

AN OVERVIEW OF THE DENDROBATID FROGS

OF VENEZUELA

Article & Photography by
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Top Left: *Allobates algorei* Top Right: *Mannophryne cordilleriana* carrying tadpoles. Bottom Left: *Allobates humilis* Bottom Right: *Allobates caribe*

Introduction

Dendrobatids are among the most attention-capturing frogs of the world, basically due to its astonishing coloration and powerful toxins. But not all dendrobatids have bright colors, or are toxic. In Venezuela, only five species of 67 are bright-colored and four are toxic.

Knowledge of dendrobatids in Venezuela augmented progressively from 10 mentioned by Rivero (1961), 30 in La Marca (1992), to 45 in Barrio-Amorós (1998), 47 in Barrio-Amorós & Fuentes (1999), 54 in Barrio-Amorós (2009) respectively to the current number of 67 (this work), increasing nine new species in seven years since the last amphibian checklist. Since Barrio-Amorós & Fuentes (1999) many changes have occurred, from the number of known species, to the current systematic allocation. It is worthy then to state a modern commented list accompanied with many illustrations of several species in question.

Grant et al. (2006) suggested, based on molecular data that the family Dendrobatidae should split in two families, Aromobatidae and Dendrobatidae. But Santos et al. (2009) rendered the two families in one again (Dendrobatidae) with two subfamilies (Aromobatinae and Dendrobatinae). They also disallowed several genera proposed by Grant et al. (2006), including *Minyobates*, and thus the taxonomic arrangement accepted herein applicable to Venezuelan species is presented in Table 1 (see end of article).

So far, there are six genera of Dendrobatidae assigned to two

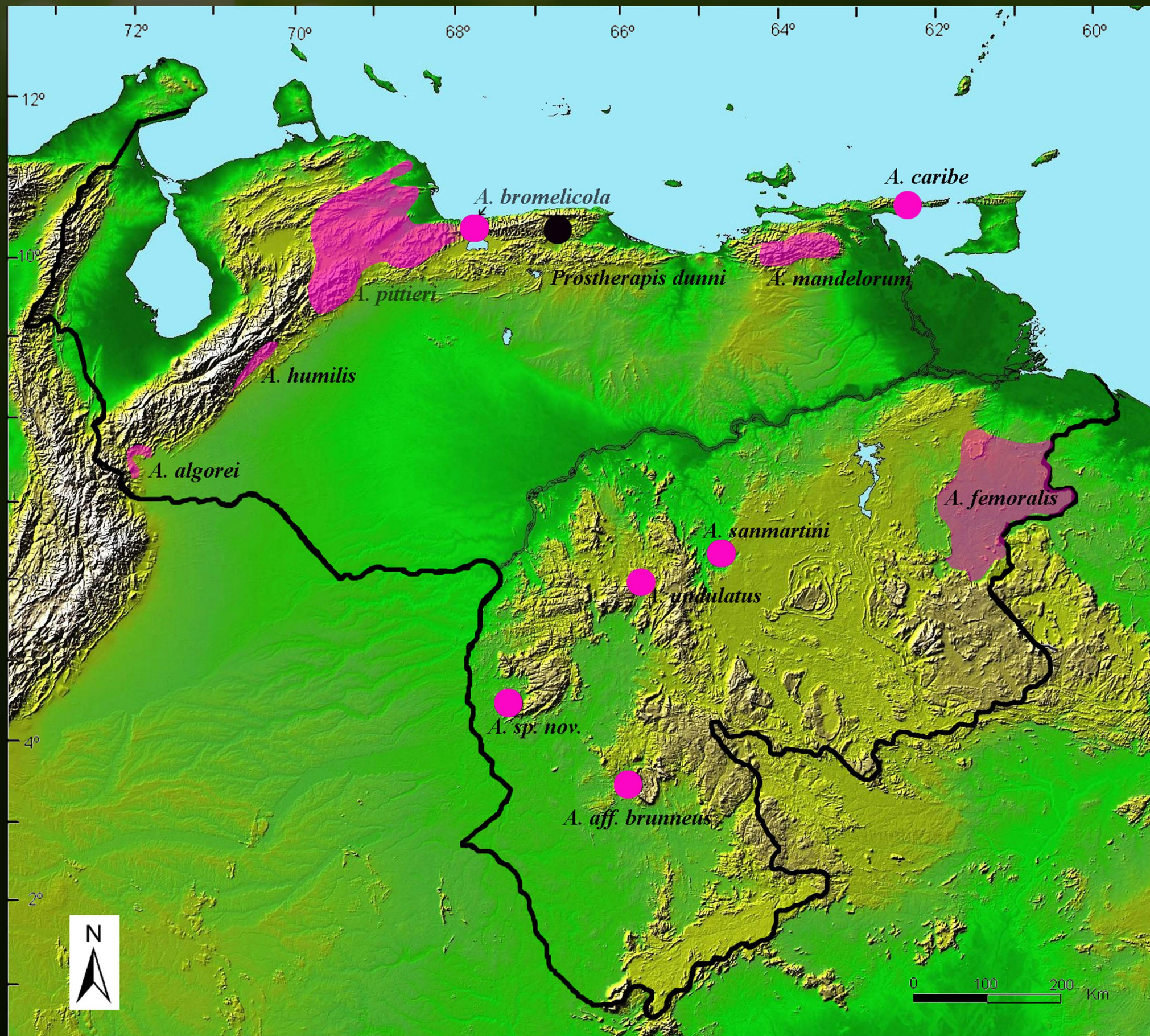
considered Incertae sedis (meaning that the generic status is not yet clear) still in a genus not used for any other taxa, *Prostherapis* (used only for *P. dunnii*)

