Therefore, since 2004, we densely sampled individuals of both suggested taxa and obtained call recordings from various localities. The results of our phylogenetic and acoustic analyses largely support the conclusions of Schulte (1999). Individuals from near Iquitos and Río Napo in Peru, Leticia in Colombia and throughout French Guiana all form a monophyletic clade with relatively low genetic diversity. This clade is sister to a widespread, diverse clade containing individuals throughout much of the eastern Andean versant and parts of the upper Amazonian basin. The latter contains individuals previously referred to as *R. ventrimaculata* or *R. variabilis* (i.e., *R. variabilis* sensu this paper). Surprisingly, *R. amazonica* and *R. variabilis* sensu this paper occur in remarkably close contact south of Iquitos and may even be sympatric in some areas along the lower Río Tigre, Loreto, Peru (M. Sanchez-Rodriguez, pers. comm.).

Additionally, call differences do exist between these two species. *Ranitomeya amazonica* has (on average) significantly fewer pulses per note and a lower pulse rate than *R. variabilis* (Table 8). However, interspecific overlap occurs in these parameters. As an example, *R. variabilis* from Cerro Yupati, Colombia and Shucushuyacu, Peru, had notes containing 19.5 and 20.6 pulses (two topotypic *R. amazonica* had notes containing 20.4 and 21.8 pulses). Also, when measuring pulse rate, one *R. variabilis* individual from Shucushuyacu had a pulse rate of 106 pulses/note, while one *R. amazonica* individual from km. 41 on the Iquitos–Nauta road (Peru) had a pulse rate of 108 pulses/note. We should note that Schulte (1999) described the call of *R. amazonica* as being shorter and more pulsed than that of *R. variabilis* sensu this paper. We did not find significant differences in note length, and the pulse-rate data indicate that *R. variabilis* (rather than *R. amazonica*) has more highly-pulsed calls (Table 5).

FIGURE 32. ***Ranitomeya*** **Plate 11**. variabilis group. **A–P:** ***Ranitomeya variabilis*** (Highland morph): A: Chazuta, San Martin, Peru; B–G: Upper Cainarachi Valley, San Martin, Peru (Ω); H & I: Borja, Loreto, Peru (24, 46Φ); J: Parque Nacional Ichigkat Muja, Amazonas (D. Rodriquez-Mercado); K: Saposoa, San Martin, Peru (Ω); L: Comparision between Saposoa and upper Cainarachi Valley populations (respectively); M: *Xanthosoma* sp. that was being used by *R. variabilis* for tadpole and egg deposition near Saposoa, San Martin, Peru; N: Saposoa, San Martin, Peru (Ω); O: Tocache, San Martin, Peru (C. Torres); P: Macas, Morona Santiago, Ecuador (J. Verkade, Ω). (nΦ = number of individual in phylogeny, Ω = population sampled in phylogeny).

FIGURE 33. ***Ranitomeya*** **Plate 12.** <u>*variabilis* group:</u> **A–P:** ***Ranitomeya variabilis*** (Lowland morph): A: Contamana, Loreto, Peru (42Φ); B: Shamboyacu, San Martin, Peru (41Φ); C: Lower Huallaga Canyon, San Martin, Peru (‡); D: Callanayacu, San Martin, Peru(‡); E: Barranquita, San Martin, Peru (‡); F: Pongo de Cainarachi, San Martin, Peru (7,8,11Φ); G & H: Bonilla, San Martin, Peru (1,3, 9 Φ); I & J: Varadero, Loreto, Peru (27Φ); K: Quebrada Blanco, Loreto, Peru (Ω); L: Rio Boncuya, Loreto, Peru (G. Gagliardi); M: Upper Rio Nanay, Loreto, Peru; N: Middle Rio Nanay, Loreto, Peru; O & P: Archidona, Napo, Ecuador (EHP and J. Verkade). (nΦ = number of individual in phylogeny, Ω = population sampled in phylogeny).

FIGURE 34. *Ranitomeya* Plate 13. variabilis group: **A–K: *Ranitomeya variabilis***: A: Archidona, Napo, Ecuador (J. Verkade); B–D: Macuma, Morona-Santiago, Ecuador (J. Verkade and EHP); E &F: Puyo, Pastaza, Ecuador (j. Verkade) G: Yupati, Vaupés, Colombia (14 Φ); H: Embryos, Archidona, Napo, Ecuador (J. Verkade); I: Breeding pair of *R. variabilis*, Archidona, Napo, Ecuador (J. Verkade); J & K: Yupati, Vaupés, Colombia (14-16 Φ). **L–Q: *Ranitomeya amazonica*:** L: Km 41 Iquitos, Loreto, Peru (ET, 26Φ); M: Km 31 Iquitos, Loreto, Peru (PPP); N & O; Km 26 Iquitos, Loreto, Peru (ET, 25, 27Φ); P: Upper Rio Mazan-Pintuyacu, Loreto, Peru (J. J. Lopez-Rojas); Q: Lower Rio Mazan, Loreto, Peru (J. J. Lopez-Rojas). (nΦ = number of individual in phylogeny).

FIGURE 35. ***Ranitomeya* Plate 14.** *variabilis* group: **A–Q: *Ranitomeya amazonica***: A–C: Iquitos, Loreto, Peru; D–K: 'Arena Blanca', Loreto, Peru (16–18, 20–24Φ); L: 30 km west of Pevas, Loreto Peru; M: Rio Sucusari, Loreto, Peru (B. Pieper); N & O: Nouragues French Guiana (EHP); P: French Guiana (B.P. Noonan, Ω); Q: Estação Científica Ferreira Penna-Caxiuanã, Para, Brazil.(nΦ = number of individual in phylogeny, Ω=population sampled in phylogeny).

Dorsal coloration and pattern do not appear to be good characters to distinguish *R. variabilis* and *R. amazonica*. Schulte (1999) recognized this by including individuals from French Guiana (which have yellow stripes) under his definition of *R. amazonica*, even though the populations near Iquitos (around km. 23 on the Iquitos–Nauta road) all have vibrant red or reddish-orange stripes. One of us (E. Twomey, unpub. data) has also found yellow individuals near Iquitos that fall within the *amazonica* clade, sampled at km. 41 on the Iquitos–Nauta road. Interestingly, individuals sampled from km. 81 (next to Nauta) all fall within the *variabilis* clade; these individuals are also yellow.

In addition to high variation in dorsal coloration in *R. amazonica*, their patterns have high levels of variation as well. In 2007, a population of *R. amazonica* was discovered by M. Pepper and M. Sanchez-Rodriguez that was strikingly similar in appearance to *R. reticulata* (Fig. 35d–k). At the time of discovery, this population was thought to potentially represent a new species; however, after extensive genetic testing (see terminals labeled "Arena Blanca" in the phylogeny), we concluded these individuals were another morph of *R. amazonica* that may be involved in a mimicry system with the sympatric *R. reticulata* (see Mimicry section).

Biogeographically, *R. amazonica* represents somewhat of an enigma, although it appears that Schulte (1999) chose the specific epithet wisely, as this species appears to be affiliated with the Amazon River. Noonan and Wray (2006) pointed out that, while *R. variabilis* sensu this paper appears to be phylogeographically structured along a latitudinal axis, the phylogeographic structuring in *R. amazonica* appears to be along the Amazon River. Inclusion of additional samples from Río Napo (Peru), Puerto Nariño (Colombia) and Leticia (Colombia) support this hypothesis. It is worth noting that there are large collection gaps between Leticia, Colombia and French Guiana, either explainable with the generally inadequate sampling in this region or natural absence (see Lötters *et al.* 2010 and discussion).

Definition and diagnosis. Assigned to the genus *Ranitomeya* due to the combination of the following characters: Small adult SVL (16–19 mm), dorsal coloration conspicuous, dorsolateral stripes highly variable and sometimes absent, but when present extend to top of thigh, ventrolateral stripes usually present (usually absent in 'Arena Blanca' populations), brightly colored throat, distinctive pale reticulation on limbs and venter, dorsal skin smooth, finger I is greatly reduced and shorter than finger II, finger discs II–IV greatly expanded, disc of finger 2.6 times wider than finger width, thenar tubercle conspicuous, toe discs III–V moderately expanded, toe webbing absent, larval vent tube dextral. Adults use arboreal phytotelmata for reproduction and deposit eggs above phytotelm, maxillary and premaxillary teeth absent. Two morphs are currently known of this species: **(i)** the Nominotypical morph (Figs. 34 l–q, 35 a–c, n–q), and **(ii)** the 'Arena Blanca' morph (Fig. 35 d–m):

(i) The Nominotypical morph has a well-defined black 'Y' on the dorsum, with the two ends terminating just medial to the eyelids and the single end terminating on the posterior dorsum. In most individuals, a small black dot is present on the snout (as in Fig. 34m), but in some individuals this spot is absent (e.g., Fig. 35c). The dorsal stripe color is variable. Most populations around Iquitos have dorsal stripe coloration ranging from red to orange, but at least one individual in the area has been found with yellow dorsal stripe coloration. Most individuals have somewhat irregular dorsolateral stripes, and an incomplete middorsal stripe that terminates between the shoulders (i.e., between the 'fork' of the black 'Y'). Ventrolateral and labial stripes are present and typically yellow. Limbs and venter are black with prominent pale reticulation that ranges from bright sky-blue to dark bronze-blue or gray. The throat is brightly colored, usually bright yellow or orange and has irregular black markings around the lateral edges. This morph occurs throughout much of the Amazon basin (see Distribution below). Red and orange individuals have been found from near Iquitos, Loreto, Peru near Río Napo and 70 km N Leticia, Amazonas, Colombia (T. Defler, pers. comm.). Yellow individuals have been found south of Iquitos, in Puerto Nariño, Leticia, throughout much of French Guiana and in extreme eastern Brazil near the Amazon river delta.

(ii) The 'Arena Blanca' (white sands) morph is a highly variable morph that may be involved in Müllerian mimicry with *R. reticulata*. This morph generally has a bright orange to red dorsum with irregular black markings. These markings can be manifested as partial stripes (i.e., Fig. 35e) or small spots (e.g., Fig. 35f). In extreme cases, these black markings can be attenuated, rendering the dorsal pattern nearly identical to that of *R. reticulata* (e.g., Fig, 35k). This morph is known only from a handful of sites in the Department of Loreto, Peru, exact locations undisclosed (available upon request).

Tadpole. The description is based on a single tadpole from lower Río Napo, Loreto, Peru. Mouthparts were verified in an individual from an unknown locality in French Guiana.

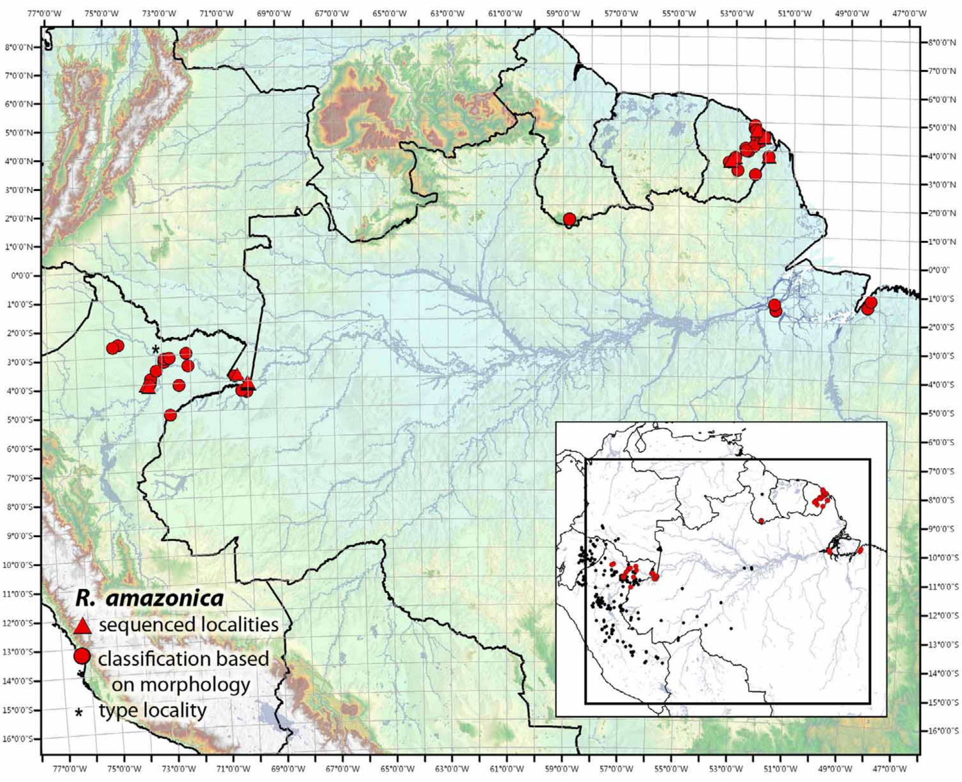

FIGURE 36. Known distribution of *Ranitomeya amazonica*. The inset map displays the geographic extent of distributions (black circles = all other *Ranitomeya*).

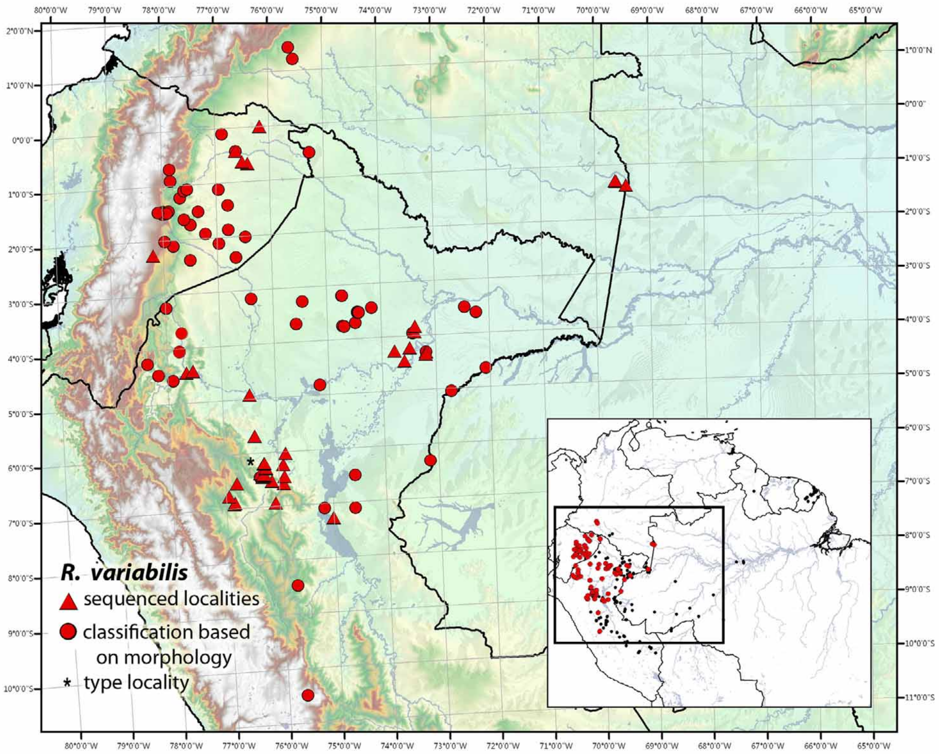

FIGURE 37. Known distribution of *Ranitomeya variabilis.* The inset map displays the geographic extent of distributions (black circles = all other *Ranitomeya*).

Tadpole in stage 29, no external gills, feeding on detritus. Body ovoid in dorsal view, wider near vent. Total length 16.6; body length 9.2; tail length 7.4, 45% of total length. Body width 7.6; body depth 5.3, 70% of body width. Eye well developed; naris small; distance from naris to anterior edge of eye 1.0. Eye positioned dorsally on head, directed dorsolaterally. Spiracle well developed, sinistral; vent tube dextral.

Tip of tail bluntly rounded. Tail muscle height at base of tail 2.5; tail muscle width at base of tail 1.9; maximum tail height 3.3. Dorsal and ventral fins approximately of same height.

Oral disc ventral, emarginated, transverse width 1.7, 22% of body width. Single row of small papillae present laterally and ventrally; dorsal gap where papillae absent. LTRF 2(2)/3(1) with A-1 developed on upper labium, A-2 with wide medial gap (one-third total width of tooth row); P-1 on lower labium with narrow medial gap; P-2 width equal to P-1; P-3 80% width of P-1.

Color in life. Head and body gray, mouthparts visible from above. Abdomen mostly transparent; intestinal coils black; heart visible. Tail musculature uniform gray, dorsal and ventral fins opaque gray.

Natural history. The natural history of *R. amazonica* (mainly French Guiana populations) has been described in detail elsewhere (e.g., Lescure & Bechter 1982; Schulte 1999; Lötters *et al.* 2007; Poelman & Dicke 2007, 2008); however, we will summarize some pertinent information here. Like other members of the *variabilis* group, *R. amazonica* breeds most frequently in bromeliads. Clutches consist of 2–6 eggs are placed in the axils of bromeliads partially submerged in water (Lötters *et al.* 2007; Poelman & Dicke 2007). Males carry tadpoles to other bromeliad axils and cannibalistic tadpoles are deposited individually. These tadpoles are abandoned (i.e., no trophic egg-feeding) and feed on mosquito larvae, algae, detritus or other tadpoles that may be unwittingly deposited in the same phytotelm.

In French Guiana, this species was observed changing its food provisioning strategy. Early in the breeding season, tadpoles subsist predominantly on food within the phytotelm, whereas later in the breeding season (apparently due to increased desiccation risk), parents deliberately deposit embryos as a food source in pools containing their offspring to ensure quick metamorphosis (Poelman & Dicke 2007, 2008).

Vocalizations. The call of *R. amazonica* consists of a series of short buzz notes, note range 0.16–0.36 sec in duration, repeated at a rate of 24–70 notes per minute.

Distribution. This species occurs in Amazonian rainforests of Brazil (States: Amapá, Amazonas, Pará), Colombia (Department: Amazonas), Guyana (Region: Upper Takutu-Upper Essequibo), French Guiana (Arrondissements: Cayenne, Saint-Laurent-du-Maroni) and Peru (Department: Loreto), Fig. 36.

Conservation Status. Following the IUCN Red List categories and criteria (IUCN 2010), we suggest listing this species as Least Concern (LC).

Ranitomeya variabilis Zimmermann & Zimmermann 1988

Account authors: J.L. Brown, E. Twomey, E.H. Poelman, M. Pepper, M. Sanchez-Rodriguez, P. Perez-Peña
Figures 3, 4, 9, 14, 32 (a–p), 33 (a–p), 34 (a–k), 37
Tables 1, 4–6, 8

Dendrobates minutus ventrimaculatus Shreve 1935 (partim): p. 213–214 [paratypes MCZ 19737, 19739 and LACM 44398 (formerly MCZ19741) collected by O.C. Felton in 1933 at "Sarayacu, Ecuador"; paratypes MCZ 19685 and MCZ 19689, collected by C. Spencer between January 1931 and August 1932 "along the Pastaza River from Canelos to the Maranon river, Ecuador"]

Dendrobates quinquevittatus (non Steindachner 1864)—Crump 1971; Silverstone 1975 (partim): p. 35; Duellman 1978: p. 125, Plate 1; Lescure & Bechter 1982: p. 26; 1983; Myers 1982: p. 13, Fig. 7; Zimmermann & Zimmermann 1988: p. 132, Schulte 1999: p. 48, Fig. DB-050.