Subfamily Aromobatinae (cryptic dendrobatids or rocket frogs)

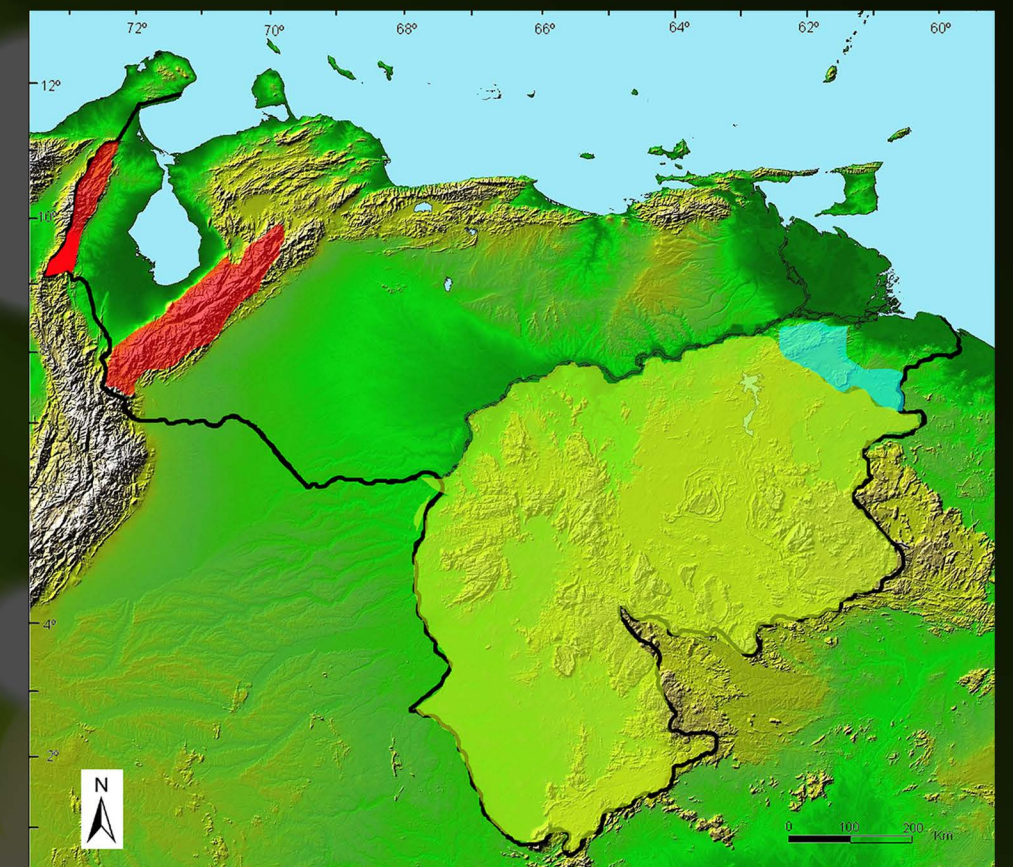
This is the dominant subfamily in Northern South America, with 62 of 66 species only in Venezuela. All species are characterized by a lack of bright colors (except *Allobates femoralis* that possesses yellow or orange flash marks on the thighs, and *Anomaloglossus rufulus*, which is orange and white ventrally). They inhabit the Andes, Cordillera de la Costa, the Orinoquian forests and tepuis (table mountains) of the Guiana Shield.