Dendrobates ventrimaculatus (non Shreve 1935)—Daly *et al.* 1987: p. 1025; Schulte 1999: p. 129; Caldwell & Myers 1990: p. 17; Summers & Amos 1997: p. 261; Fujitani *et al.* 1998: p. 74; Summers 1999: p. 557, Figs. 1–7; Summers & Earn 1999: p. 517; Summers & Symula 2001: p. 17; Symula *et al.* 2001: p. 2415, Table 1, Figs. 1–3; 2003: p. 453, Figs. 1–6; ; Cisneros-Heredia 2003; Christmann 2004: p. 5, Figs. on p. 15, 42, 98, 100, 147, 151; Brown *et al.* 2006: p. 55, Table 2, Fig. 1; 2008a: p. 1157; 2008b: p. 2; 2009b: p. 478; Noonan & Wray 2006: p. 1008, Table 2, Figs. 4, 5; Roberts *et al.* 2006a: p. 378, Table 1, Figs. 1, 3, 4

Dendrobates variabilis Zimmermann & Zimmermann 1988: p. 132 [SMNS 7054 (holotype) collected by Rainer Schulte from "Departamento San Martín, Peru"; restricted to "km 27 auf der Straße von Tarapoto nach Yurimaguas" by Henle 1992: p. 102];—Caldwell & Myers 1990: p. 17; Henle 1992: p. 102; Schulte 1999: p. 39–46, Figs. DB-067, DB-044, DB-063, DB-

009; Summers & Earn 1999: p. 517; Symula *et al.* 2001: p. 2415, Table 1, Figs. 1–3, 2003: p. 453, Figs. 1–6; Lötters *et al.* 2003: p. 1909; Christmann 2004: p. 5, Figs. on p. 25, 121; Noonan & Wray 2006: p. 1008, Table 2, Figs. 4, 5; Roberts *et al.* 2006a: P. 378, Table 1, Figs. 2–4; Brown *et al.* 2006: p. 55, Table 2, Fig. 1; 2008a: p. 1140, Table 1; 2008b: p.1, Table 1, Figs. 1–3; 2009b: p. 478, Tables 1–4, Fig. 3; 2009c: p. 148, Fig. 1; Santos *et al.* 2009, by implication

Ranitomeya variabilis—Grant *et al.* 2006: p. 171, Fig. 76, Fig. 76; Lötters *et al.* 2007: p. 500, Figs. 630–633; Brown *et al.* 2008c: p. 9; 2009a: p. 1877, Table 1, 2010: p. 436, Figs. 1, 2, 4, 5; Perez-Peña *et al.* 2010: p. 18, Fig. 13; Schulte *et al.* 2010

Ranitomeya ventrimaculata (non Shreve 1935)—Grant *et al.* 2006: p. 171, Fig. 76; Lötters *et al.* 2007: p. 504, Figs. 634, 636, 637; Brown *et al.* 2009a: p. 1877, Table 1; Perez-Peña *et al.* 2010: p. 18, Fig. 13

Background information. Technically, this species did not receive a formal taxonomic name until Zimmermann & Zimmermann (1988) described a morph of this species as *Dendrobates variabilis*. Prior to that, most members of this group were referred to as *Dendrobates ventrimaculatus* or *Dendrobates quinquevittatus*. Shortly after its description Caldwell & Myers (1990) stated “at present it is not diagnosable from all other populations of *D. ventrimaculatus* s.l.” and considered *Dendrobates variabilis* sensu Zimmermann & Zimmermann (1988) as a junior synonym of *Dendrobates ventrimaculatus* Shreve 1935. Symula *et al.* (2003) responded to Caldwell & Myers’ synonymy, stating “there are acoustic differences between the advertisement calls of *D. variabilis* and *D. ventrimaculatus*… Furthermore, *D. variabilis* is restricted to the summits of mid-level mountains, whereas *D. ventrimaculatus* is confined to lowland habitats”. They urged future research, particularly hybridization studies, before a conclusion on the specific status could be reached. Certainly, *R. variabilis* sensu Zimmermann & Zimmermann (1988) and nearby lowland populations of *R. ventrimaculata* sensu Schulte (1999) have diverged from each other in some regards (as is apparent in their morphology); however, unlike stated by Symula e*t al* (2003), we are not able to recover any consistent acoustic differences between *R. variabilis* sensu Zimmermann & Zimmermann (1988) and nearby populations of *R. ventrimaculata* sensu Schulte (1999); (see *R. amazonica* account for discussion of acoustic differences between *R. variabilis* and *R. amazonica*).

Interestingly, we have found evidence of four independent origins of “spotted highland” populations (i.e., morphologically similar to *variabilis* sensu Zimmermann & Zimmermann 1988) in our molecular phylogenetic analyses. To reconcile the monophyly of either species (*R. ventrimaculata* sensu Schulte (1999) and *R. variabilis* sensu Zimmermann & Zimmermann (1988)—using only the type populations), so that each is a distinct species, several additional populations would have to be elevated to specific status. Based on the lack of phylogenetic and acoustic data and consistent morphological or ecological differences, we consider *R. variabilis* sensu Zimmermann & Zimmermann (1988) to be synonymous with *R. ventrimaculata* sensu Schulte (1999). Because members of this group were erroneously considered *R. ventrimaculata* (see *R. ventrimaculata* acount), the name *R. variabilis* gains precedence.

The evolution of spots seems to coincide with the transition to montane forests from lowland ancestors. The exact cause of this trend is unclear and not all montane populations are spotted; however, generally speaking the trend is prevalent. Additionally, we do not have molecular data for several populations of *R. variabilis* sensu Zimmermann & Zimmermann (1988). To further complicate the situation, it is common within populations of spotted frogs to observe transitional morphs or an entirely lowland morph. This phenomenon gets to the heart of the problems scientists face when trying to clarify the taxonomy of this group. Under any species criterion, no taxonomy can portray the diversity scientists perceive with complete satisfaction. This species is highly nomadic and appears to be tolerant of suboptimal habitats (in terms of geology, climate and reproductive resources) and is often found in areas unoccupied by any other *Ranitomeya* (e.g., seasonally flooded forests). This behavior likely reduces the possibility of isolation for periods long enough to result in speciation. Thus, like *R. sirensis* (sensu this paper), these groups appear to be widely dispersed species with the propensity for local adaptation– though not enough to result in complete speciation.

Definition and diagnosis. Assigned to the genus *Ranitomeya* due to the combination of the following characters: adult SVL < 18.0 mm, dorsal coloration conspicuous, dorsolateral stripes present (in lowland populations), stripes complete when present, extending to top of thigh, brightly colored throat, distinctive pale reticulation on limbs and venter, dorsal skin smooth, finger I greatly reduced and shorter than finger II, finger discs II–IV greatly expanded, disc of finger two times wider than finger width, thenar tubercle conspicuous, toe discs III–V moderately expanded, toe webbing absent, larval vent tube dextral, maxillary and premaxillary teeth absent. Adults use arboreal phytotelmata for reproduction and deposit eggs above or in water. Two main morphs of this species are currently known: **(i)** the Highland morph (*R. variabilis* sensu Zimmermann & Zimmermann 1988, Fig. 32a–p) and **(ii)** the Lowland morph (*R. ventrimaculata* sensu Schulte 1999, Figs. 33a–p, 34a–k). All morphs possess a large black spot on the snout, anterior to orbits:

(i) The Highland morph possesses regular yellow-green reticulation, creating ovoid and large black spots on dorsum. The dorsal coloration often transitions from yellow-green anteriorly to blue-green posteriorly. Venter and limbs are green to blue and typically are evenly stippled with medium to large black spots. The throat is yellow and gular spots are commonly present. This morph is known to occur within rainforests in Ecuador (Province Morona-Santiago) and Peru (Department Amazonas, San Martín, Pasco).

(ii) The Lowland morph has thin yellow dorsolateral, middorsal and oblique lateral stripes. The ventrolateral and dorsolateral stripes are typically complete; however, the middorsal stripe typically terminates around the axilla and creates a distinctive black 'Y' on the dorsum (Fig. 2g-i). In some populations, dorsal coloration is orange (e.g., near Varadero, Department Loreto, Peru); middorsal stripe is largely complete (e.g., populations near Shamboyacu, Department San Martín, Peru); or dorsolateral and oblique lateral stripes fuse near the axilla (e.g., populations near Pongo de Cainarachi, Department San Martín, Peru; Quebrada Blanco, Department Loreto, Peru; Puyo, Province Morona-Santiago, Ecuador). The ventral and limb coloration is typically blue-green to light gray to blue. The limbs and venter are finely reticulated. This morph occurs predominantly though the lowland forests adjacent to eastern Andean versant, though some populations also occur far from mountains (e.g., those in La Pedrera, Department Vaupés, Colombia; Rio Tahuayo, and Contamana, Department Loreto, Peru). This morph is known from the rainforests of Brazil (State Amazonas), Colombia (Departments Amazonas, Caquetá, Putumayo (tentative), Vaupés), Ecuador (Provinces Napo, Orellana, Pastaza, Sucumbíos) and Peru (Departments Amazonas, Loreto, San Martín, Ucayali).

The highland morph is similar in appearance to the local *R. imitator* and in some populations is involved in a mimicry complex, however, populations of *R. imitator* that are similar in appearance possess paired nose spots (versus a single nose spot in *R. variabilis*). For a detailed list of characters see Brown *et al.* (2008b). The lowland morph is similar in appearance to *R. amazonica*, *R. toraro* sp. nov. and some populations of *R. imitator, R. ventrimaculata* and *R. sirensis*. *Ranitomeya variabilis* lacks a large belly spot (present in *R. sirensis*) and bears a conspicuous black 'Y' on the dorsum (versus stripes parallel and extending to vent in *R. toraro*, *R. imitator, R. sirensis* and *R. uakarii*). Distinguishing the lowland morph of *R. variabilis* and *R. amazonica* can be difficult if nothing is known about the origin of the individual. Where the species co-exist near Iquitos, *R. variabilis* typically has thin-yellow dorsal stripes and *R. amazonica* has broad bright red or orange dorsal stripes (though they can also be yellow). Individuals of *R. amazonica* from the Guiana Shield are almost identical in appearance to some *R. variabilis* individuals from Pongo de Cainarachi or Quebrada Blanco in Peru, possessing thin-yellow dorsolateral stripes that fuse with the ventrolateral stripe near the axilla. To confidently identify these populations, genetic or locality data must be used.

TABLE 8. Bioacoustic parameters of *R. amazonica* and *R. variabilis.* Sample sizes refer to the number of individuals included. For each individual, 1-5 calls were measured and averaged. Localities included were: *R. amazonica*: km. 23 Iquitos-Nauta road (7 individuals), 'Arena Blanca' (1 individual), French Guiana (1 individual): *R. variabilis*: km. 81 Iquitos-Nauta road (1 individual), Shucushuyacu (1 individual), Río Tahuayo (2 individuals), Cainarachi Valley (2 individuals), Saposoa (1 individual), Pongo de Cainarachi (1 individual), Cerro Yupati (2 individuals), Shamboyacu (1 individual). Mean recording temperatures were compared to show that there was no systematic difference in recording temperatures between the two species.

species	n	mean temp. (C)	dom. freq. (Hz)	note length (s)	pulses per note	pulse rate (pulses/note length)	inter note interval (s)	notes per second
amazonica	9	26	4930 ± 445	0.261 ± 0.061	27.7 ± 9.8	106.3 ± 16.2	1.44 ± 0.73	0.74 ± 0.20
variabilis	11	26	5157 ± 341	0.280 ± 0.113	67.0 ± 43.8	235.2 ± 137.9	1.16 ± 0.46	0.86 ± 0.17
P-value		0.913	0.203	0.639	**0.02**	**0.01**	0.29	0.15

TABLE 9.Table of major phylogenetic groups and corresponding support values. Bremer Support Values (BSV) represents the number of changes for a tree with the particular group and the number without it, posterior probabilities (PP), Bayes Factors (BF), Bootstrap Values (BV). Overall Support was calculated by using the following metric: [(Sum of (BSV values ≥ 10 = 1, <10 = 0; PP values ≥ 95 = 1, <95 = 0; BF values 0-10 = 0, >10 = 1; BS = values ≥ 70 = 1, < 70 = 0) / n of values for which data is reported)*100]. Metric values interpreted are as Overall Support indices: > 90 = high, 90-80 = medium-high, 80-60 = medium, 60-0 = low.

Study	Grant *et al.* 2006	Twomey & Brown 2008	Santos *et al.* 2009	This study	Overall Support
Test Criterion/ Method of Support Values	BSV	PP/BF	BV/PP	mtDNA PP/ nDNA PP/ BF	Index (Value)
Genera					
Adelphobates	37	88/1.13	98/100	100/42/*	Med-High (71)
Andinobates	22	100/*	100/100	100/100/8.52	High (100)
Excidobates	*	98/0.71	100/100	100/*/*	High (100)
***Dendrobates* (sensu Grant)**	79	100/1.76	100/100	100/100/*	High (100)
***Dendrobates* (sensu Silverstone)**	9	100/*	99/100	79/100/*	Med (67)
Minyobates	1	*/*	98/100	100/*/*	Med (75)
Oophaga	114	100/0.37	100/100	100/99/*	High (100)
Phyllobates	132	*/*	100/100	100/100/*	High (100)
***Ranitomeya* (sensu this study)**	33	100/*	98/100	100/100/9.96	High (100)
***Ranitomeya* (sensu Grant *et al.* 2006)**	13	100/2.41	98/100	100/42/*	Med-High (86)

Tadpole. The description is based on a tadpole from the Cainarachi Valley, San Martín, Peru. Mouthparts were verified in three individuals from same locality.

Tadpole in stage 28; no external gills; feeding on detritus. Body ovoid in dorsal view, wider near mouth. Total length 18.1; body length 8.6; tail length 9.5, 52% of total length. Body width 5.2; body depth 3.1, 60% of body width. Eyes well developed; naris small; distance from naris to anterior edge of eye 1.6. Eye positioned dorsally on head, directed dorsolaterally. Spiracle well developed, sinistral; vent tube dextral.

Tip of tail bluntly rounded. Tail muscle height at base of tail 1.8; tail muscle width at base of tail 1.3; maximum tail height 2.0. Dorsal and ventral fins approximately same height.

Oral disc ventral, emarginated, transverse width 1.9, 37% of body width. Single row of small papillae present laterally and ventrally; dorsal gap where papillae absent. LTRF 2(2)/3(1) with A-1 developed on upper labium, A-2 with wide medial gap (1/3 total width of A-1); P-1 on lower labium with narrow medial gap; P-2 width equal to P-1; P-3 75% width of P-1.

Color in life. Head and body gray, mouthparts visible from above. Abdomen mostly transparent; intestinal coils black. Tail musculature uniform gray, dorsal and ventral fins opaque gray.

Natural history. Zimmermann & Zimmermann (1984) reported that captive specimens of *R. variabilis* exhibited biparental care. In contrast, observations in the field indicate that this species has a promiscuous mating system: unrelated tadpoles are commonly deposited within the same phytotelm and females do not return to pools to perform egg-feeding. Oviposition usually takes place at the edge of the water within phytotelmata; clutches contain 3–6 eggs. After 10–15 days, the male transports tadpoles to separate small phytotelmata, where they are deposited individually and thereafter abandoned (Summers 1999; Summers & Amos 1999; Lötters *et al.* 2007; Brown *et al.* 2008b). Alternatively, within the same population, clutches can be abandoned shortly after reproduction and all the tadpoles fall into the pool below, often resulting in cannibalism of all but one tadpole (Brown *et al.* 2008b). The degree of embryo cannibalism varies between populations. Near Tarapoto, Peru, tadpoles were never observed cannibalizing embryos that were deposited in their pools (Brown *et al.* 2008a, 2009c), whereas in populations from Sucumbíos Province, Ecuador, tadpoles were frequently observed cannibalizing embryos (Summers 1999, Summers & Amos 1999). In both populations, the tadpoles would frequently consume other congeneric tadpoles.

This species occupies primary and secondary forests where bromeliads are abundant. It commonly breeds in *Guzmania* spp. and *Aechmia* spp. Occasionally this species has been observed breeding in tree holes and in the axils of *Heliconia*, *Dieffenbachia* and *Xanthosoma* plants. Most individuals are transient and in mark-and-recapture studies they demonstrate little site fidelity (Summers & Amos 1999, Brown *et al.* 2009b).

Vocalizations. The call of *R. variabilis* is a series of short buzz notes, note range 0.14–0.44 sec in length, repeated at 34–62 notes per minute.

Distribution. This species occurs in Amazonian rainforests of Brazil (States: Amazonas), Colombia (Departments: Amazonas, Caquetá, Putumayo (tentative), Vaupés), Ecuador (Provinces: Morona-Santiago, Napo, Orellana, Pastaza, Sucumbíos) and Peru (Departments: Amazonas, Loreto, San Martín, Ucayali), Fig. 37.

Conservation status. Following the IUCN Red List categories and criteria (IUCN 2010), we suggest listing this species as Least Concern (LC). It has a large distribution and occurs within several protected areas.

Incertae sedis

Ranitomeya rubrocephala Schulte 1999

Account authors: E. Twomey, J.L. Brown, S. Lötters
Fig. 38
Table 1

Dendrobates rubrocephalus Schulte 1999: p. 138 [CRS BD 5, "Ceja de Selva, Ostandenabhang und vielleicht vorgelagerte Ostkordilleren, Dep. Pasco und Junín, Höhe vermutlich zwischen 600 und 1500 m" (= Ceja de Selva, eastern Andean versant and perhaps outlaying eastern cordilleras, Departments Pasco and Junin, elevation assumingly between 600 and 1500 m.a.s.l.), unknown collector];—Lötters & Vences 2000: p. 254; Santos *et al.* 2009, by implication
Ranitomeya rubrocephala—Grant *et al.* 2006: p. 171; Lötters *et al.* 2007: p. 514

Background information. This suggested species was described on the basis of two specimens, collected likely in 1956 by an unknown collector and deposited at MUSM. Initially four specimens (two lost, two now with the describer) were said to originate from the "Ceja de Selva" (= east-Andean versant) in the Department Pasco, as stated on the original label, which is a more than vague locality. According to the original description, another vague report states that this putative species occurs near Chanchamayo-San Ramón, Department Junín (Schulte 1999: p. 143). Moreover, Schulte suggested that this poison frog may originate from the Cordillera Yanachaga or Cordillera San Matéo. Schulte (1999) described the frog as being small (adult SVL < 15 mm) and entirely black in preservative with a reddish-orange head and throat patch. He speculated that the black color in preservative may be green in life and that *R. sirensis* (sensu Aichinger 1991) was a related taxon. Additionally, the two specimens available for the original description had two unusual characters: the finger formula was 1 < 4 < 2 < 3, unknown in related small poison frogs which have 1 < 2 < 4 < 3 (according to Schulte 1999), although in our experience fingers 2 and 4 are almost equal in length for most species. Second, Schulte (1999) noted a large central hook on the front of the lower jaw and a respective notch in the upper jaw. Based on Schulte's description, *R. rubrocephala* resembles *R. benedicta* which is known only from parts of the Departments Loreto and San Martín.

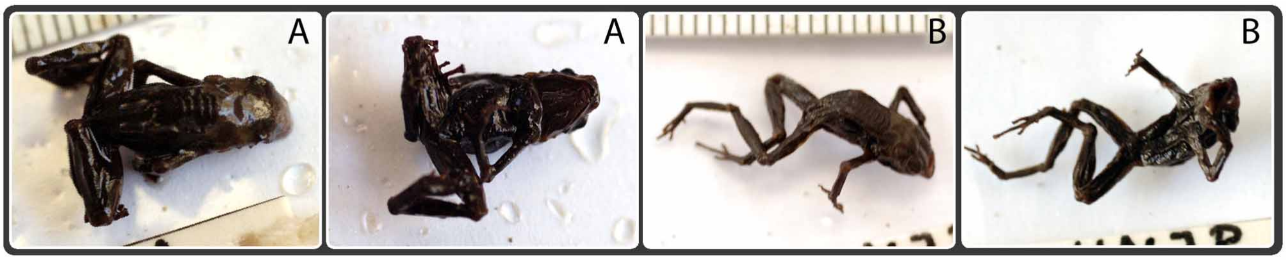

FIGURE 38. Type series of *Dendrobates rubrocephalus* Schulte 1999. A. Holotype (BD 5H, MHNJP 408) and **B.** Paratype (BD 6P, MHNJP 408).