Allobates (Nurse frogs)

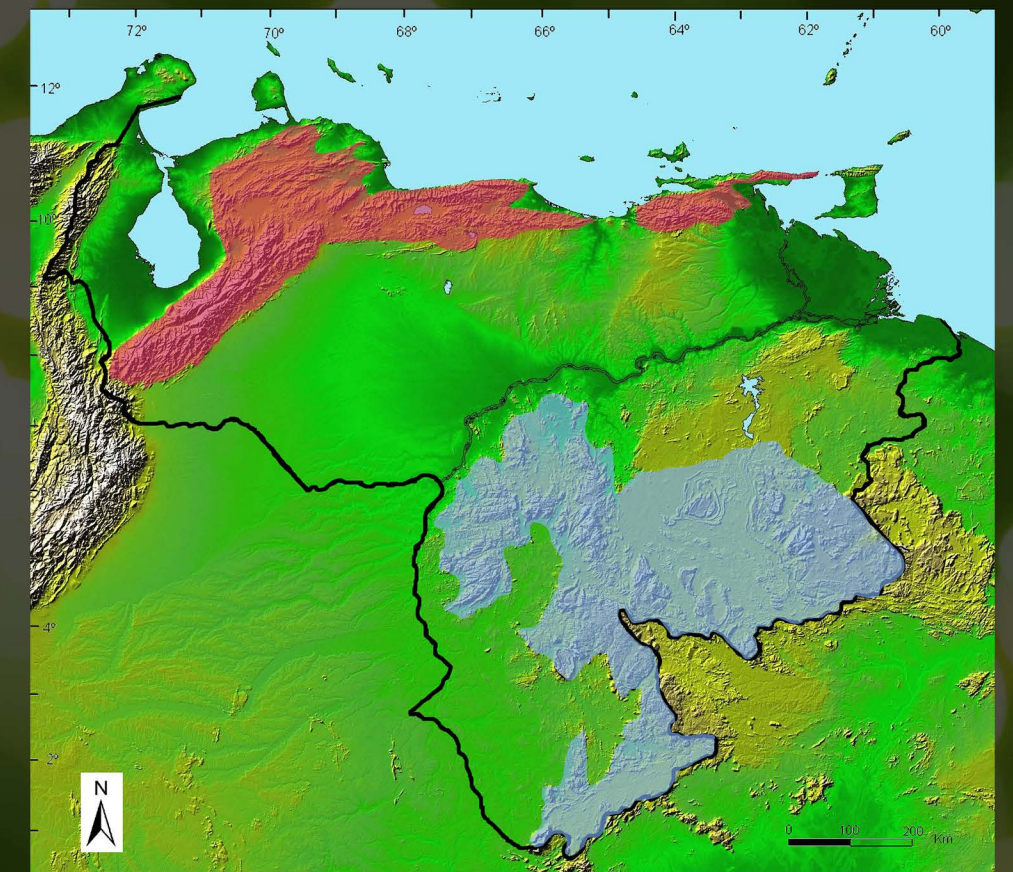
Allobates (sensu Grant et al. 2006) is a genus that though proved monophyletic, can be artificial as many species have never been genetically tested. In Venezuela 9 species are known, two more are recognized as similar to other species (probably only one species, named in different works *A. aff. marchesianus* and *A. aff. brunneus*), and one more is waiting for description (*A. sp. nov.* from the Venezuelan Amazonas state). The genus is widely distributed along all Venezuela except Los Llanos region, and the Maracaibo Lake basin. Three are known from the Andes (*A. algorei*, *A. humilis* and *A. pittieri*), four from the Coastal range (*A. bromelicola*, *A. caribe*, *A. mandelorum* and *A. pittieri*) and the rest are distributed south of the Orinoco at the Guiana Shield (*A. sanmartini*, *A. femoralis*, *A. undulatus*, *A. aff. marchesianus* and *A. aff. brunneus*).