Lötters & Vences (2000), despite their apparent skepticism, supported *R. rubrocephala* as a valid species on the basis of coloration and the unique hand morphology. However, because the original description fails to mention an adequate type locality, because no photos or descriptions exist of live specimens and the two type specimens are so badly degraded (being almost entirely black and badly shriveled with unusual posturing and twisted limbs; Fig. 38), it will be exceedingly difficult to ever confidently ascribe any newly collected specimen as belonging to this species. Further, it is possible that characters described for this species, including the two unusual characters mentioned above, could be artifacts of the poor condition of the specimens. As a consequence, we consider *Ranitomeya rubrocephala* Schulte 1999 as a *nomen dubium*.

Discussion

Phylogenetics

The mitochondrial phylogenetic results of this study are largely similar to those of Grant *et al.* (2006), Twomey & Brown (2008) and Santos *et al.* (2009). These studies utilized more gene regions (both nuclear and mitochondrial) and more base-pairs, but contained fewer individuals of *Ranitomeya* and *Andinobates* species. In these studies all the major groups received considerable support (Table 9) and the relationships among most groups were largely consistent. The placement of *Minyobates steyermarki* continues to challenge phylogeneticists. In Grant *et al.* (2006*), M. steyermarki* was found to be sister to a group containing *Andinobates*, *Adelphobates*, *Dendrobates*, *Excidobates*, *Oophaga* and *Ranitomeya*. In this study and in Twomey & Brown (2008), *Minyobates* was found to be sister to a clade containing *Adelphobates*, *Dendrobates* and *Oophaga*. We place higher credence in the placement of *Minyobates* as sister to *Adelphobates*, as in Twomey & Brown 2008 and Santos *et al.* (2009), given that the gene regions sequenced in these studies were aimed to address more recent phylogenetic relationships. Further, in the current study, the nodes in the phylogeny adjacent to *Minyobates* received little support, suggesting the placement of this species was unstable (including the node that would place it sister to *Adelphobates*).

Our analysis of nuclear sequence data resulted in novel phylogenetic arrangements among many dendrobatine genera. When using mitochondrial data, most genera are well supported; however, in a concatenated nuclear phylogeny, the relationships among the genera changed dramatically and almost all relationships among genera received little support. These results suggest that researchers need to consider additional nuclear markers when dealing with dendrobatine phylogenetics. When single genes are analyzed independently, these relationships vary considerably and, in some instances, they reflect mitochondrial phylogenies, whereas others result in novel arrangements. It appears that these differences do not dramatically influence the results of combined analyses of nuclear and mitochondrial analyses, because topologies are similar to mitochondrial-only analyses. This also could be due to a much stronger signal in the mitochondrial data when compared to the limited variation observed within the nuclear genes.

Notes on Taxonomic Changes and the Use of the Name *Ranitomeya*

> *…the taxonomy of poison-arrow frogs, at the family and generic levels, has been and remains confused and controversial*
>
> P.A. Silverstone 1975, p. 1

In 2006, shortly after the publication of the taxonomy of Grant *et al.* (2006), feeling this taxonomy was unnecessary and confusing; we (J.L. Brown and E. Twomey) set out to synonymize the proposed genera for *Dendrobates* (sensu Silverstone 1975). Grant *et al.* (2006) subdivided the former *Dendrobates* into five genera at that time. Due the burgeoning body of literature on species concepts, we were surprised by a paucity of scientific discussion regarding higher-level taxonomy. Like many species concepts, the few generic concepts we were able to find were predominantly theoretical and difficult to implement. Following is a brief summary of many prevalent ideas regarding generic concepts. Mayr & Ashlock (1991) stated “the species category signifies singularity, distinctness and difference, while the higher categories have the function of grouping and ordering by emphasizing affinities among groups of species… (and) a genus (generic taxon) is a monophyletic group composed of one or more species that are separated from other generic taxa by a decided gap." Other generic concepts were modified species concepts, such as that proposed by Dubois (1988), stating that evidence for morphological, ecological and genetic discontinuities should be considered, and that taxonomists should use a modified biological species concept and species should be placed in the same group (genus) if able to produce viable hybrids. Winston (1999) stated:

> *Genera are defined not by one character, but by a group of carefully chosen characters. Usually at least some of them are correlated either functionally or genetically and so are present in all members of the groups. The members of the genus do not have to share all characters, however. One or more species in a genus may lack one or more of the diagnostic characters.*
>
> J.E. Winston 1999, p. 341

Quicke (1993) defined a genus as "one or more species that are believed to be closely related." In vertebrate taxonomy, the only absolute rule of genera we uncovered was the requirement of common ancestry (Wiley 1981; Dubois 1988; Myer & Ashlock 1991; Quicke 1993; Winston 1999). We advocate that genera represent "natural groups" of closely related species that are easily diagnosable via synapomorphies (morphological, behavioral and genetic).

One of us (J.L.Brown) reanalyzed the data of Grant *et al.* (2006) using Bayesian versus parsimony-based analyses. We generated new molecular data (see Twomey & Brown 2008), thinking this might reveal inconsistencies in the taxonomy proposed by Grant *et al.* 2006. However, we gradually realized that our frustration with the taxonomy proposed by Grant *et al.* (2006) was not scientific, but based on personal preferences (only a disdain for the new names applied to the taxa we affectionately called "*Dendrobates*"). In fact, any argument we proposed to justify the synonymy of Grant *et al.*'s taxonomy could just as easily be applied in their favor (i.e., monophyly, cohesiveness and diagnosability).

More recently, Santos *et al.* (2009) proposed to synonymize the genera of Grant *et al.* (2006), stating that:

> *…for the purpose of this paper, some corrections to the Grant et al.'s taxonomy must be made in order to have a nomenclature concordant with well-supported clades, and to avoid ambiguity and subsequent confusion in the literature of this family…*Dendrobates *sensu lato (including* Adelphobates, Dendrobates, Excidobates, Minyobates, Oophaga, *and* Ranitomeya*) was found to be a well-supported monophyletic group (as it was previously); thus the splitting of Dendrobates into several genera is unnecessary (e.g.,* Excidobates*) and Grant et al. did not provide an unambiguous list of synapomorphies for their generic concepts.…. Therefore, we synonymize* Adelphobates, Excidobates, Minyobates, Oophaga, *and* Ranitomeya *in the genus* Dendrobates.
>
> J.C. Santos *et al.* 2009, p. 44 of supplemental material

Like our initial criticisms, we think these criticisms are unnecessarily conservative, incorrect and possibly unscientific. To revert *Dendrobates* sensu Silverstone (1975) to a single genus (rather than 7 genera) ignores the considerable cohesion that the genera proposed by Grant *et al.* (2006), Twomey & Brown (2008) and this paper reflect (herein simply referred to as the "Grant *et al.*'s taxonomy"). Much of this unity has been recognized by dendrobatid taxonomists for the last 40 years, e.g., Silverstone's (1975) classification of the *pumilio* group (now *Oophaga*), or Myers' *quinquevittatus* (now *Ranitomeya*; 1982) and *minutus* groups (formerly *Minyobates* minus *steyermarki*, now *Andinobates*; Myers 1987). The synonymy of Santos *et al.* (2009) largely undervalues the existence of morphological and life-history characteristics associated with these genera (see below).

Under the more exclusive taxonomy, i.e., Grant *et al.* (2006), *Oophaga* is a group of poison frogs that: lacks conspicuous limb reticulation, has an entirely cartilaginous omosternum, has a sacrum fused with vertebra 8, engages cloacal touching during courtship/oviposition, uses small phytotelmata for tadpole deposition, has females as nurse frogs, has males that display a chirp call, has tadpoles that possess a single anterior and posterior larval keratodont rows, and has obligate egg feeding by females. Additionally, *Dendrobates* (sensu Grant *et al.*) is a group of relatively larger frogs with conspicuous coloration that lack oblique lateral and ventrolateral stripes, and have smooth dorsal skin texture. Adults are predominanty terrestrial, eggs are deposited terrestrially, and tadpoles are transported, often communally, into larger terrestrial pools. Parental care is done by males and females perform mate guarding. Lastly, *Ranitomeya* is classified as a group of small Amazonian poison frogs that possess the synapomorphies of reticulated netting on limbs, greatly expanded finger discs, conspicuous throat coloration and unfused vertebrae 2 and 3.

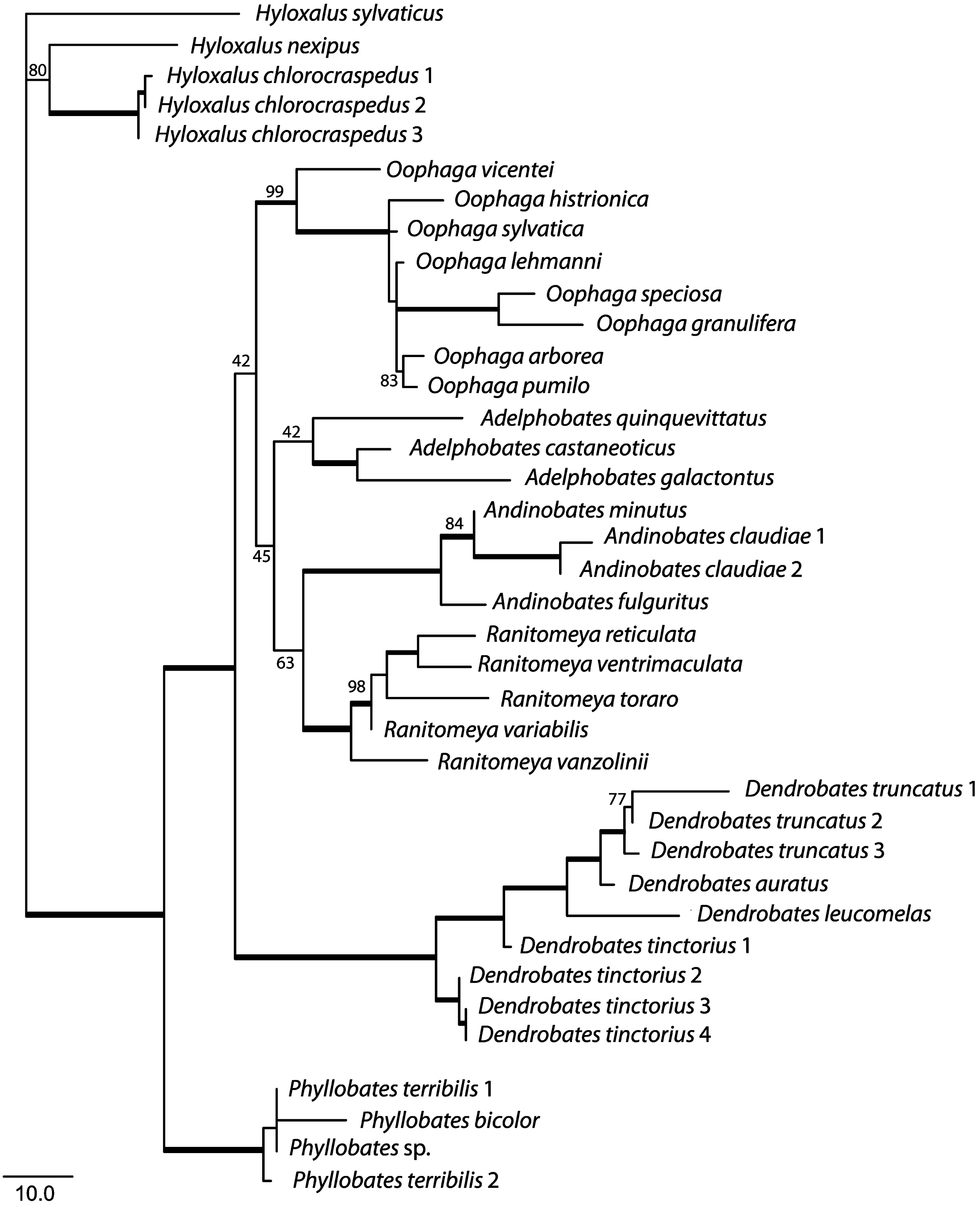

FIGURE 39. A consensus Bayesian phylogeny based on 2262 base pairs of nuclear DNA from five genes (Rag1, Rhodopsin, Histone H3, 28s, 7th in Absentia). Thickened branches represent nodes with posterior probabilities higher than 85 (those which are not labeled are 100). In addition, some branches of interest with posterior probabilities lower than 85 are labeled.

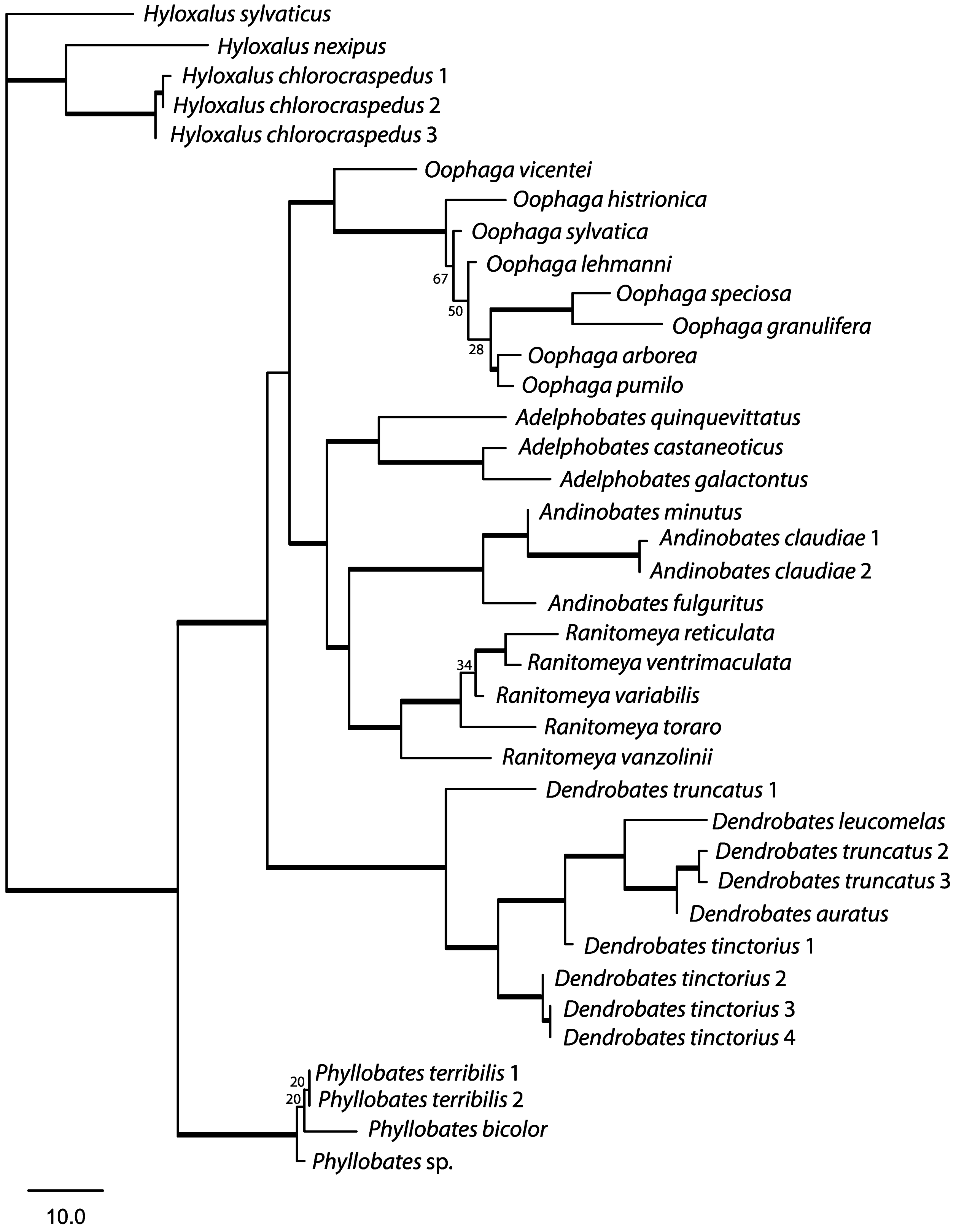

FIGURE 40. Consensus of 820 most parsimonious trees for 2622 base pairs of five nuclear genes (Rag1, Rhodopsin, Histone H3, 28s, 7th in Absentia). Thickened branches represent nodes with a consensus percentage of 100%.

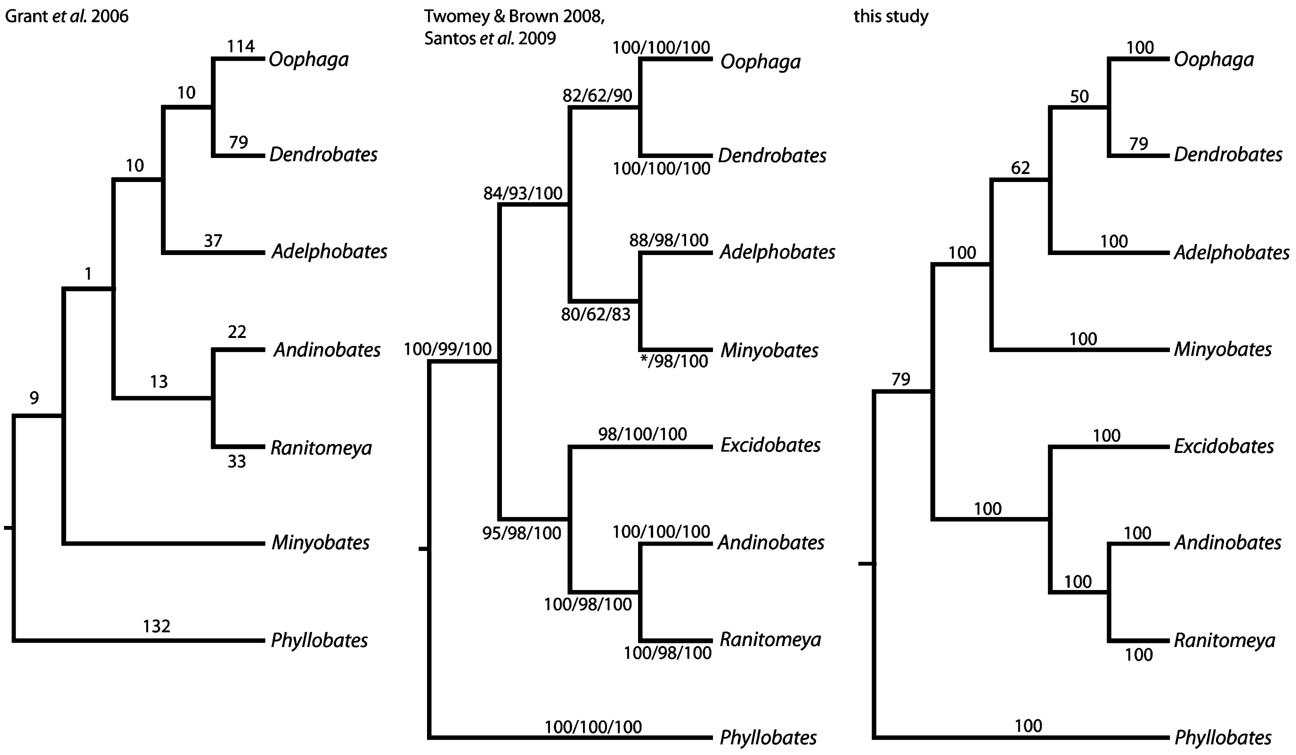

FIGURE 41. Phylogenetic relationships of genera. Left**:** Relationships between genera of Grant *et al.* 2006 based on ca. 6100 bp of nDNA and mtDNA, optimality criterion: maximum parsimony, numbers on branches depict Bremer support values. Center: Relationships between genera of Twomey & Brown 2008 based on 2124 bp of nDNA and mtDNA (Bayesian analysis) and Santos *et al.*2009 based on 2895 bp of nDNA and mtDNA (Bayesian and maximum likelihood analyses). Number on branches depict: posterior probabilities from Twomey & Brown 2008 / bootstrap values from Santos *et al.* 2009 / posterior probabilities from Santos *et al.* 2009. Right: Relationships between genera from this study based on 1011 bp of mtDNA, Bayesian analysis, number on branches depict posterior probabilities. If genus was excluded, focal study lacked corresponding taxa.

The diversity described for the more exclusive genera is on par with the differences observed when comparing *Phyllobates* to its sister group *Dendrobates* sensu Silverstone (1975). The continued use of *Dendrobates* sensu Silverstone inaccurately exaggerates the differences between *Phyllobates* and all other dendrobatines and undervalues the dramatic diversity within this subfamily. Under the broader definition of *Dendrobates* sensu Silverstone, the previously mentioned variation is contained within a single genus. The genus *Dendrobates* sensu Silverstone is most commonly diagnosed by appressed first finger noticeably shorter than second (an exception in *Adelphobates quinquevittatus, A. castaneoticus, Excidobates mysteriosus, Minyobates steyermarki, Dendrobates truncatus* and *Andinobates daleswansoni* in which fingers are barely shorter or are equal in length), lack of webbing between toes (however, in *Andinobates dorisswansonae* and *A. daleswansoni* toes IV and V are fused), finger discs conspicuous, enlarged in adults to at least twice finger width in fingers II, III and IV (however, in most *Andinobates, Excidobates* and *Minyobates* finger discs are moderately expanded and often less than two times finger width) and absence of premaxillary and maxillary teeth (Silverstone 1975; Myers 1982).

Santos *et al.* 2009, stated that "some of the putative synapomorphies for genera used by Grant *et al.* are ambiguous and others are problematic", but unfortunately, these authors did not explicitly describe these problems so that we cannot address them specifically. However, these same criticisms can be said about *Dendrobates* sensu Silverstone (1975). Poison frog systematists have frequently ignored inconsistent characters and typically only report those that agree with the definition of their focal taxon. Further, those characters most commonly used (discussed above) do not provide any obvious diagnostic advantages to those mentioned for the seven genera (in that they are not absolute indicators of the genus/genera). Santos *et al.* 2009 followed by stating:

> *These include those with sequence errors…,those that are polymorphic intraspecifically (coloration pattern and alkaloid presence), poorly defined (e.g., advertisement call type), or undetermined in*

> *most species (e.g., larvae morphology, chromosome number, alkaloid profile, and type of parental care).*
>
> J.C. Santos *et al.* 2009, p. 44 of supplemental material

Given that all the groups were well supported and were demonstrated to be statistically monophyletic by Twomey & Brown (2008), whose topology is almost identical to their own, no phylogenetic support exists for their justification (i.e., para- or polyphyletic genera). Furthermore, the claim that the presence of "sequencing errors" invalidates these genera is also incorrect, and as mentioned above, their topologies for this group are very similar. We are unsure what support "those that are polymorphic intraspecifically (coloration pattern and alkaloid presence)" provides in favor of *Dendrobates* sensu Silverstone (1975) versus sensu Grant *et al*. All dendrobatine genera proposed by Grant *et al.* (2006) are diagnosable in the absence of alkaloid data. Further, most intraspecific polymorphisms in coloration/pattern actually favor the more exclusive genera of Grant *et al.* (2006). This is because the latter taxonomy reduces the number of species within a genus and genera are composed of taxa that are more closely related; resulting in the presence of synapomorphies that are absent in the larger group *Dendrobates* sensu Silverstone. More importantly, the synapomorphies commonly used to diagnose *Dendrobates* sensu Silverstone are not unambiguous and are problematic (with the exception of presence/absence of premaxillary and maxillary teeth, a character intended by Silverstone (1975) to be used only in conjuction with finger disc size and finger length)(discussed above).

Despite their claims that much is "undetermined," the genera *Adelphobates*, *Excidobates*, *Minyobates*, *Oophaga*, *Ranitomeya*, *Andinobates and Dendrobates* have been the focal subjects of hundreds of studies (over 300 counted at the time of writing, including several books; e.g., see Lötters *et al.* 2007), and Dendrobatidae is one of the more thoroughly studied anuran families. To claim that exhaustive data on all these species is necessary before new taxonomies can be considered is unnecessarily conservative. Further, when characters are placed in a phylogenetic context, there is considerable phylogenetic affinity for many of the characters proposed (e.g., call data: Erdtmann & Amézquita 2009, Table 5; e.g., behavior, Table 6: see Summers & McKeon 2004, Brown *et al.* 2009; e.g., tadpoles: Grant *et al.* 2006, this paper, Table 4), thus, some missing data are not likely to dramatically affect these taxonomies. Lastly the specific characters they mentioned (larval morphology, chromosome number, alkaloid profile and type of parental care) were never listed as explicit synapomorphies by Grant *et al.* (2006) for dendrobatine genera, but rather were included as known characteristics of these genera in addition to the unambiguous synapomorphies.

Recently, several systematists have argued that taxonomic changes affecting genera should be minimized to maintain communication among the biological community and in place of creating new genera, subgenera (or unranked taxa) should be created to formally recognize diversity to facilitate nomenclatural continuity (D.C. Cannatella, pers. comm.). We agree that researchers should refrain from needlessly creating genera. The creation of subgroups to maintain consistency, however, downplays a group's cohesiveness (when compared to the creation of a new genus). This also entrenches taxonomists in previously described genera and can greatly attenuate the biological unity observed in taxonomies resulting from detailed molecular taxonomies (many times replacing genera prescribed from purely morphological taxonomies). Lastly from the point of view of conservation, it is important for all non-specialists to realize how diverse a taxonomic group actually is, rather than masking the diversity within described genera.

Ultimately, the current discussion regarding generic classification has little to do with taxonomic code, and more to do with the tradeoff between nomenclatural consistency on one side and adequately depicting a group's cohesiveness on the other, and hence is open to debates among the scientists. In the case of *Ranitomeya*, and likely in other dendrobatine genera, it is impossible to maintain taxonomic continuity because of numerous alpha-taxonomic problems, genus-level debates aside. We think it is important that taxonomies be challenged and exhaustively discussed; we hope for generations to come taxonomists will continue to feverishly work to perfect taxonomies. Further, no taxonomic change should be apathetically accepted: continued dialogue (e.g., that of Santos *et al.* 2009) and careful attention to details will ultimately reduce unnecessary confusion from nomenclatural irresponsibility. Regarding the use of *Dendrobates* sensu Silverstone (1975), we feel it is time move forward, and we have presented our case in this paper.

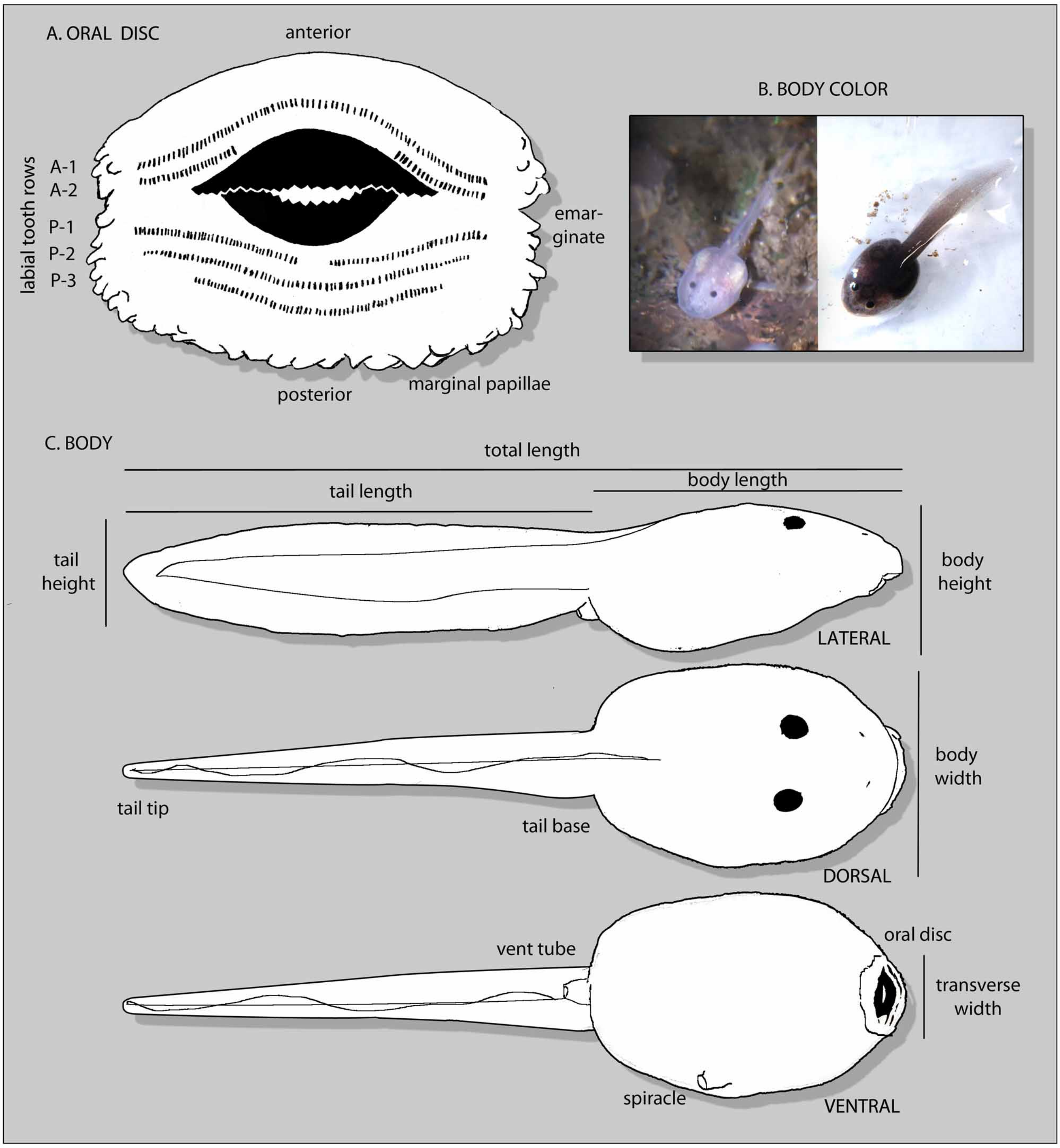

FIGURE 42. ***Ranitomeya* tadpole morphology.** Major features of: **A.** Oral disc morphology, **B.** Body coloration, **C.** Body morphology.

Tadpole Morphology

Relatively few tadpoles of species of *Andinobates* and *Ranitomeya* have been thoroughly described. Among the 28 species, tadpoles of five species are unknown (Table 4). Among the known tadpoles, some descriptions are incomplete and others are based on only one tadpole or only on back-riding tadpoles. Descriptions based on a series of specimens are available for only two species. Back-riding tadpoles that are collected from an adult frog may not have all characters developed. In particular, very small back-riding tadpoles may not have developed labial tooth rows or they may have developed only one anterior and two posterior rows. Even small tadpoles in stages 25 or 26 may not have rows fully developed. Upper and lower tail fins may change in height or shape in older tadpoles, and proportions of various characters may change as tadpoles develop.

The lack of sufficient tadpole specimens for description is a result of several factors. Species in these two genera typically have small clutch sizes, and tadpoles develop in small phytotelmata, such as bromeliads, axils of various plant species, and vineholes or treeholes. Thus, collecting a reasonable series of tadpoles of any species at one time can be difficult. Tadpoles are more easily located for those species that use axils of plants such as *Heliconia* that occur in stands. Other species use widely spaced bromeliads or treeholes, and their tadpoles, which often occur singly, can only be located by following adult frogs when they visit tadpole nurseries to transport a tadpole or to provide nutritive eggs, or by locating and searching phytotelmata for tadpoles.

In addition, relative few researchers work with tadpoles. Understandably, many researchers are interested in adult frogs, which may be poorly known and are necessary to understand relationships and construct phylogenies. Coupled with the fact that many of these species have very restricted ranges often in remote areas means that locating tadpoles is not the highest priority. However, good tadpole descriptions can add to our knowledge of the species and provide valuable clues to relationships (Caldwell *et al.* 2002).

In the future, we encourage investigators to preserve good series of tadpoles from as many localities as possible. We realize that in this paper most of the new tadpole descriptions used only a couple of specimens from a single locality. In this case, our attention (J.L. Brown) to collecting complete tadpole series, regrettably, actualized shortly after completing most the field work for this project. Ideally, specimens in a variety of stages of development will add to the completeness of the description. Only with a good series of well-preserved tadpoles (preserved and permanently stored in 10% formalin) can investigators provide complete descriptions, assess variation, and document how morphological changes occur during development.

Müllerian Mimicry

Mimicry appears to be more common than previously documented among *Ranitomeya* species (Symula *et al.* 2001). The striking similarities among populations of *Ranitomeya uakarii* (which possess yellow dorsolateral and middorsal stripes) and *Ranitomeya toraro* sp. nov., some syntopic populations *R. amazonica* and *R. reticulata*, and Varadero populations of *R. imitator*, *R. fantastica* and *R. variabilis* are similar to those in the Müllerian mimicry systems observed by Symula *et al.* (2001). Assuming the aforementioned cases are in fact a result of Müllerian mimicry, this would mean half of all extant *Ranitomeya* species are involved in mimicry systems (Fig. 43). In other species, it is apparent that other factors affecting phenotype do not fit a mimicry model. For instance, the reoccurring origins of spotting in montane populations of *R. variabilis* or the considerable variation observed in *R. sirensis* suggest that other factors (i.e., sexual selection, genetic linkage, or stochastic processes) played a key role in the evolution of phenotypic diversity.

Dendrobatid Frogs and the Pet Trade

Smuggling for the pet trade remains a serious threat to native populations, including *Ranitomeya*. Despite having brought attention to this (Gorzula 1996; Pepper *et al.* 2007; Lötters *et al.* 2008; Brown *et al.* 2008c; Nijman & Shepard 2010), the pet trade continues to drive the market for smuggled animals (Table 10). For example, shortly after describing *R. benedicta* (Brown *et al.* 2008c), publishing new pictures of new morphs of *R. imitator* (ca. 2006 on www.dendrobates.org), or publishing the rediscovery of *E. captivus* (Twomey & Brown 2008), the result was the almost immediate arrival of illegal specimens in trade shows in North America and Europe. These acts appear to have had negative impacts on at least some populations. For example, during recent trips to Shucushuyacu (in 2008 and 2010), the type locality of *R. benedicta*, we were faced with the dismal reality that locals were cutting trees to access the large *Aechmea* bromeliads growing in the canopies in search of this species. If the hobby is to have a sustainable future, these trends need to cease and hobbyists need to make educated and ethical decisions when purchasing new frogs. Today, consumers have an unprecedented number and variety of sustainably produced frogs available. These choices include captive-bred specimens (particularly those whose founding stock are of legal origin), wild caught individuals imported legally via controlled quotas, and those frogs sustainably bred in the country of origin.

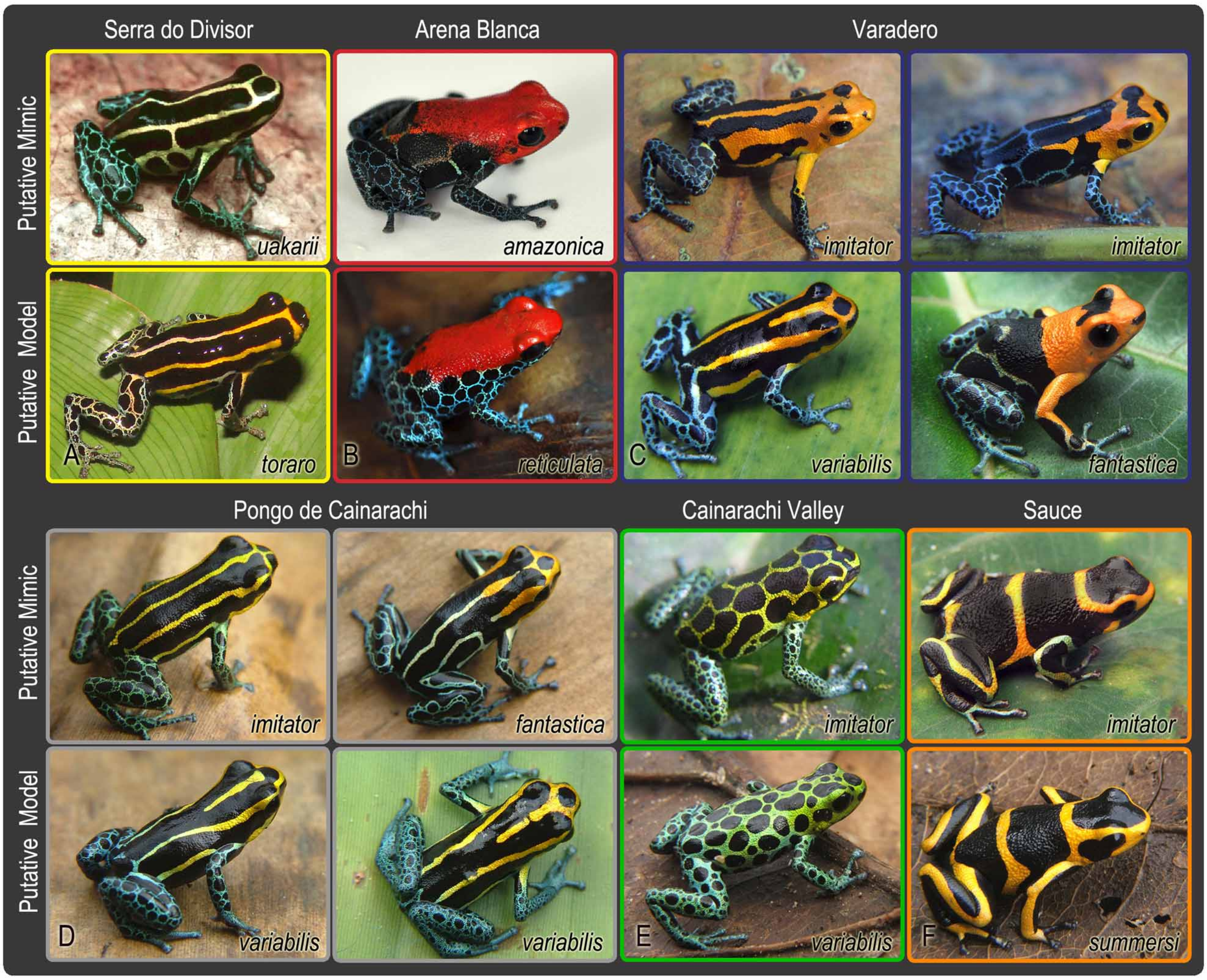

FIGURE 43. Potential examples of mimicry in *Ranitomeya*. A. *Ranitomeya uakarii* and *R. toraro* from western Brazil. **B.** *Ranitomeya amazonica* and *R. reticulata* from undisclosed locality in Loreto, Peru. **C.** *Ranitomeya imitator*, *R. variabilis*, *R. fantastica* from Varadero, Loreto, Peru. In this population, individuals of *R. imitator* display a cline of morphologies, usually closely resembling local morphs of either *R. variabilis* or *R. fantastica*. **D.** *Ranitomeya imitator*, *R. variabilis* and *R. fantastica* from Pongo de Cainarachi, San Martin, Peru. In this population (and surrounding areas), individuals of *R. imitator* and *R. fantastica* (nearby populations possess considerably more orange on the head and dorsum and lack the appearance of 2 black stripes down the dorsum) appear similar to widespread lowland morph of *R. variabilis*. **E.** *Ranitomeya imitator* and *R. variabilis* from Cainarachi Valley, San Martin, Peru. **F.** *Ranitomeya imitator* and *R. summersi* from Sauce, San Martin, Peru. See Symula *et al.* 2001 for analyses of D, E and F as cases of Müllerian mimicry.