Distribution of species of *Allobates* (disjunct populations) – in pink; and “*Prostherapis*” – black dot- in Venezuela.



Distribution of *Aromobates* (Pink), *Dendrobates* (yellow) and *Ameerega* (light blue) in Venezuela.



Distribution of *Mannophryne* (pink) and *Anomaloglossus* (light blue) in Venezuela.

Of them, the affinities are unknown for *A. bromelicola*, *caribe*, *mandelorum*, and *sanmartini*. Interestingly, *A. femoralis*, a common Amazonian dweller, is only known in Venezuela still through two recordings (Barrio-Amorós & Santos 2010). One of the Andean species, *A. algorei* was dedicated to Al Gore due to his endless efforts to educate people about the global warming (Barrio-Amorós & Santos 2009).

Anomaloglossus (Lingual frogs)

Anomaloglossus (literally= anomalous tongue) is the genus proposed by Grant et al. (2006) for some former *Colostethus* that present an appendix in the middle of the tongue. The use of this character is unknown, but it is convenient to distinguish them among other dull colored Aromobatines. *Anomaloglossus* is distributed in eastern Panama, Chocóan Ecuador and Colombia and the Magdalena River Valley also in Colombia (5 species); and throughout the Guiana Shield (24 species). It is unclear how these species are related, as no *Anomaloglossus* from the western part of South America or Central America have been genetically tested and compared with Guiana Shield representatives. Dealing only with Venezuela, 16 species are known widespread through the lowlands, uplands and highlands of the Guiana Shield, from 80 masl (*A. veerbeksnyderorum*) to 2700 m (*A. roraima*). There is an implicit problem in the recognition of some of these species. As some of them were described based on old and badly preserved specimens (and based on one individual), it is very difficult to compare among species and specimens. Only a comprehensive work involving morphometry, genetics and

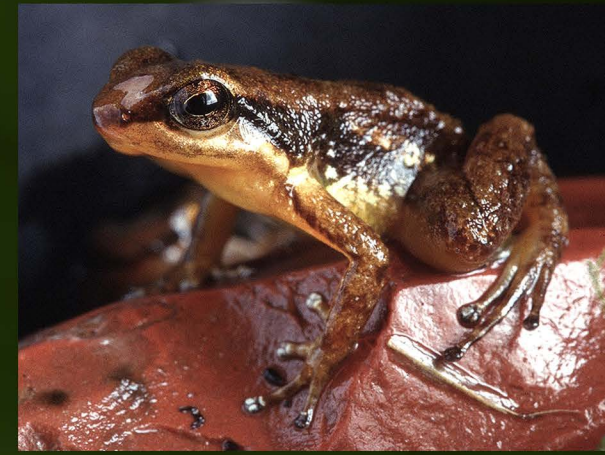
bioacoustics can proof their validity. This problem happens with species described by La Marca (1999), who named 7 species based on poorly preserved material (sometimes single, juvenile specimens), and afterwards is impossible to compare with other taxa satisfyingly. Describe species in such complicated genera using only one or few bad preserved specimen can introduce many taxonomic problems, like synonyms from previous species, and generates poor literature to compare with newly preserved specimens. Along with Phillippe Kok, I have been looking for *A. parkerae* at Sierra de Lema, with no luck. In order to make a comprehensive genetic comparison among species it is vital to find this species which is one of the first described in eastern Venezuela (Meinhardt & Parmalee 1996), and can be the senior synonym of many others described after (P. Kok and Barrio-Amorós, own data).