One aspect of amphibian smuggling that is largely overlooked is the process by which most frogs arrive to the market. Simply put, the number of individuals for sale does not reflect the number of individuals removed from the wild. Most illegal specimens are exposed to horrendous shipping and living conditions on the way to the market (Fig. 44). At trade shows only the few specimens that arrived in fair physical condition are encountered. Only the smugglers know the exact mortality rates and number of frogs that are illegally harvested. Based on observations of confiscated shipments, it is apparent most smugglers give little consideration to maximizing the survival of each specimen. Frogs are often packed inhumanely in crowded containers or cages and often food-deprived for days (INRENA personal comm. 2005). Because new frogs (of known illegal origin) continue to arrive at trade shows, many thousands of individuals likely die worldwide each year.

For example, in Peru hundreds to thousands of animals are collected by local farmers and held for a middleman until numbers are sufficient to warrant travel costs (Pepper *et al.* 2007). A smuggled frog can be sold for over 500 times their initial investment (for example in 2008, the first specimens of *R. benedicta* were sold for over $500 each in Europe). This recipe makes exploitation not only affordable for the smugglers but also so potentially lucrative that there is little incentive to "invest" in proper care of frogs during transit.


A
B
C
D
E

FIGURE 44. Illegal traffic of poison frogs. A. A cage for poison frogs containing ca. 50 *A. silverstonei* awaiting collection for illegal trade (near Tingo Maria, June 2007) **B.** Inside view of cage. **C.** 500 ml soda bottles and **D.** wooden boxes containing dozens of *R. imitator*, *R. variabilis* and *R. fantastica* awaiting collecting for illegal trade (near Varadero, Loreto, August 2007). **E.** Dead *Ranitomeya vanzolini* and *Excidobates mysteriosus* (an endangered species) found hidden amongst a shipment of tropical fish and destined for a major distributor of frogs in Europe in 2005. Over 400 frogs were discovered in this shipment, concealed among tropical fish exports from Iquitos, Loreto, Peru. The frogs themselves were packed against each other, with no room to move, inside plastic tubes with a diameter of about 3 cm. Nearly half of the animals were dead upon seizure in Lima. The remaining live animals were immediately released to the custody of Zoocriadero Exotics Frogs in Iquitos, and despite considerable effort, more than 80% of the survivors died shortly thereafter. Assuming many more perished during the collection of these animals and transport to Iquitos (as both species habitats occur greater than 600 km from Iquitos), it is easy to speculate that several hundred additional animals perished during this single export. The shipping conditions observed here are standard practice in the illegal trade of poison frogs.

TABLE 10: Summary of information known regarding the current state of smuggling poison frogs for the pet trade.

Number – Species	Case Info	Mortality	Punishment	Citation
580 - *O. pumilio* 22 - *D. auratus*	In 2004 CITES officials discovered over 600 frogs packed into more than 200 film canisters. Each canister contained 2 to 3 frogs. Three Belgian citizens, arriving from Panama, were arrested.	10%	Arrested, punishment not disclosed	TRAFFIC 2011
196 - *O. histrionica*	In 2000 a Panamanian man was arrested in Bogota, Colombia transporting Harlequin poison frogs and 344 Matamata Turtles (*Chelus fimbriatus*). (Destination unspecified, presumed Panama)	Unknown	2 years imprisonment and fined $13,864 USD	TRAFFIC 2011
770 - *D. leucomelas*	In 2000, Frankfurt, Germany customs officials seized 770 poison frogs hidden in three plastic containers hidden within the hand luggage of the person traveling from Venezuela.	Unknown	Unknown	TRAFFIC 2011
32 - adults of the following species: *D. tinctorius*, *R. amazonica*, *Allobates femoralis*	In 2006, Belgian federal police stopped 7 Belgians and a French person returning from French Guiana. The latter had the 32 frogs in film canisters in the bottom half of a drink thermos. Belgian police searched their residences and confiscated 10 additional '*Dendrobates*' specimens.	Unknown	Two perpetrators were fined 2000 Euros each, another 800 Euros. In addition, the three were fined a joint sum of 3000 Euros.	TRAFFIC 2011
373 - of the following species: *O. pumilio* and *D. auratus*	Frogs were found in plastic tubes in the suit case of a British passenger arriving from Panama. Resulted in raids on several premises in southern England; additional poison frogs were seized	Unknown	Unknown	TRAFFIC 2011
330 - *O. pumilio* 30 - *D. auratus*	Collected in Costa Rica, a German citizen attempted to hide the specimens in a concealed compartment of a sport bag. Frogs were contained in three plastic boxes.	50% were found dead on arrival, or died since arriving.	Unknown	TRAFFIC 2011
279 - *A. galactonotus* 281 - *D. tinctorious*	In 1999, the 560 frogs destined for Germany were confiscated in Guarulhos International Airport, Brazil packed individually in film canisters inside of two suitcases.	Unknown	Unknown	Postoni & Felipe-Toledo (2010)
400 of the following species: *E. mysteriosus* and *R. vanzolinii*	In 2005 in Lima, Peru officials discovered 400 frogs pack tightly inside of small plastic tubes (ca. 3cm) hidden amongst a shipment of tropical fish arriving from Iquitos intended for Europe.	50% were dead upon discovery, more than 90% eventually died.	Unknown	M. Pepper, M. Sanchez-Rodriguez, unpub. data

Below we offer some anecdotal reports which we hope give insight to the ramifications of illegal smuggling practices.

Atalaya, Ucayali, Peru

A small isolated town on the east versant of the Cordillera El Sira, (Atalaya, Peru) was often visited by foreigners in search of *R. vanzolinii*. In 2007, we (M. Pepper) arrived here and before leaving the airport, we were approached by an airport security worker with an offer to purchase this species. This offer was made without solicitation or any indication that we had come looking for the frog. After three days of searching near Atalaya, we failed to find a single individual of *R. vanzolinii*. Subsequent trips to Atalaya in 2007 and 2008 (by M. Sanchez-Rodriguez), as well Shepahua, where *R. vanzolinii* was also once common, resulted in only one animal being found. Around that time, large numbers of this species arrived in Europe and the US, despite neither Peru nor Brazil ever having issued CITES export permits for the species for non-scientific purposes.

Tingo Maria, Huánuco, Peru

Local farmers from the mountains east of Tingo Maria (locally known as the "Divisoria") recount the times in the late nineties when they would sell frogs to certain "gringos." One villager claimed that 900 *R. sirensis* (at the time, known as *lamasi*) were sold on a single occasion. It is impossible to determine exactly how many frogs were collected for the pet trade; however, it is evident that this unique morph, known only from this area (the Divisoria morph), once was frequently available in the pet trade. Despite frequent visits and arduous searches by several of the authors over the last five years (J.L. Brown, E. Twomey, M. Pepper, M. Sanchez-Rodriguez), we have failed to locate this morph in the wild. Another victim is *Ameerega silverstonei*, also part of this trade circuit. This species continues to be collected for illegal exportation —one farmer stated that he continues to sell "40–60 adult *A. silverstonei* a month" and has done so for the last several years (name undisclosed, pers. comm.; Fig. 44). Despite this, relatively few *A. silverstonei* have arrived on the black markets, suggesting to us that most of them probably died during transit through the sweltering lowland cities of Iquitos and Pucallpa.

Unfortunately, these practices are not restricted to Atalaya or Tingo Maria. We have encountered similar situations in dozens of villages and towns throughout our travels in Peru (e.g., Chazuta, Pongo de Cainarachi, Iquitos, Tarapoto, Shucushuyacu and Puerto Inca).

While doing the final revisions of this monograph, we decided to remove several localities and pictures because we feared that this information would be exploited by smugglers. We realize that this is not standard procedure; however, people who work with or study marketable species must consider the potential impact on wild populations resulting from novel information published (both in manuscripts and on the internet). These actions detract from the completeness of this research, in essence slowing scientific progress by inhibiting the dissemination of information.

It should be noted that the authors are not opposed to keeping poison frogs as pets, in fact the contrary. We feel that dendrobatids play an important role in captivity. They serve as ambassadors to not only the plight of the world's amphibians but also, more importantly, to the plight of the tropical forests and other natural wonderlands across the globe (e.g., Madagascar). While in captivity, these frogs have become for many a tangible connection to tropical rainforests in far off places. For the many that will not be as fortunate as we are, to have had the opportunity to search amidst the rainforest for these frogs, the only contact they may have with these remarkable forests and their inhabitants are through the exposure to animals in captivity.

Future Directions

Ironically, one of the biggest factors impeding anuran taxonomy in South America is the arduous and often long process to obtain collection and export permits (both for whole specimens and genetic samples). Without increased governmental support, rigorous taxonomic studies containing large type series (distributed at multiple museums) are not possible (for both national and international researchers). Recent restrictions on the export of genetic samples, with particular fear of "biopiracy" have further complicated this process. It is impossible to plan out effective conservation strategies without basic knowledge of biodiversity. In recent decades, this has become particularly important; we are now witnessing unnaturally high extinction rates (Barnosky *et al.* 2011). We are among the first generation of scientists to be commonly confronted with the challenge of describing species as they disappear. This problem is further exacerbated by the decreasing emphasis being placed on taxonomy as an important science. In recent decades, funding for collection and taxonomic training has been greatly reduced (both in developed and developing nations), despite wide acknowledgement that quantifying biodiversity is one of the most fundamental requirements for effective conservation (McClain 2011).

In regard to the taxonomy of *Ranitomeya*, we still lack basic life history information for several species (e.g., mating system, reproductive resource types, tadpole development and ecology). Though this information is partially known for most species and, at minimum, for species groups, detailed knowledge of this information can be very important in context of evolutionary studies. Numerous geographic areas remain underexplored or lack genetic material and whole specimens, including adults and especially tadpoles. We have classified three key areas in need of basic exploration based on current collection data and ecological niche modeling: 1. Amazonian Colombia northwest of La Pedrera. 2. Western Brazil (specifically the Rio Jurua and Purus drainages south of Rio Amazonas and the Rio Negro drainage to the north) 3. Southeastern Venezuela (Roraima region and central Guyana). These areas may or may not contain *Ranitomeya* species; however, they appear to be climatically suitable and are geographically proximate to known populations (see Lötters *et al.* 2010). In many areas, even if we understand the composition of the *Ranitomeya* communities, we lack crucial genetic material (see Fig. 45).

We hope this revision has revealed some of the problems poison frog taxonomists encounter when delimiting species solely on morphological characters. Still, when using molecular data, researchers also need to proceed with caution, as these tools are not absolute barometers of a species. Factors such as historical introgressive hybridization, incomplete lineage sorting, recombination and gene duplication are increasingly reported (Brown & Twomey 2008, Shimada *et al.* 2010; Hauswaldt *et al.* 2010). These phenomena make it difficult to discern a "true" species tree from a gene tree. Arbitrary genetic metrics such as branch lengths or genetic distances (which only vaguely depict common ancestry) can be difficult to interpret and can be misleading. These metrics can be sensitive to the breadth of genetic sampling, demographic processes (i.e., population size and dispersal potential), and the biogeography of the species. Often high genetic divergence can be explained simply by isolation-by-distance rather than speciation. For example, in this study we observed high genetic divergence within *R. variabilis*; however, when we classify the morphological divergence within this group in context of the mitochondrial phylogeny, we are not presented with any natural subgroups that display consistent differences in morphology —both adult and larval — acoustics, ecology or behavior. In contrast, the *R. fantastica* species complex (sensu Brown *et al.* 2008c) occupies a considerably smaller geographic range and demonstrates about a quarter of the genetic divergence observed in *R. variabilis*. However, the three recognized species within this group differ acoustically, morphologically and phylogenetically. If we were to use the observed genetic divergence of the *fantastica* species complex as the rule for genetic divergence per species in *Ranitomeya*, this would suggest that the *R. variabilis* is a complex containing multiple species, rather than being a single, widespread species.

In conclusion, we urge future taxonomists to consider behavioral, morphological (both adult and larval), ecological and phylogenetic data when classifying new dendrobatine species. The inclusion and careful consideration of these data can reduce unnecessary taxonomic confusion and will facilitate the designation of other new species. This revision resulted in the synonymy of five species (*R. ignea*, *R. duellmani*, *R. biolat*, *R. lamasi* and *R. intermedia*), description of one new species (*R. toraro*), redescriptions of three species (*R. uakarii*, *R. variabilis* and *R. sirensis*), a restriction of *Ranitomeya* resulting in the description of one new genus (*Andinobates*) and placement of one species as *nomen dubium*.

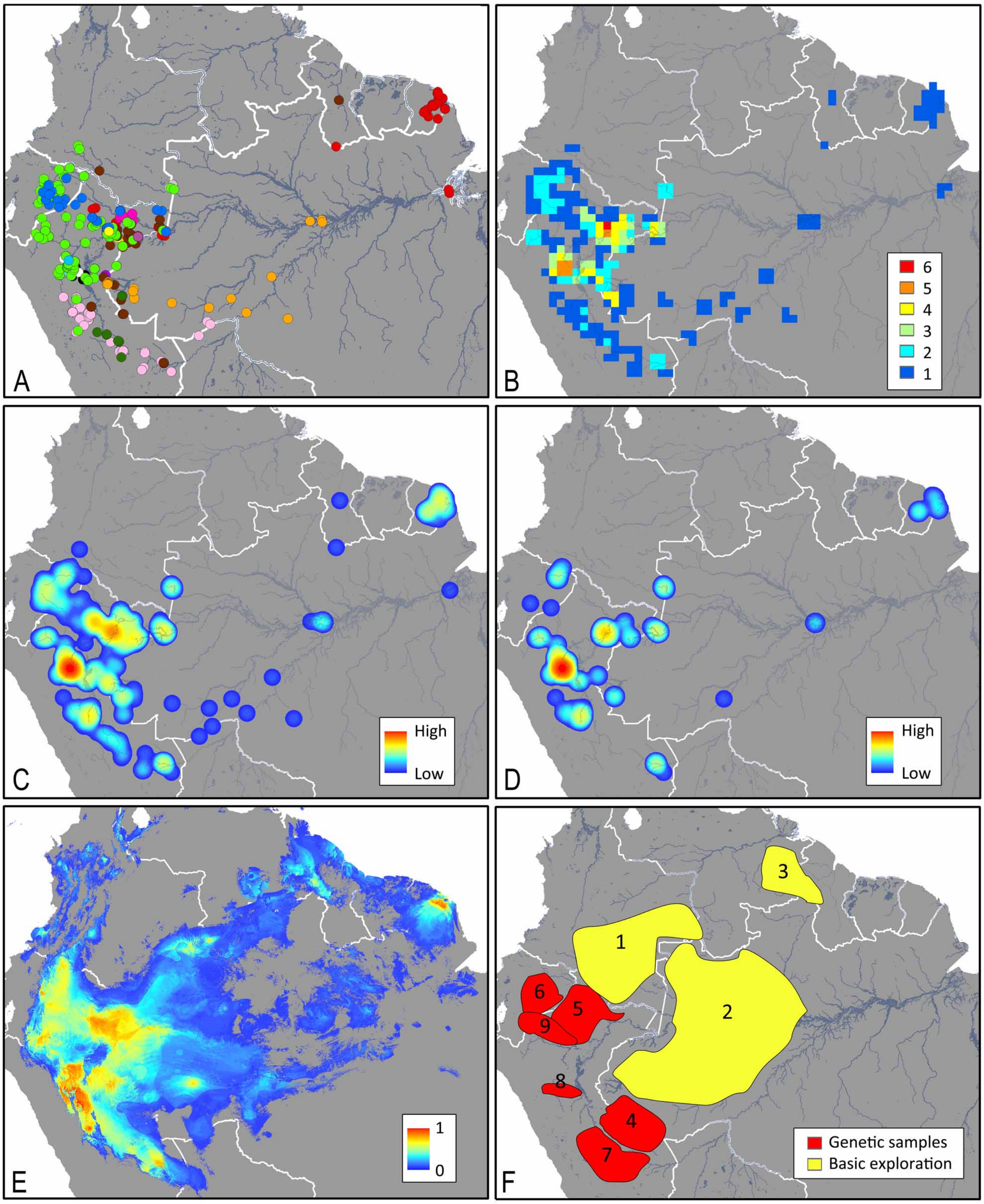

FIGURE 45. **Geospatial distribution of our current sampling of *Ranitomeya*. A.** Distribution of *Ranitomeya* species (each color represents a different species). In figures A–F; warmer colors represent high values. **B.** Species richness. Spatial density of observations: **C.** reported localities and **D.** available genetic material. **E.** Species distribution model of the genus *Ranitomeya*. Higher values (represented by warmer colors) depict areas of high habitat suitability. **F.** Key areas in need of future research (red= areas in need of genetic exploration, yellow= areas in need of basic exploration). Google Earth files downloadable from: http://www.jasonlee-brown.org/Ranitomeya_GoogleEarth.zip

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DNA sequences: *Incertae sedis*

The following list represents DNA sequences of dubious origins (both in terms of tissue source or the locality applied to the tissue source) or those that differ considerably from other individuals from similar populations (whereas other gene regions sequenced share considerable similarity). In some cases we cannot rule out that these sequences are not the "true" sequences; however, if used in the future, results should be interpreted with caution.

1. DQ502302.1: *Phyllobates lugubris* isolate 329 histone H3 gene. Matches (100%) a caecilian (*Caecilia tentaculata*) histone H3a gene and is not similar to any *Phyllobates*.
2. DQ371305.1: *Dendrobates uakarii* (now considered *R. uakarii*) 12S ribosomal RNA gene. This sequence is very similar to several individuals of *Adelphobates castaneoticus* individuals rather than other *Ranitomeya*. Since this realization, this individual has been resequenced and the new, correct 12S sequence is available (see Apendix II). This error can be definitively attributed to a "tracking error" during post DNA sequencing processing. This explains the extremely long branch lengths observed in Roberts *et al.* (2006a) and Brown *et al.* (2006).
3. AF482773.1: *Dendrobates quinquevittatus* (now considered *A. quinquevittatus*) 12S ribosomal RNA gene. This is 99% identical to *Excidobates mysteriosus*, and not similar to other *Adelphobates quinquevittatus* individuals. The inclusion of this sample could explain why Roberts *et al.* (2006a) found a novel placement of this taxon.
4. AF482794.1: *Dendrobates biolat* (now considered *R. sirensis*) 16S ribosomal RNA gene. This sequence is very similar to other sequences of *R. fantastica* and not very similar to other members of the *vanzolinii* group or, more importantly, to other *R. sirensis*.
5. All Brazilian *D. ventrimaculatus* from Symula *et al.* (2003) and Roberts *et al.* (2006a) due to ambiguous labels on both the vial containing received tissue and corresponding DNA extraction, locality cannot be attributed with certainty to either locality/species. At the time of DNA extraction this information may have been clear; however, as outsiders, we cannot determine any locality with certainty.

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Appendix I. Species names, collection localities, and GenBank accession numbers (where available) for taxa included in the phylogenetic analysis.