Unfortunately, *A. parkerae* seems a very rare species or have suffered a severe declination, as it is apparently absent from pristine streams along an altitudinal gradient in la Escalera region from 300 to 1400 m (see Duellman 1997 for an extensive description of the region).

Usually *Anomaloglossus* species can be locally abundant, though very seasonal (*A. veerbeksnyderorum*, *A. rufulus*). *Anomaloglossus tepuyensis* is the best known species due to the redescription and variation made by Myers & Donnelly (2008). Modern descriptions using fresh material, genetic markers and bioacoustics offer a wider spectrum of information, and *A. praderioi*, *A. roraima*, *A. rufulus*, and *A. veerbeksnyderorum* are the best characterized species in Venezuela until



Anomaloglossus moffetti



Anomaloglossus breweri - Photo by Charles Brewer-Carías



Anomaloglossus tepuyensis



Anomaloglossus rufulus



Anomaloglossus triunfo



Anomaloglossus wothuja



Aromobates meridensis



Aromobates ornatissimus



Aromobates zippeli



Aromobates ericksonae

now (Kok 2010; Kok et al. 2013; Barrio-Amorós & Santos 2010; Barrio-Amorós et al. 2010). A review of the genus is urgently needed.

Aromobates (Cloud frogs)

The genus *Aromobates* is endemic from the Venezuelan Andes (Cordillera de Mérida, Venezuelan side of the Cordillera Oriental de Colombia and Sierra de Perijá) and one or two undescribed species are mentioned in the Colombian part of the Cordillera Oriental de Colombia. The genus was created to allocate a rather unique species, the largest so far known Dendrobatid, *Aromobates nocturnus*, Myers, Polillo et Daly 1991, but also the only nocturnal and aquatic dendrobatid. It smells like a skunk and so is called, the skunk frog. Until 2006, it was regarded as monotypic in its own genus.

Other dull colored species of the Venezuelan Andes, known as pertaining to the *Colostethus alboguttatus* group, were gathered in a new genus by La Marca in 1994, *Nephelobates*. This genus was problematic since its inception, as it was based on little clear morphological characters, like long teeth (long compared to what?), and presence of anal sheath (usually due to preservation artifacts) presented as synapomorphies of the genus (but also present in other genera). Grant et al. (2006) used a few species of *Nephelobates* in their phylogenies and found that they were nested with *Aromobates*. Barrio-Amorós & Santos (2012) created a more comprehensive phylogeny with 10 of the 17 known species.

At least two more species are in process of being described.



Mannophryne riveroi (male)



Mannophryne collaris



Mannophryne cordilleriana



Mannophryne leonardo



Mannophryne obliterata



Left: *Mannophryne .aff caquetio* Above: *Mannophryne orellana*



Mannophryne vulcano



Mannophryne venezuelensis



Mannophryne urticans

All *Aromobates* except the type species, are small to moderate frogs (20-40 mm), inhabiting terrestrial to riparian microhabitats, from 700 (*A. ericksonae*) to 3400 m (*A. leopardalis*) in the Venezuelan Andes. *Aromobates nocturnus* can grow as large as 65 mm, being the largest dendrobatid, though with an odd morphology (apparently the only nocturnal and aquatic Dendrobatid as well). *Aromobates* are not colored frogs, and only *A. haydeae* (orange belly). *A. meridensis* (yellow belly with dark spots) and *A. ornatissimus* (green to orange dorsum with reticulated belly) stand out for its beauty.