Name in Tree	Locality (Country:Province/ Department/State: locality)	Coordiantes		Study	Genbank Info		
current name (former name) #		Lat	Long		*12S*	*16S*	*CytB*
amazonica (*ventrimaculata*) 1	French Guiana: Maripa	NA	NA	Noonan and Wray 2006	DQ163088	DQ163080	DQ163069
amazonica (*ventrimaculata*) 2	French Guiana: Maripa	NA	NA	Noonan and Wray 2006	DQ163085	-	DQ163067
amazonica (*ventrimaculata*) 3	French Guiana: Maripa	NA	NA	Noonan and Wray 2006	DQ163086	DQ163078	DQ163068
amazonica (*ventrimaculata*) 4	French Guiana: Pic Matecho	NA	NA	Noonan and Wray 2006	DQ163083	DQ163075	DQ163066
amazonica (*ventrimaculata*) 5	French Guiana	NA	NA	Roberts *et al.* 2006	DQ371302	DQ371313	DQ371332
amazonica (*ventrimaculata*) 6	French Guiana: Saul	NA	NA	Noonan and Wray 2006	DQ163084	DQ163081	DQ163070
amazonica (*ventrimaculata*) 7	Unknown	NA	NA	Fouquet *et al.* 2007	-	EU201083	-
amazonica (*ventrimaculata*) 8	Colombia: Amazonas, Leticia, Km 11 (Leticia-Tarapaca)	-4.11228	-69.93964	this study	JN635787	JN635842	JN635915
amazonica (*amazonica*) 9	Peru: Loreto: Near ACEER camp, north bank of Napo River	NA	NA	Symula *et al.* 2003	AF482781	AF482796	AF482811
amazonica (*ventrimaculata*) 10	French Guiana: Guyane	NA	NA	Santos *et al.* 2009	EU342681	EU342681	JN635885
amazonica (*ventrimaculata*) 11	French Guiana: Kaw	NA	NA	Noonan and Wray 2006	DQ163087	DQ163076	DQ163073
amazonica 12	Unknown	NA	NA	Fouquet *et al.* 2007	-	EU201084	-
amazonica 13	French Guiana	NA	NA	Vences *et al.* 2003	-	AY263248	-
amazonica (sp. aff. *fantastica*) 14	Peru: Loreto: Pevas	NA	NA	this study	JN635788	JN635843	JN635916
amazonica (*ventrimaculata*) 15	Colombia: Amazonas: Puerto Nariño	NA	NA	this study	-	JN635878	JN635936
amazonica 16	Peru: Loreto: undisclosed locality 'arena blanca 1'	AUR	AUR	this study	-	JN651251	JN635940
amazonica 17	Peru: Loreto: undisclosed locality 'arena blanca 2'	AUR	AUR	this study	-	JN651255	JN635944
amazonica 18	Peru: Loreto: undisclosed locality 'arena blanca 2'	AUR	AUR	this study	-	JN651252	JN635941
amazonica 19	Peru: Loreto: undisclosed locality 'arena blanca 1'	AUR	AUR	this study	-	JN651254	JN635943
amazonica 20	Peru: Loreto: undisclosed locality 'arena blanca 1'	AUR	AUR	this study	-	JN651249	JN635938
amazonica 21	Peru: Loreto: undisclosed locality 'arena blanca 1'	AUR	AUR	this study	-	JN651271	JN635958
amazonica 22	Peru: Loreto: undisclosed locality 'arena blanca 2'	AUR	AUR	this study	-	JN651272	JN635959
amazonica 23	Peru: Loreto: undisclosed locality 'arena blanca 2'	AUR	AUR	this study	-	JN651273	JN635960
amazonica 24	Peru: Loreto: undisclosed locality 'arena blanca 2'	AUR	AUR	this study	-	JN651274	JN635961
amazonica 25	Peru: Loreto: km 26 on the road from Iquitos to Nauta	-3.96400	-73.40500	this study	JN635785	JN635840	JN635913
amazonica (*ventrimaculata*) 26	Peru: Loreto: km 41 on the road from Iquitos to Nauta	-4.07500	-73.46200	this study	JN635786	JN635841	JN635914
amazonica 27	Peru: Loreto: km 26 on the road from Iquitos to Nauta	-3.96400	-73.40500	this study	JN635784	JN635839	JN635912
amazonica (*amazonica*) 28	Peru: Loreto: Almendras	-3.83411	-73.38975	Symula *et al.* 2003	AF482770	AF482777	AF482792
arborea	Panama	NA	NA	Clough and Summers 2000	AF128611	AF128610	AF128612
auratus	Panama	NA	NA	Clough and Summers 2000	AF128602	AF098745	AF128603
benedicta	Peru: Loreto: nearby Shucushuyacu	-6.03209	-75.85700	Brown *et al.* 2008	EU736204	EU736219	EU736191

Name in Tree		Coordiantes			Genbank Info		
current name (former name) #	Locality (Country:Province/ Department/State: locality)	Lat	Long	Study	*12S*	*16S*	*CytB*
bicolor	Colombia: Choco	NA	NA	Clough and Summers 2000	AF128578	AF128577	AF128579
bombetes 1	Colombia: Valle del Cauca: Buga, Buga-Buenaventura road, 1610 masl	NA	NA	Santos *et al.* 2009	EU342668	EU342668	-
bombetes 2	Colombia: Quindio: Barbas, Finlandia, Hacienda Lusitania, 1958 masl	4.67000	-75.67000	Santos *et al.* 2009	EU342669	EU342669	JN635880
bombetes 3	Colombia	NA	NA	this study	-	JN635869	-
captivus (sp. nov.) 1	Ecuador: Zamora Chinchipe: near Panguitza, 870 masl	NA	NA	Santos *et al.* 2009	EU342666	EU342666	JN635879
captivus 2	Peru: Amazonas: Rio Santiago near the cofluence of the Rio Marañon	-4.44670	-77.64360	Twomey and Brown 2008	EU325898	EU325900	EU325902
captivus (sp. nov.) 3	See *captivus* (sp. nov.) 1	NA	NA	Santos *et al.* 2009	EU342665	EU342665	-
captivus 4	See *captivus* 2	-4.44011	-77.61493	Twomey and Brown 2008	EU325899	EU325901	-
castaneoticus	Brazil: Para: 101 km South, 15 km East of Santarem	-3.15067	-54.84247	Symula *et al.* 2003	AF482774	AF482789	AF482804
claudiae 1	Panama: Bocas del Toro, S end of Isla Popa, 1 km E Sumwood Channel	NA	NA	Frost *et al.* 2009	Q283042	Q283042	-
claudiae 2	See *claudiae* 1	NA	NA	Frost *et al.* 2009	DQ502024	DQ502024	JN635926
claudiae 3	Panama: Bocal del Toro	NA	NA	Roberts *et al.* 2006	DQ371304	DQ371315	DQ371334
claudiae 4	Panama: Bocas del Toro: Isla Colon, Bocas del Drago, 11 masl	NA	NA	Santos *et al.* 2009	EU342671	EU342671	JN635882
claudiae 5	Panama: Bocas del Toro, Isla Colon, La Gruta	NA	NA	Grant *et al.* 2006	DQ502027	DQ502027	DQ502457
Colostethus talamancae	Costa Rica	NA	NA	Clough and Summers 2000	AF128587	AF128586	AF128588
cyanovitatta	Peru: Loreto: Rio Blanco Basin near to the Zona Reservada Sierra del Divisor, 206 m elevation	-6.92000	-73.84583	Perez-Peña *et al.* 2010	HM038419	HM038422	HM038425
toraro (*ventrimaculata* sensu lato) 1	Brazil: location uncertain (either Acre: Porto Walter or Amazonas: near Manaus)	NA	NA	Roberts *et al.* 2006	DQ371308	DQ371319	DQ371338
toraro (*ventrimaculata* sensu lato) 10	Colombia: Amazonas, Leticia, Km 11 (Leticia-Tarapaca)	-4.11228	-69.93964	this study	JN635753	JN635807	JN635889
toraro (*ventrimaculata* sensu lato) 2	Brazil: location uncertain (either Acre: Porto Walter or Amazonas: near Manaus)	NA	NA	Roberts *et al.* 2006	DQ371307	DQ371318	DQ371337
toraro (*ventrimaculata* sensu lato) 3	See *toraro* 2	NA	NA	Symula *et al.* 2003	AF482782	AF482797	AF482812
toraro (*ventrimaculata* sensu lato) 4	Brazil: Amazonas: Castanho, ca. 40 km S Manaus at km 12 on road to Autazes, 40 masl	-3.51451	-59.82809	Santos *et al.* 2009	EU342676	EU342676	-
toraro (*ventrimaculata* sensu lato) 5	Sames as *toraro* 4	-3.51451	-59.82809	Grant *et al.* 2006	DQ502232	DQ502232	DQ502665
toraro (*ventrimaculata* sensu lato) 6	Brazil: Amazonas: Rio Ituxi at the Scheffer Madeireira; left bank, 110 masl			Grant *et al.* 2006	DQ502072	DQ502072	DQ502503
toraro (*ventrimaculata* sensu lato) 7	Brazil: Amazonas: Rio Ituxi, Scheffer Madeireira	-8.76333	-42.99333	Grant *et al.* 2006	DQ502071	DQ502071	DQ502502
toraro (*ventrimaculata* sensu lato) 8	Brazil: Amazonas: Rio Ituxi, Scheffer Madeireira	-8.76333	-42.99333	Brown et al. 2006	JN635804	JN635877	JN635934
toraro (*ventrimaculata* sensu lato) 9	Brazil: Amazonas: "Solimoes"	NA	NA	Noonan and Wray 2006	DQ163089	DQ163079	DQ163074

Name in Tree		Coordiantes			Genbank Info		
current name (former name) #	Locality (Country:Province/ Department/State: locality)	Lat	Long	Study	*12S*	*16S*	*CytB*
defleri 1	Colombia: Vaupés: north bank of Mosiro Itájura (an oxbow lake off Río Apaporis, also known as ‘Lago Taraira’), 98 m elevation, approximately 0.2 km SW of Estación Biológica Caparú	-1.07707	-69.51426	this study	-	JN635834	JN635907
defleri 2	See *defleri* 1	-1.07707	-69.51426	this study	JN635780	JN635835	JN635908
defleri 3	See *defleri* 1	-1.07707	-69.51426	this study	JN635779	JN635833	JN635906
defleri 4	Colombia: Vaupés: north bank of Río Caquetá near Puerto Córdoba (a village 16.6 km NW from La Pedrera), 68 m elevation	-1.28100	-69.71954	Twomey and Brown 2009	GU062190	GU062191	GU062192
dorisswansonae 1	Colombia	NA	NA	this study	-	JN635861	-
dorisswansonae 2	Colombia	NA	NA	this study	-	JN635863	-
fantastica 1	Peru: San Martin: Lower Huallaga Canyon	-6.52791	-75.92121	Brown *et al.* 2008	EU736200	EU736215	EU736185
fantastica 2	Peru: San Martin: Lower Huallaga Canyon	-6.44761	-75.89488	Brown *et al.* 2008	AF412469	AF412469	EU36194
fantastica 3	Peru: Amazonas: Pongo de Manseriche	AUR	AUR	this study	JN635793	-	JN635920
fantastica 4	Peru: Amazonas: Pongo de Manseriche	AUR	AUR	this study	JN635794	JN635848	JN635921
fantastica 5	Peru: San Martin: km 26 road from Tarapoto to Yurimaguas	-6.42717	-76.29080	Brown *et al.* 2008	-	EU736216	EU736186
fantastica 7	Peru: Loreto: Varadero	-5.68744	-76.41832	Brown *et al.* 2008	EU736195	EU736208	EU736180
fantastica 7	Peru: San Martin: km 42 road from Tarapoto to Yurimaguas	-6.43058	-76.66098	Symula *et al.* 2003	AF4112447	AF412475	EU736193
fantastica 8	Peru: San Martin: Bocatoma near Tarapoto	-6.45467	-76.34885	Brown *et al.* 2008	EU736196	EU736209	EU736181
flavovitatta 1	Peru: Loreto: Tahuayo	-4.35842	-73.18444	this study	-	JN635858	JN635928
flavovitatta 2	Peru: Loreto: Tahuayo	-4.35842	-73.18444	this study	-	JN635862	JN635930
flavovitatta 3	Peru: Loreto: Tahuayo	-4.35842	-73.18444	this study	-	JN635864	-
flavovitatta 4	Peru: Loreto: Tahuayo	-4.35842	-73.18444	Roberts et. al. 2006	DQ371306	DQ371317	DQ371336
flavovitatta 5	Peru: Loreto: Tamshiyacu-Tahuayo	-4.00908	-73.10076	this study	-	JN635860	JN635929
fulguritus 1	Unknown	NA	NA	Vences *et al.* 1999	-	AF124116	-
fulguritus 2	Colombia: Choco: Bahia Solano, Sierra Mecana, 260 m	6.25847	-77.35560	Grant *et al.* 2006	DQ502106	DQ502106	DQ502538
galactonotus 1	Brazil	NA	NA	Roberts *et al.* 2006	DQ371300	DQ371311	DQ371330
galactonotus 2	Brazil: Amazonas	NA	NA	Santos *et al.* 2009	EU342641	EU342641	-
granulifera	Costa Rica	NA	NA	Clough and Summers 2000	AF128608	AF098749	AF128609
histrionica 1	Ecuador	NA	NA	Clough and Summers 2000	AF128617	AF128616	U70154
histrionica 2	Ecuador	NA	NA	Vences *et al.* 2000	AF124098	AF124117	AF173766
Hyloxalus nexipus 1	Peru: San Martin: Cainarachi Valley	-6.43000	-76.29000	Santos *et al.* 2009	EU342714	EU342714	-
Hyloxalus nexipus 2	Peru: San Martin: Cataratas Ahuashiyacu, 14 km NE Tarapoto, 730 masl	-6.46554	-76.30888	Santos *et al.* 2009	EU342713	EU342713	-
imitator 1	Peru: San Martin: Central Huallaga Canyon near Chazuta	-6.54000	-76.11000	Symula *et al.* 2001	AF412448	AF412476	AF412504
imitator 2	Peru: San Martin: Pongo de Cainarachi	-6.28681	-76.23179	Symula *et al.* 2001	AF412459	AF412487	AF412515

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current name (former name) #		Lat	Long		*12S*	*16S*	*CytB*
leucomelas	Venezuela	NA	NA	Clough and Summers 2000	AF128593	AF124119	AF128594
lugubris 1	Nicaragua: Rio San Juan: Rio San Juan, Near Isla de Diamante (ca. 15 km SE El Castillo on Rio San Juan), 80 masl	10.93400	-84.30000	Grant *et al*. 2006	DQ502061	DQ502061	DQ502492
lugubris 2	Panama: Bocas del Toro, S end of Isla Popa, 1 km E Sumwood Channel	NA	NA	Grant *et al*. 2006	DQ283043	DQ283043	DQ502456
minutus 1	Panama: Cocle, El Cope, Parque Nacional General de Division 'Omar Torrijos Herrera	NA	NA	Grant *et al*. 2006	DQ502168	DQ502168	DQ502603
minutus 2	Panama	NA	NA	Clough and Summers 2000	AF128590	AF128589	MMU70163
mysteriosus 1	Peru: Amazonas: Tissues from captive individuals housed in Santa Rosa from Tupire Reserve	-5.43904	-78.55452	this study	JN635803	JN635866	JN635931
mysteriosus 2	See *mysteriosus* 1	-5.43904	-78.55452	this study	-	JN635868	-
mysteriosus 3	Unknown	NA	NA	Roberts *et al.* 2006	AF128590	AF128589	MMU70163
pumilio	Panama: Bocas del Toro	NA	NA	Clough and Summers 2000	AF128614	AF128613	U70147
quinquevittatus 1	Brazil: Amazonas: Rio Ituxi at the Madeireira Scheffer; left bank, 110 masl	NA	NA	Santos *et al.* 2009	EU342644	EU342644	-
quinquevittatus 2	Brazil: Rondonia: Rio Formoso, Parque Estadual Guajara-Mirim, 90 km N Nova Mamore, 180 masl	NA	NA	Santos *et al.* 2009	EU342646	EU342646	-
quinquevittatus 3	See *quinquevittatus* 2	NA	NA	Santos *et al.* 2009	EU342645	EU342645	-
quinquevittatus 4	Brazil: Rondonia, Parque Estadual Guajara-Mirim	-10.32144	-64.56331	Grant *et al*. 2006	DQ502063	DQ502063	DQ502496
quinquevittatus 5	Brazil: Amazonas, Rio Ituxi, Scheffer Madeireira	-8.47939	-65.71656	Grant *et al*. 2006	DQ502063	DQ502063	DQ502494
quinquevittatus 6	Brazil: Amazonas, Rio Ituxi, Scheffer Madeireira	-8.47939	-65.71656	Grant *et al*. 2006	DQ502064	DQ502064	DQ502495
quinquevittatus 7	Brazil: Rondonia, Parque Estadual Guajara-Mirim	-10.32144	-64.56331	Grant *et al*. 2006	DQ502066	DQ502066	DQ502497
quinquevittatus 8	Brazil: Amazonas, Rio Ituxi, Scheffer Madeireira	-8.47939	-65.71656	Grant *et al*. 2006	DQ502234	DQ502234	DQ502667
quinquevittatus 9	Brazil	NA	NA	Vences *et al.* 2003	AY263253	AY263253	-
reticulata 1	Peru	NA	NA	Darst *et al*. 2004	AY326029	AY326029	-
reticulata 2	Peru	NA	NA	Santos *et al.* 2003	AY364567	AY364567	-
reticulata 3	Peru: Loreto: "Puerto Almendras, 20 km WSW of Iquitos"	-3.82700	-73.37600	Santos *et al.* 2009	EU342686	EU342686	JN635900
reticulata 4	Peru: Loreto: km 55 (Puente Itaya) off of Iquitos- Nauta road	-4.22000	-73.48000	Symula *et al.* 2003	AF482772	AF482787	AF482802
reticulata 5	Unknown	NA	NA	Vences *et al.* 2003	-	AY263245	-
reticulata 6	Peru	NA	NA	Symula *et al.* 2001	AF412439	AF412467	AF412495
reticulata (*D*. sp. Itaya) 7	Peru: Loreto: km 66 (across Itaya River going to Nauta) off of Iquitos- Nauta road	-4.27420	-73.51269	Symula *et al.* 2003	AF482777	AF482792	AF482807
reticulata 8	Peru: Loreto: km 26 (Allpahuayo) off of Iquitos-Nauta road	-3.96700	-73.41700	Grant *et al*. 2006	DQ502119	DQ502119	-
reticulata 9	Peru: Loreto: km 13.5 off of Iquitos-Nauta road	-3.89125	-73.34797	Symula *et al.* 2003	AF482771	AF482786	AF482801