Phylogenetically *Aromobates* stands with its sister genus *Mannophryne* at a basal position among Aromobatinae (Grant et al, 2006; Barrio-Amorós & Santos 2012) being sister genera to *Anomaloglossus*. *Aromobates ornatissimus* is apparently the most ancient species of the genus (Barrio-Amorós et al. 2011). This genus seems to have suffered extensively a severe declination and currently a few species are common. Only the recently described *Aromobates cannatellae*, *A. ericksonae*, *A. ornatissimus* plus *A. saltuensis* are common at their type localities (Barrio-Amorós & Santos 2012). *Aromobates zippeli* is a páramo dweller and is highly threatened by pesticides in its surroundings.

Aromobates alboguttatus, *A. durantei*, *A. haydeae*, *A. leopardalis*, *A. mayorgai*, *A. molinarii*, *A. orostoma* and *A. serranus* have been not found in recent attempts by the author and other herpetologists. I conducted a census of *A. meridensis* in 2006, and I found only a remnant population close to the type locality (extinct at the type locality) of

56-129 adults. This numbers are smaller than any possible species can stand (Barrio-Amorós et al. 2010). Nothing is known after that date. I am afraid that *A. nocturnus*, one of the most extraordinary frogs in the world, is already extinct, as recent expeditions by different herpetologists failed to find it at its type locality (Barrio-Amorós 2001; Barrio-Amorós et al. 2010).

***Mannophryne* (Collared frogs)**

Mannophryne are the collared frogs. They are dominant amphibian elements in many sites at the Venezuelan Andes and Cordillera de la Costa. Of 19 extant species, 17 are endemic to Venezuela (only *M. trinitatis* from Trinidad and *M. olmonae* from Tobago are known outside Venezuela). The genus is not known from Colombia, though one species (*M. orellana*) is present in the Venezuelan side of the Cordillera Oriental de Colombia (Barrio-Amorós et al. 2010) and should be found in the Colombian side.

Some of the morphological synapomorphies are the presence of a black collar and a yellow throat (especially obvious in females). Also, elaborated fights occur among females to defend their territories (Dole & Durant 1974). There are two clades within the genus, one is mainly of Andean origin with few Coastal representatives (*collaris*, *cordilleriana*, *larandina*, *yustizi*, *lamarcai*, *caquetio* and *herminae*, with *oblitterata* as basal), and the other is Coastal (*trinitatis*, *venezuelensis*, *leonardo*, *olmonae* and *riveroi*) (Manzanilla et al. 2009). Seems that due to the major apparent speciation at the Coastal Range (or Cordillera de la Costa), *Mannophryne*'s origin is probably the northern coastal mountain chain of

Venezuela. Other recently described species of the genus must prove its phylogenetic position (*M. orellana*, *M. speeri*, *M. trujillensis*, *M. urticans* and *M. vulcano*).

Mannophryne species are normally abundant through their distribution. In some cases the distribution is restricted to a small area (*M. urticans*, *trujillensis*, *speeri*, *larandina*, *lamarcai*, *caquetio*, *oblitterata*). Other species are more widely distributed (*M. collaris*, *cordilleriana*, *vulcano*, *herminae sensu lato*, *leonardo*, *riveroi* and *yustizi*). The only three *Mannophryne* mentioned as threatened are *M. caquetio*, *M. lamarcai* and *M. neblina*. I don't have first hand information about *M. lamarcai*, but I have seen abundant populations of *M. aff. caquetio* in appropriate creeks. I cannot speculate the cause of the decimation of *M. neblina*, as *M. herminae*, a sympatric species, is still abundant at neblina's type locality.

Subfamily Dendrobatinae (real poison frogs)

The subfamily Dendrobatinae includes all bright colored Dendrobatids. In Venezuela only 4 species are known.

Ameerega

There are only two species in the genus *Ameerega* in Venezuela, *A. picta* and *A. trivittata*. The center of speciation is far from northern South America, in the Upper Amazon. Both species share the same distribution in the country, far East Estado Bolivar. Both are also similar (young *A. trivittata* could be easily mistaken for an adult *A. picta*), but adult *trivittata* is double size (40 mm vs 23 mm). Heatwole et al. (1965) described *Dendrobates pictus*

guayanensis, which is currently not recognized. If there is sufficient genetic divergence between the topotypic *Ameerega picta* from Bolivia and the eastern Venezuelan specimens, the name *Ameerega guayanensis* should be used. Lotters et al. (2007) map of *A. hahneli* includes extreme Southern Venezuela, but this is not based in any voucher or scientifically reported specimen. I reject herein the presence of that species until it is proved with a voucher.

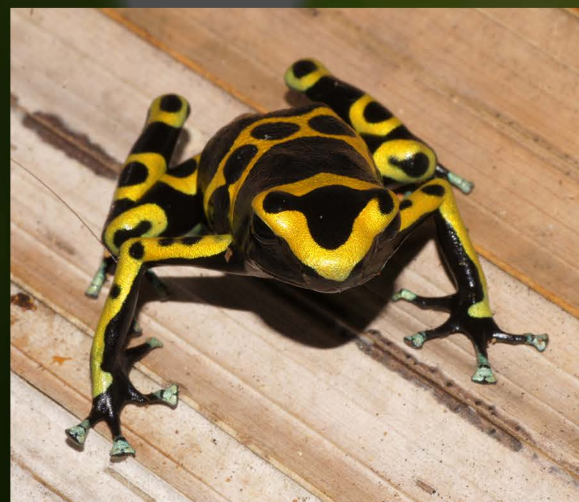
Dendrobates

Dendrobates is a large genus that was split by Grant et al (2006) and further authors (Twomey & Brown, 2008) in different genera accounting each subclade appeared in their genetic studies (*Adelphobates*, *Dendrobates*, *Excidobates*, *Minyobates*, *Oophaga*, *Ranitomeya*). However, Santos et al. (2009) find *Dendrobates* as a well-supported monophyletic group, and recovered a comprehensive *Dendrobates* synonymizing all these genera with *Dendrobates*. Brown et al. (2011) describe a further genus, *Andinobates* for some Andean and Central American former *Minyobates* (*Ranitomeya* afterwards). We must take in count that some of these generic arrangements are depending how one understands the philosophy of systematic and how one applies that. While Grant et al. (2006), Brown et al (2011) see useful to name subclades of a major clade as genera, Santos et al. (2009) don't. The only real living entities are species.

Returning to Venezuela, there are only two species of *Dendrobates*, the black and yellow poison frog *Dendrobates leucomelas*, and the Demonic Poison Frog, *D. steyermarki*.



Ameerega trivittata



Dendrobates leucomelas



Dendrobates steyermarki - Photo by Wolfgang Schmidt



Ameerega picta

While *D. leucomelas* is widely distributed south of the Orinoco River (Barrio-Amorós & Fuentes 1998; Lötters et al. 2007), inhabiting rainforest, gallery and dry forest and even savanna, the Demonic Poison Frog is highly restricted to the summit and slopes of a small tepui (table mountain) in extreme west Guiana Shield, named Yapacana in Estado Amazonas. *Dendrobates leucomelas* is a still abundant species at many places, but *D. steyermarki* is probably one of the most endangered frogs in the world. Only occurring at the summit and higher slopes of the tepui, with less than 30 Km² of extension, Yapacana is threatened by gold mining, even if it is a national park. The continued use of mercury at all levels, and destruction of wide sectors of the mountain precludes a near future extinction. Also, *D. steyermarki* was target of several illegal expeditions that extracted several hundreds of specimens in the nineties. All specimens in Europe are descendant of such extractions. Here we can also introduce the dilemma that in the worst scenario, some illegal specimens can save a species from extinction if the type locality is destroyed.