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reticulata 10	Peru: Loreto: UNAP forests off of Rio Napo	NA	NA	this study	JN635756	JN635810	-
sirensis (*lamasi*) 1	Peru: Loreto: nearby Contamana	-7.27412	-75.00242	this study	JN635790	JN635845	JN635918
sirensis (*lamasi*) 2	Peru: Loreto: nearby Contamana	-7.19854	-74.95244	this study	-	JN635872	-
sirensis (*lamasi*) 3	Peru: Loreto: nearby Contamana	NA	NA	this study	JN635774	JN635828	-
sirensis (*lamasi*) 4	Peru: San Martin: nearby Ishinga a small village outside of Tocache	-8.33047	-76.56894	this study	-	JN635849	JN635923
sirensis (*lamasi*) 5	Peru: Pasco: nearby Palcazu	-9.82086	-74.96331	this study	JN635796	JN635850	-
sirensis (*lamasi*) 6	Peru: Pasco: nearby Palcazu	-9.82086	-74.96331	this study	JN635797	JN635851	-
sirensis (*lamasi*) 7	Unknown; likely from Peru: Junin: nearby Iscozacin	NA	NA	this study	JN635792	JN635847	JN635919
sirensis (*lamasi*) 8	Peru: Huánuco: Puetro Inca	-9.36716	-74.93792	this study	JN635798	JN635852	-
sirensis (*lamasi*) 9	Peru: Huánuco: Puetro Inca	-9.45182	-74.80820	this study	JN635799	JN635853	-
sirensis (*sirensis*) 10	Peru: Huánuco: western versant of Cordillera El Sira, 4 km from type locality	-9.46360	74.81748	this study	JN635771	JN635825	-
sirensis (*sirensis*) 11	See *sirensis* (*sirensis*) 10	-9.46360	74.81748	this study	JN635772	JN635826	-
sirensis (*lamasi*) 12	Unknown	NA	NA	this study	JN635770	JN635824	-
sirensis (*lamasi*) 13	Unknown; likely from Peru: Junin: nearby Iscozacin	NA	NA	this study	JN635791	JN635846	-
sirensis (*lamasi*) 14	Unknown	NA	NA	this study	JN635752	JN635806	JN635883
sirensis (*biolat*) 15	Peru: Madre de Dios: Los Amigos Research Center at the confluence of Rios Los Amigos and Madre de Dios	-12.56700	-70.10000	Roberts *et al.* 2006	AF482779	AF482794	AF482809
sirensis (*lamasi*) 16	Peru: Huánuco: Tingo Maria, forest near the Universidad Nacional Agraria de la Selva, (exact paratype locality)	-9.30000	-76.00000	Symula *et al.* 2003	AF482778	AF482793	AF482808
sirensis (*lamasi*) 17	Peru: "Rio Pachitea"	NA	NA	this study	JN635769	JN635823	-
sirensis (*biolat*) 18	See *sirensis* (*biolat*) 15	-12.59653	-20.08967	this study	-	JN635870	JN635932
sirensis (*biolat*) 19	See *sirensis* (*biolat*) 15	-12.59653	-20.08967	this study	-	JN635874	JN635933
sirensis (*lamasi*) 20	Peru: Huánuco: nearby Codo del Pozuzo on the road to Pozuzo	-9.73488	-75.51036	this study	JN635802	JN635856	JN635925
sirensis (*lamasi*) 21	Peru: Loreto: unspecifed locality	NA	NA	this study	JN635776	JN635830	JN635903
sirensis (*lamasi*) 22	See *sirensis* (*biolat*) 16	-9.30000	-76.00000	this study	JN635800	JN635854	JN635924
sirensis (*lamasi*) 23	Peru: Huánuco: nearby Tingo Maria	-9.31492	-75.99280	this study	JN635801	JN635855	
sirensis (*lamasi*) 24	Peru: Loreto: nearby Contamana	-7.19854	-74.95244	this study	JN635775	JN635829	JN635902
sp. "Quibdo"	Colombia: Choco: Quibdo, La Troje, 50 masl	NA	NA	Santos *et al.* 2009	EU342670	EU342670	JN635881
sp. "supata" 1	Colombia: Cundinamarca, Supatá	-5.05000	-74.25000	this study	-	JN635865	-
sp. "supata" 2	Colombia: Cundinamarca, Supatá	-5.05000	-74.25000	this study	-	JN635867	-
speciosa	Panama	NA	NA	Clough and Summers 2000	AF128596	AF098747	AF128597
steyermarki 1	Venezuela	NA	NA	Roberts *et al.* 2006	DQ371310	DQ371321	DQ371340
steyermarki 2	Venezuela	NA	NA	Vences *et al.* 2003	-	AY263244	-
summersi 1	Peru: San Martin: Chipaota	-6.57687	-76.08260	Brown *et al.* 2008	EU736201	EU736217	EU736187

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summersi 2	Peru: San Martin: Sauce	-6.72453	-76.25318	Brown *et al.* 2008	EU736202	EU736218	EU736188
summersi 3	Peru: San Martin: Chazuta	-6.54319	-76.11097	this study	JN635789	JN635844	JN635917
sylvatica	Ecuador	NA	NA	Santos *et al.* 2003	AY364569	AY364569	AF324041
terribilis 1	Unknown	NA	NA	Grant *et al.* 2006	DQ502180	DQ502180	DQ502616
terribilis 2	Colombia: Cauca, Quebrada Guangui, 0.5 km above Rio Patia (upper Saija drainage), 100-200 m	NA	NA	Grant *et al.* 2006	DQ502157	DQ502157	DQ502593
tinctorius	Captive specimen: presumed from French Guiana	NA	NA	Clough and Summers 2000	AF128605	AF128604	AF128606
tolimensis 1	Colombia: Tolima: Municipio de Falan, Cordillera Central of Colombia	-5.01889	-75.04194	this study	-	JN635857	-
tolimensis 2	See *tolimensis* 1	-5.01889	-75.04194	this study	-	JN635859	-
uakarii (*ventrimaculata* sensu lato) 1	Brazil: location uncertain (either Acre: Porto Walter or Amazonas: near Manaus)	NA	NA	Roberts *et al.* 2006	DQ371301	DQ371312	DQ371331
uakarii (*ventrimaculata* sensu lato) 2	See *uakarii* (*ventrimaculata* sensu lato) 1	NA	NA	Symula *et al.* 2003	AF482783	AF482798	AF482813
uakarii (*ventrimaculata* sensu lato) 3	Brazil: Acre: near 5 km N Porto Walker, inland from the Rio Jurua, 200 masl	-8.25867	-72.77697	Grant *et al.* 2006	DQ502233	DQ502233	DQ502666
uakarii 4	Peru: Madre de Dios: Los Amigos Research Center at the confluence of Rios Los Amigos and Madre de Dios	-12.59653	-20.08967	this study	-	JN651270	JN635957
uakarii (*ventrimaculata* sensu lato) 5	See *uakarii* (*ventrimaculata* sensu lato) 3	-8.25867	-72.77697	Grant *et al.* 2006	DQ502070	DQ502070	DQ502501
uakarii (cf. *uakarii*) 6	Peru: Huánuco: nearby Tournavista	-8.94822	-74.76783	this study	JN635755	JN635809	-
uakarii (cf. *uakarii*) 7	Peru: Huánuco: nearby Tournavista	-8.95347	-74.77928	this study	JN635762	JN635816	JN635895
uakarii 8	Peru: Loreto: Tamshiyacu-Tahuayo, Quebrada Blanco	-4.35842	-73.18444	this study	JN635757	JN635811	JN635890
uakarii 9	Peru: Loreto: Tamshiyacu-Tahuayo, near Tamshiyacu village	-4.00908	-73.10075	this study	JN635761	JN635815	JN635894
uakarii 10	Peru: Loreto: Rio Manati	-3.65201	-72.20045	this study	JN635759	JN635813	JN635892
uakarii 11	Peru: Loreto: Rio Manati	-3.65201	-72.20045	this study	JN635760	JN635814	JN635893
uakarii 12	Peru: Loreto: Tamshiyacu-Tahuayo, Quebrada Blanco	-4.35842	-73.18444	this study	JN635758	JN635812	JN635891
uakarii 13	Peru: Loreto: Tamshiyacu-Tahuayo, Quebrada Blanco	-4.35842	-73.18444	Roberts *et al.* 2006	JN635805	DQ371316	DQ371335
vanzolinii 1	Brazil: Acre: Porto Walter	-8.25867	-72.77697	Grant *et al.* 2006	DQ502067	DQ502067	DQ502498
vanzolinii 2	Brazil: Acre: Porto Walter	-8.25867	-72.77697	Grant *et al.* 2006	DQ502236	DQ502236	DQ502669
vanzolinii 3	Brazil: Acre: Porto Walter	-8.25867	-72.77697	Grant *et al.* 2006	DQ502068	DQ502068	DQ502499
vanzolinii 4	Brazil: Acre: near 5 km N Porto Walter, inland from the Rio Jurua, 200 masl	-8.25867	-72.77697	Santos *et al.* 2009	EU342673	EU342673	-
vanzolinii 5	See *vanzolinii* 4	-8.25867	-72.77697	Santos *et al.* 2009	EU342674	EU342674	-
vanzolinii 6	Brazil: Acre: Porto Walter	-8.25867	-72.77697	Clough and Summers 2000	AF128599	AF128598	AF128600
variabilis (*ventrimaculata*) 1	Peru: San Martin: Bonilla km 44 on road from Tarapoto to Yurimaguas	-6.21007	-76.27226	Symula *et al.* 2001	AF412466	AF412522	AF412494
variabilis (*variabilis*) 2	Peru: San Martin: km 26 road from Tarapoto to Yurimaguas "Cainarachi Valley"	-6.42717	-76.29080	Symula *et al.* 2001	AF412521	AF412519	AF412491
variabilis (*ventrimaculata*) 3	See *variabilis* (*ventrimaculata*) 1	-6.21007	-76.27226	Symula *et al.* 2001	AF412465	AF412521	AF412493

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current name (former name) #		Lat	Long		*12S*	*16S*	*CytB*
variabilis (*variabilis*) 4	See *variabilis* (*variabilis*) 2	-6.42717	-76.29080	Symula *et al.* 2001	AF412520	AF412492	AF412520
variabilis (*variabilis*) 5	See *variabilis* (*variabilis*) 4	-6.42717	-76.29080	Santos *et al.* 2009	EU342679	EU342679	-
variabilis (*variabilis*) 6	Peru: San Martin: km 27 road from Tarapoto to Yurimaguas "Cainarachi Valley"	-6.43373	-76.28358	Santos *et al.* 2009	EU342680	EU342680	JN635884
variabilis (*ventrimaculata*) 7	Peru: San Martin: km 7 road from Pongo to Barranquita	-6.28681	-76.23179	this study	-	JN651247	JN635935
variabilis (*ventrimaculata*) 8	Peru: San Martin: nearby Pelejo	-6.24352	-75.90925	this study	-	JN651258	JN635947
variabilis (*ventrimaculata*) 9	See *variabilis* (*variabilis*) 3	-6.19754	-76.25838	this study	-	JN651257	JN635946
variabilis (*variabilis*) 10	Unknown	NA	NA	Vences *et al.* 2003	-	AY263249	
variabilis (*ventrimaculata*) 11	Peru: San Martin: km 7 road from Pongo to Barranquita	-6.28681	-76.23179	this study	-	JN651260	-
variabilis (*ventrimaculata*) 12	Peru: Loreto: nearby Shucushuyacu	-6.03209	-75.85700	this study	-	JN651248	JN635937
variabilis (*ventrimaculata*) 13	Peru: Loreto: nearby Shucushuyacu	-6.03209	-75.85700	this study	-	JN651263	JN635950
variabilis (*ventrimaculata*) 14	Colombia: Vaupés: north bank of Río Caquetá 2 km NW of La Pedrera	-1.31053	-69.59990	this study	JN635778	JN635832	JN635905
variabilis (*ventrimaculata*) 15	See *variabilis* (*ventrimaculata*) 14	-1.31053	-69.59990	this study	JN635782	JN635837	JN635910
variabilis (*ventrimaculata*) 16	See *variabilis* (*ventrimaculata*) 14	-1.31053	-69.59990	this study	JN635783	JN635838	JN635911
variabilis (*ventrimaculata*) 17	Colombia: Vaupés: north bank of Río Caquetá 5 km W of La Pedrera	-1.29720	-69.62690	this study	JN635781	JN635836	JN635909
variabilis (*ventrimaculata*) 18	Peru: Amazonas: nearby Centro de Espiritualidad TUNAANTS Santa María de Nieva	-4.58000	-77.90000	this study	JN635795	-	JN635922
variabilis (cf. *variabilis*) 19	Ecuador: Morona Santiago: nearby Macas	NA	NA	this study	-	-	JN635927
variabilis (*ventrimaculata*) 20	Peru: Loreto: nearby Nauta	-4.46300	-73.58200	this study	-	JN651250	JN635939
variabilis (*ventrimaculata*) 21	Peru: Loreto: nearby Puente Nauta	NA	NA	this study	-	JN651264	JN635951
variabilis (*ventrimaculata*) 22	Peru: Loreto: from across Itaya river going to Nauta	-4.26667	-73.76167	Symula *et al.* 2003	AF482784	-	AF482814
variabilis (*ventrimaculata*) 23	Peru: Loreto: nearby San Lorenzo, south side of Rio Marañon	-4.92631	-76.48445	this study	-	JN651268	JN635955
variabilis (*ventrimaculata*) 24	Peru: Amazonas: Cordillera Campanquiz	-4.42767	-77.52502	this study	-	JN651267	JN635954
variabilis (*ventrimaculata*) 25	Peru: Loreto: Tahuayo	NA	NA	Santos *et al.* 2009	EU342678	EU342678	-
variabilis (*ventrimaculata*) 26	Peru: Loreto: Tahuayo	-4.30750	-73.17778	this study	JN635766	JN635820	JN635898
variabilis (cf. *variabilis*) 27	Ecuador: Morona Santiago: nearby Macas	NA	NA	this study	JN635763	JN635817	JN635962
variabilis (*ventrimaculata*) 28	Peru: Loreto: Varadero	-5.68742	-76.41825	this study	-	JN651256	JN635945
variabilis (*ventrimaculata*) 29	Ecuador: Sucumbios: Pompeya	-0.43000	-76.62000	Symula *et al.* 2003	AF482780	AF482795	AF482810
variabilis (*ventrimaculata*) 30	Ecuador: Sucumbios: Pompeya	-0.43000	-76.62000	Summers *et al.* 1999	-	AF098746	AF120013
variabilis (*ventrimaculata*) 31	Ecuador: Sucumbios: Pompeya	-0.43000	-76.62000	Clough and Summers 2000	AF128621	AF128619	AF128620
variabilis (*ventrimaculata*) 32	Ecuador: Sucumbios, Estacion Cientifica de Universidad Catolica near Reserva Faunistica Cuyabeno, 220 m	0.00000	-76.16700	Grant *et al.* 2006.	DQ502069	DQ502069	DQ502500
variabilis (*ventrimaculata*) 33	Colombia: Vaupés: north bank of Río Caquetá 2 km NW of La Pedrera	-1.31053	-69.59990	this study	JN635777	JN635831	JN635904

Name in Tree		Coordiantes			Genbank Info		
current name (former name) #	Locality (Country:Province/ Department/State: locality)	Lat	Long	Study	*12S*	*16S*	*CytB*
variabilis (*ventrimaculata*) 34	Ecuador: Francisco de Orellana: Parque Nacional Yasuni-Estacion PUCE, 230 masl	-0.67131	-76.40050	Santos *et al.* 2003	AY364570	AY364570	-
variabilis (*ventrimaculata*) 35	Ecuador	NA	NA	this study	JN635754	JN635808	-
variabilis (*ventrimaculata*) 36	Peru: Loreto: Tamshiyacu-Tahuayo, Quebrada Blanco	-4.35842	-73.18444	this study	JN635767	JN635821	JN635899
variabilis (*ventrimaculata*) 37	Peru: Loreto: Tamshiyacu-Tahuayo, Quebrada Blanco	-4.35842	-73.18444	this study	-	JN651259	-
variabilis (*ventrimaculata*) 38	Peru: Loreto: nearby San Lorenzo, south side of Rio Marañon	-4.92631	-76.48445	this study	-	JN651262	JN635949
variabilis (*ventrimaculata*) 39	Peru: Loreto: Allpahuayo	NA	NA	Symula *et al.* 2003	AF482776	AF482791	AF482806
variabilis (*ventrimaculata*) 40	Peru: Loreto: nearby Shamboyacu on the trail to Puesto 15	-6.94224	-76.07806	this study	-	JN651266	JN635953
variabilis (*ventrimaculata*) 41	See *variabilis* (*ventrimaculata*) 41	-6.94224	-76.07806	this study	-	JN651269	JN635956
variabilis (*ventrimaculata*) 42	Peru: Loreto: nearby Contamana	-7.27412	-75.00242	this study	-	JN651265	JN635952
variabilis (cf. *variabilis*) 43	Peru: San Martin: nearby Saposoa on the trail to Cataratas Shima	-6.77107	-76.94127	this study	JN635764	JN635818	JN635896
variabilis (cf. *variabilis*) 44	Peru: San Martin: nearby Shima	-6.89859	-76.83324	this study	JN635765	JN635819	JN635897
variabilis (cf. *variabilis*) 45	Peru: San Martin: nearby Saposoa on the trail to Cataratas Shima	-6.77107	-76.94127	this study	-	JN651261	JN635948
variabilis (*ventrimaculata*) 46	Peru: Amazonas: Cordillera Campanquiz	-4.44670	-77.64360	this study	-	JN651253	JN635942
ventrimaculata (*duellmani*) 1	Ecuador: Francisco de Orellana: Parque Nacional Yasuni-Estacion PUCE, 230 masl	-0.67131	-76.40050	Santos *et al.* 2009	EU342688	EU342688	JN635887
ventrimaculata (*duellmani*) 2	See *ventrimaculata* (*duellmani*) 1	-0.67131	-76.40050	Santos *et al.* 2009	AY364566	AY364566	JN635888
ventrimaculata (*duellmani*) 3	Unknown	NA	NA	Vences *et al.* 2003	AY263246	AY263246	-
ventrimaculata (*duellmani*) 4	See *ventrimaculata* (*duellmani*) 1	-0.67131	-76.40050	this study	JN635768	JN635822	-
ventrimaculata (*D.* sp. G) 5	Ecuador	NA	NA	Santos *et al.* 2003	AY364568	AY364568	-
ventrimaculata 6	Peru: Loreto: 40 west of Iquitos north of Rio Nanay	-3.84000	-73.62000	this study	JN635773	JN635827	JN635901
ventrimaculata (*duellmani*) 7	Colombia: Amazonas, Leticia, Km 11 (Leticia-Tarapaca)	-4.11228	-69.93964	Grant *et al.* 2006	DQ502266	DQ502266	DQ502697
ventrimaculata (*D.* sp. Kapawi) 8	Ecuador: Pastaza: Kapawi Lodge, 239 masl	-2.54100	-76.85857	Santos *et al.* 2009	EU342687	EU342687	JN635886
virolinensis 1	Colombia: Santander: Virolin, Costilla de Fara, 1767 masl	NA	NA	Santos *et al.* 2009	EU342667	EU342667	-
virolinensis 2	See *virolinensis* 1	NA	NA	this study	-	JN635873	-
virolinensis 3	Colombia: Santander: Socorro	6.47000	73.26000	this study	-	JN635875	-
virolinensis 4	Colombia: Santander: Virolin, Costilla de Fara, 1767 masl	NA	NA	this study	-	JN635871	-
virolinensis 5	Colombia: Santander: Socorro	6.47000	73.26000	this study	-	JN635876	-
yavaricola 1	Peru: Loreto:17 km W of Estiron de Ecuador, 120 m elevation	-4.45972	-71.75097	Perez-Peña *et al.* 2010	HM038420	HM038423	HM038427
yavaricola 2	See *yavaricola* 1	-4.45972	-71.75097	Perez-Peña *et al.* 2010	HM038421	HM038424	HM038428
yavaricola 3	See *yavaricola* 1	-4.45972	-71.75097	Perez-Peña *et al.* 2010	-	-	HM038426

Appendix II. Material Examined and current taxonomic status (museum-catalog number _classification at time of examination, current taxonomic classification*_).

LACM-71972 _Dendrobates altobueyensis_ (Holotype), _Andinobates altobueyensis*;_ **LACM-71973** _Dendrobates altobueyensis_ (Paratype), _Andinobates altobueyensis*;_ **LACM-71974** _Dendrobates altobueyensis_ (Paratype), _Andinobates altobueyensis*;_ **LACM-71975** _Dendrobates altobueyensis_ (Paratype), _Andinobates altobueyensis*;_ **LACM-71976** _Dendrobates altobueyensis_ (Paratype), _Andinobates altobueyensis*;_ **LACM-71977** _Dendrobates altobueyensis_ (Paratype), _Andinobates altobueyensis*;_ **LACM-43802** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43803** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43819** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43820** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43821** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43822** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43830** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43835** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43836** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43837** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43838** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43843** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43844** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43845** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43846** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43847** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43848** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43854** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43855** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43856** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43857** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43858** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43859** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43860** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43861** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43862** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43863** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43864** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43874** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43875** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43877** _Dendrobates minutus, Andinobates minutus*;_ **LACM-43878** _Dendrobates minutus, Andinobates minutus*;_ **LACM-45568** _Dendrobates minutus, Andinobates minutus*;_ **LACM-45569** _Dendrobates minutus, Andinobates minutus*;_ **LACM-61024** _Dendrobates minutus, Andinobates minutus*;_ **LACM-61025** _Dendrobates minutus, Andinobates minutus*;_ **LACM-61066** _Dendrobates minutus, Andinobates minutus*;_ **LACM-61068** _Dendrobates minutus, Andinobates minutus*;_ **LACM-71931** _Dendrobates minutus, Andinobates minutus*;_ **LACM-71935** _Dendrobates minutus, Andinobates minutus*;_ **LACM-71941** _Dendrobates minutus, Andinobates minutus*;_ **LACM-71946** _Dendrobates minutus, Andinobates minutus*;_ **LACM-71949** _Dendrobates minutus, Andinobates minutus*;_ **LACM-71958** _Dendrobates minutus, Andinobates minutus*;_ **LACM-71959** _Dendrobates minutus, Andinobates minutus*;_ **LACM-71961** _Dendrobates minutus, Andinobates minutus*;_ **LACM-44397** _Dendrobates minutus ventrimaculatus_ (Paratype), _Ranitomeya ventrimaculata*;_ **LACM-44398** _Dendrobates minutus ventrimaculatus_ (Paratype), _Ranitomeya variabilis*;_ **LACM-43880** _Dendrobates opisthomelas, Andinobates opisthomelas*;_ **LACM-43882** _Dendrobates opisthomelas, Andinobates opisthomelas*;_ **LACM-43891** _Dendrobates opisthomelas, Andinobates opisthomelas*;_ **LACM-43894** _Dendrobates opisthomelas, Andinobates opisthomelas*;_ **LACM-43898** _Dendrobates opisthomelas, Andinobates opisthomelas*;_ **LACM-43899** _Dendrobates opisthomelas, Andinobates opisthomelas*;_ **LACM-71964** _Dendrobates opisthomelas, Andinobates opisthomelas*;_ **LACM-71965** _Dendrobates opisthomelas, Andinobates opisthomelas*;_ **LACM-71968** _Dendrobates opisthomelas, Andinobates opisthomelas*;_ **LACM-71969** _Dendrobates opisthomelas, Andinobates opisthomelas*;_ **LACM-71970** _Dendrobates opisthomelas, Andinobates opisthomelas*;_ **LACM-42305** _Dendrobates quinquevittatus, Ranitomeya amazonica*;_ **LACM-42306** _Dendrobates quinquevittatus, Ranitomeya amazonica*;_ **LACM-42307** _Dendrobates quinquevittatus, Ranitomeya amazonica*;_ **LACM-42308** _Dendrobates quinquevittatus, Ranitomeya amazonica*;_ **LACM-72645** _Dendrobates quinquevittatus, Ranitomeya variabilis *;_ **LACM-42309** _Dendrobates quinquevittatus, Ranitomeya amazonica*;_ **LACM-72062** _Dendrobates quinquevittatus, Ranitomeya variabilis*;_ **LACM-72063** _Dendrobates quinquevittatus, Ranitomeya variabilis*;_ **LACM-64596** _Dendrobates reticulatus, Ranitomeya reticulata*;_ **USNM-306529** _Dendrobates biolat_ (Paratype), _Ranitomeya sirensis*;_ **USNM-537561** _Dendrobates biolat, Ranitomeya sirensis*;_ **USNM-537562** _Dendrobates biolat, Ranitomeya sirensis*;_ **USNM-537563** _Dendrobates biolat, Ranitomeya sirensis*;_ **USNM-537564** _Dendrobates biolat, Ranitomeya sirensis*;_ **USNM-537565** _Dendrobates biolat, Ranitomeya sirensis*;_ **USNM-537557** _Dendrobates biolat, Ranitomeya sirensis*;_ **USNM-537558** _Dendrobates biolat, Ranitomeya sirensis*;_ **USNM-268842** _Dendrobates biolat_ (Paratype), _Ranitomeya sirensis*;_ **USNM-537559** _Dendrobates biolat, Ranitomeya sirensis*;_ **USNM-268843** _Dendrobates biolat_ (Paratype), _Ranitomeya sirensis*;_ **USNM-537560** _Dendrobates biolat, Ranitomeya sirensis*;_ **USNM-268844** _Dendrobates biolat_ (Paratype), _Ranitomeya sirensis*;_ **USNM-332406** _Dendrobates biolat, Ranitomeya sirensis*;_ **USNM-332407** _Dendrobates biolat, Ranitomeya sirensis*;_ **USNM-342778** _Dendrobates biolat, Ranitomeya sirensis*;_ **USNM-342881** _Dendrobates biolat, Ranitomeya sirensis*;_ **USNM-342882** _Dendrobates biolat, Ranitomeya sirensis*;_ **USNM-268841** _Dendrobates biolat_ (Paratype), _Ranitomeya sirensis*;_ **USNM-269059** _Dendrobates biolat_ (Paratype), _Ranitomeya sirensis*;_ **USNM-306528** _Dendrobates biolat_ (Paratype), _Ranitomeya sirensis*;_ **USNM-306530** _Dendrobates biolat_ (Paratype), _Ranitomeya sirensis*;_ **USNM-306531** _Dendrobates biolat_ (Paratype), _Ranitomeya sirensis*;_ **USNM-306532** _Dendrobates biolat_ (Paratype), _Ranitomeya sirensis*;_ **USNM-306533** _Dendrobates biolat_ (Paratype), _Ranitomeya sirensis*;_ **USNM-127197** _Dendrobates fantasticus, Ranitomeya benedicta*;_ **USNM-127198** _Dendrobates fantasticus, Ranitomeya benedicta*;_ **USNM-127933** _Dendrobates fantasticus, Ranitomeya benedicta*;_ **USNM-299726** _Dendrobates imitator, Ranitomeya imitator*;_ **USNM-299727** _Dendrobates imitator, Ranitomeya imitator*;_ **USNM-299728** _Dendrobates imitator, Ranitomeya imitator*;_ **USNM-299729** _Dendrobates imitator, Ranitomeya imitator*;_ **USNM-324338** _Dendrobates lamasi, Ranitomeya sirensis*;_ **USNM-166905** _Dendrobates lamasi, Ranitomeya sirensis*;_ **USNM-166906** _Dendrobates lamasi, Ranitomeya sirensis*;_ **USNM-314946** _Dendrobates reticulatus, Ranitomeya reticulata*;_ **USNM-331413** _Dendrobates reticulatus, Ranitomeya reticulata*;_ **USNM-222373** _Dendrobates reticulatus, Ranitomeya reticulata*;_ **USNM-222374** _Dendrobates reticulatus, Ranitomeya reticulata*;_ **USNM-166756** _Dendrobates vanzolinii_ (Paratype), _Ranitomeya vanzolinii*;_ **USNM-266119** _Dendrobates ventrimaculatus,_ Not specified*; **USNM-320762** _Dendrobates ventrimaculatus,_ Not specified*; **USNM-537566** _Dendrobates ventrimaculatus,_ Not specified*; **USNM-127199** _Dendrobates ventrimaculatus,_ Not specified*; **USNM-127200** _Dendrobates ventrimaculatus,_ Not specified*; **USNM-317194** _Dendrobates ventrimaculatus,_ Not specified*; **USNM-317195** _Dendrobates ventrimaculatus,_ Not specified*; **USNM-346308** _Dendrobates ventrimaculatus,_ Not specified*; **USNM-520916** _Dendrobates ventrimaculatus,_ Not specified*; **USNM-520918** _Dendrobates ventrimaculatus,_ Not specified*; **USNM-520919** _Dendrobates ventrimaculatus,_ Not specified*; **USNM-520920** _Dendrobates ventrimaculatus,_ Not specified*; **USNM-520917** _Dendrobates ventrimaculatus,_ Not specified*; **MCZ-A-19734** _Dendrobates minutus ventrimaculatus_ (Holotype),*; **MCZ-A-19684** _Dendrobates quinquevittatus_ (Paratype), _Ranitomeya ventrimaculata*;_ **MCZ-A-19685** _Dendrobates quinquevittatus_ (Paratype), _Ranitomeya variabilis*;_ **MCZ-A-19686** _Dendrobates quinquevittatus_ (Paratype), _Ranitomeya ventrimaculata*;_ **MCZ-A-19687** _Dendrobates quinquevittatus_ (Paratype), _Ranitomeya ventrimaculata*;_ **MCZ-A-19688** _Dendrobates quinquevittatus_ (Paratype), _Ranitomeya ventrimaculata*;_ **MCZ-A-19689** _Dendrobates quinquevittatus_ (Paratype), _Ranitomeya variabilis*;_ **MCZ-A-19690** (currently in LACM as 44397)

Dendrobates quinquevittatus (Paratype), *Ranitomeya ventrimaculata*;* **MCZ-A-19735** *Dendrobates quinquevittatus* (Paratype), *Ranitomeya ventrimaculata*;* **MCZ-A-19736** *Dendrobates quinquevittatus* (Paratype), *Ranitomeya ventrimaculata*;* **MCZ-A-19737** *Dendrobates quinquevittatus* (Paratype), *Ranitomeya variabilis*;* **MCZ-A-19738** *Dendrobates quinquevittatus* (Paratype), *Ranitomeya ventrimaculata*;* **MCZ-A-19739** *Dendrobates quinquevittatus* (Paratype), *Ranitomeya variabilis*;* **MCZ-A-19740** *Dendrobates quinquevittatus* (Paratype), *Ranitomeya ventrimaculata*;* **MCZ-A-19741** (currently in LACM as 44398) *Dendrobates quinquevittatus* (Paratype), *Ranitomeya variabilis*;* **MCZ-A-24444** *Dendrobates quinquevittatus, Ranitomeya sirensis*;* **MCZ-A-26050** *Dendrobates quinquevittatus, Ranitomeya uakarii*;* **MCZ-A-28061** *Dendrobates quinquevittatus, Ranitomeya defleri*;* **MCZ-A-37625** *Dendrobates quinquevittatus, Ranitomeya amazonica*;* **MCZ-A-89562** *Dendrobates quinquevittatus,* Cannot ID species- poor quality*; **MCZ-A-92502** *Dendrobates quinquevittatus, Ranitomeya variabilis*;* **MCZ-A-92503** *Dendrobates quinquevittatus, Ranitomeya variabilis*;* **MCZ-A-93643** *Dendrobates quinquevittatus, Ranitomeya uakarii*;* **MCZ-A-93644** *Dendrobates quinquevittatus, Ranitomeya uakarii*;* **MCZ-A-93645** *Dendrobates quinquevittatus, Ranitomeya uakarii*;* **MCZ-A-94730** *Dendrobates quinquevittatus, Ranitomeya uakarii*;* **MCZ-A-95697** *Dendrobates quinquevittatus, Ranitomeya amazonica*;* **MCZ-A-96207** *Dendrobates quinquevittatus, Ranitomeya amazonica*;* **MCZ-A-96369** *Dendrobates quinquevittatus, Ranitomeya uakarii*;* **MCZ-A-96760** *Dendrobates quinquevittatus, Ranitomeya variabilis*;* **MCZ-A-97976** *Dendrobates quinquevittatus, Ranitomeya variabilis*;* **MCZ-A-107797** *Dendrobates quinquevittatus, Ranitomeya duellmani*;* **MCZ-A-107798** *Dendrobates quinquevittatus, Ranitomeya reticulata*;* **MCZ-A-107799** *Dendrobates quinquevittatus, Ranitomeya ventrimaculata*;* **MCZ-A-107812** *Dendrobates quinquevittatus, Ranitomeya amazonica*;* **MCZ-A-19684-90**, not labeled #1, *Ranitomeya ventrimaculata*;* **MCZ-A-19684-90**, not labeled #2, *Ranitomeya ventrimaculata*;* **MPEG-13838** *Dendrobates ventrimaculatus* (Holotype), *Ranitomeya toraro*;* **MPEG-13839** *Dendrobates ventrimaculatus* (Paratype), *Ranitomeya toraro*;* **MPEG-13840** *Dendrobates ventrimaculatus* (Paratype), *Ranitomeya toraro*;* **MPEG-13841** *Dendrobates ventrimaculatus* (Paratype), *Ranitomeya toraro*;* **MPEG-13842** *Dendrobates ventrimaculatus* (Paratype), *Ranitomeya toraro*;* **OMNH-37438** *Dendrobates ventrimaculatus* (Paratype), *Ranitomeya toraro*;* **OMNH-37439** *Dendrobates ventrimaculatus* (Paratype), *Ranitomeya toraro*;* **OMNH-37440** *Dendrobates ventrimaculatus* (Paratype), *Ranitomeya toraro*;* **OMNH-37441** *Dendrobates ventrimaculatus* (Paratype), *Ranitomeya toraro*;* **OMNH-37442** *Dendrobates ventrimaculatus* (Paratype), *Ranitomeya toraro*;* **MPEG-13036** *Dendrobates ventrimaculatus* (Paratype), *Ranitomeya toraro*;* **MPEG-13037** *Dendrobates ventrimaculatus* (Paratype), *Ranitomeya toraro*;* **OMNH-36666** *Dendrobates ventrimaculatus* (Paratype), *Ranitomeya toraro*;* **OMNH-36667** *Dendrobates ventrimaculatus* (Paratype), *Ranitomeya toraro*;* **OMNH-36062** *Dendrobates ventrimaculatus, Ranitomeya uakarii*;* **MPEG-12394** *Dendrobates ventrimaculatus, Ranitomeya uakarii*;* **MPEG-12395** *Dendrobates ventrimaculatus, Ranitomeya uakarii*;* **MUSM-26957** *Ranitomeya benedicta* (Holotype), *Ranitomeya benedicta*;* **MUSM-26956** *Ranitomeya benedicta* (Paratype), *Ranitomeya benedicta*;* **MUSM-26958** *Ranitomeya benedicta* (Paratype), *Ranitomeya benedicta*;* **MUSM-26959** *Ranitomeya benedicta* (Paratype), *Ranitomeya benedicta*;* **MUSM-26960** *Ranitomeya benedicta* (Paratype), *Ranitomeya benedicta*;* **MUSM-26961** *Ranitomeya benedicta* (Paratype), *Ranitomeya benedicta*;* **MUSM-26962** *Ranitomeya benedicta* (Paratype), *Ranitomeya benedicta*;* **MUSM-26855** *Ranitomeya lamasi, Ranitomeya sirensis*;* **MUSM-26891** *Ranitomeya lamasi, Ranitomeya sirensis*;* **MUSM-26812** *Ranitomeya lamasi, Ranitomeya sirensis*;* **MUSM-26844** *Ranitomeya lamasi, Ranitomeya sirensis*;* **MUSM-26809** *Ranitomeya lamasi, Ranitomeya sirensis*;* **MUSM-24935** *Ranitomeya lamasi, Ranitomeya sirensis*;* **MUSM-24936** *Ranitomeya lamasi, Ranitomeya sirensis*;* **MUSM-24937** *Ranitomeya lamasi, Ranitomeya sirensis*;* **MUSM-24938** *Ranitomeya lamasi, Ranitomeya sirensis*;* **MUSM-24039** *Ranitomeya lamasi, Ranitomeya sirensis*;* **MUSM-29072** *Ranitomeya lamasi, Ranitomeya sirensis*;* **MUSM-29086** *Ranitomeya lamasi, Ranitomeya sirensis*;* **MUSM-21734** *Ranitomeya lamasi, Ranitomeya sirensis*;* **MUSM-3625** *Ranitomeya ventrimaculata, Ranitomeya variabilis*;* **MUSM-3626** *Ranitomeya ventrimaculata, Ranitomeya variabilis*;* **MUSM-3527** *Ranitomeya ventrimaculata, Ranitomeya variabilis*;* **MUSM-3628** *Ranitomeya ventrimaculata, Ranitomeya variabilis*;* **MUSM-28623** *Ranitomeya ventrimaculata, Ranitomeya variabilis*;* **MUSM-27457** *Ranitomeya ventrimaculata, Ranitomeya variabilis*;* **MUSM-27454** *Ranitomeya ventrimaculata, Ranitomeya variabilis*;* **MUSM-RVM-132** *Ranitomeya duellmani, Ranitomeya ventrimaculata*;* **MUSM-RVM-138** *Ranitomeya uakarii, Ranitomeya uakarii*;* **MUSM-23246** *Ranitomeya uakarii* (Holotype), *Ranitomeya uakarii*;* **MUSM-23247** *Ranitomeya uakarii* (Paratype), *Ranitomeya uakarii*;* **MUSM-23248** *Ranitomeya uakarii* (Paratype), *Ranitomeya uakarii*;* **MUSM-23249** *Ranitomeya uakarii* (Paratype), *Ranitomeya uakarii*;* **MUSM-23250** *Ranitomeya uakarii* (Paratype), *Ranitomeya uakarii*;* **MUSM-26994** *Ranitomeya summersi* (Paratype), *Ranitomeya summersi*;* **MUSM-26991** *Ranitomeya summersi* (Paratype), *Ranitomeya summersi*;* **MUSM-26992** *Ranitomeya summersi* (Paratype), *Ranitomeya summersi*;* **MUSM-26993** *Ranitomeya summersi* (Paratype), *Ranitomeya summersi*;* **MUSM-26949** *Ranitomeya summersi* (Paratype), *Ranitomeya summersi*;* **MUSM-26967** *Ranitomeya summersi* (Paratype), *Ranitomeya summersi*;* **NHML-1947.2.15.1** *Ranitomeya fantasica* (Holotype), *Ranitomeya fantasica*;* **NHML-1947.2.15.2** *Ranitomeya fantasica* (Paratype), *Ranitomeya fantasica*;* **NHML-1947.2.15.3** *Ranitomeya fantasica* (Paratype), *Ranitomeya fantasica*;* **NHML-1947.2.15.4** *Ranitomeya fantasica* (Paratype), *Ranitomeya fantasica*;* **PUJB-JLB08-001 (field number)** *Ranitomeya ventrimaculata* (Paratype), *Ranitomeya defleri*;* **PUJB-JLB08-002 (field number)** *Ranitomeya ventrimaculata* (Paratype), *Ranitomeya defleri*;* **PUJB-JLB08-003 (field number)** *Ranitomeya ventrimaculata* (Paratype), *Ranitomeya defleri*;* **PUJB-JLB08-004 (field number)** *Ranitomeya ventrimaculata* (Paratype), *Ranitomeya defleri*;* **PUJB-JLB08-005 (field number)** *Ranitomeya ventrimaculata, Ranitomeya variabilis*;* **PUJB-JLB08-006 (field number)** *Ranitomeya ventrimaculata, Ranitomeya variabilis*;* **PUJB-JLB08-007 (field number)** *Ranitomeya ventrimaculata, Ranitomeya variabilis*;* **MZUNAP-01-520** *Ranitomeya yavaricola* (Holotype), *Ranitomeya yavaricola*;* **MZUNAP-01-519** *Ranitomeya yavaricola* (Paratype), *Ranitomeya yavaricola*;* **MZUNAP-01-518** *Ranitomeya yavaricola* (Paratype), *Ranitomeya yavaricola*;* **CORBIDI-2266** *Ranitomeya cyanovittata* (Paratype), *Ranitomeya cyanovittata*;* **CORBIDI-2991** *Ranitomeya cyanovittata* (Paratype), *Ranitomeya cyanovittata*;* **MUSM-JLB08-011 (field number)** *Ranitomeya ventrimaculata, Ranitomeya variabilis*;* **MUSM-JLB08-012 (field number)** *Ranitomeya ventrimaculata, Ranitomeya variabilis*;* **MUSM-JLB08-013 (field number)** *Ranitomeya ventrimaculata, Ranitomeya variabilis*;* **MUSM-JLB08-014 (field number)** *Ranitomeya ventrimaculata, Ranitomeya variabilis*;* **MUSM-408** (specimens were on loan to R. Schulte) *Dendrobates rubrocephalus* (Type), *incertae sedis.*