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TABLE 1

Family *Dendrobatidae* Cope 1865

Subfamily *Aromobatinae* Grant, Frost, Caldwell, Gagliardo, Haddad, Kok, Means, Noonan, Schargel, et Wheeler, 2006

Those with an asterisk (*) proof to be endemic from Venezuela

Genus *Allobates* Zimmermann et Zimmermann, 1988

Allobates algorei Barrio-Amorós et¹ Santos 2009)*

Allobates bromelicola (Test, 1956)*

Allobates aff. *brunneus* (Cope, 1887)

Allobates caribe (Barrio-Amorós, Rivas et Kaiser, 2006)*

Allobates femoralis (Boulenger, 1884)

Allobates humilis (Rivero, 1980)*

Allobates mandelorum (Schmidt, 1932)*

Allobates aff. *marchesianus* (Melin, 1941)²

Allobates pittieri (La Marca, Manzanilla, et Mijares-Urrutia, 2004)*

Allobates sanmartini (Rivero, Langone, et Prigioni, 1986)*

Allobates undulatus (Myers et Donnelly, 2001)*

Genus *Anomaloglossus* Grant, Frost, Caldwell, Gagliardo, Haddad, Kok, Means, Noonan, Schargel et Wheeler, 2006

Anomaloglossus ayarzaguenai (La Marca 1997)*

Anomaloglossus breweri (Barrio-Amorós, 2006)*

Anomaloglossus guanayensis (La Marca, 1997)*

Anomaloglossus moffetti Barrio-Amorós et Brewer-Carías, 2008*

Anomaloglossus murisipanensis (La Marca, 1997)*

Anomaloglossus parimae (La Marca, 1997)*

Anomaloglossus parkerae (Meinhardt et Parmalee, 1996)*

Anomaloglossus praderioi (La Marca, 1997)*

Anomaloglossus roraima (La Marca, 1997)*

Anomaloglossus rufulus (Gorzula, 1990)*



Anomaloglossus shrevei (Rivero, 1961)*
Anomaloglossus tamacuarensis (Myers et Donnelly, 1997)
Anomaloglossus tepuyensis (La Marca, 1997)*
Anomaloglossus triunfo (Barrio-Amorós, Fuentes et Rivas, 2004)*
Anomaloglossus verveeksnyderorum Barrio-Amorós, Santos et Jovanovic 2009*
Anomaloglossus wothuja (Barrio-Amorós, Fuentes et Rivas, 2004)*

Genus *Aromobates* Myers, Paolillo et Daly, 1991

Aromobates alboguttatus (Boulenger, 1903)*
Aromobates cannatellai Barrio-Amorós et Santos, 2011*
Aromobates capurinensis (Péfaur, 1993)*
Aromobates durante (Péfaur, 1985)*
Aromobates ericksonae Barrio-Amorós et Santos, 2011*
Aromobates haydeeeae (Rivero, 1978)*
Aromobates leopardalis (Rivero, 1978)*
Aromobates mayorgai (Rivero, 1980)*
Aromobates meridensis (Dole et Durant, 1973)*
Aromobates molinarii (La Marca, 1985)*
Aromobates nocturnus Myers, Paolillo, et Daly, 1991*
Aromobates ornatissimus Barrio-Amorós, Rivero et Santos, 2011*
Aromobates orostoma (Rivero, 1978)*
Aromobates saltuensis (Rivero, 1980)*
Aromobates serranus (Péfaur, 1985)*
Aromobates tokuko Rojas-Runjaic, Infante et Barrio-Amorós, 2011*
Aromobates walterarpi La Marca et Otero, 2012*
Aromobates zippeli Barrio-Amorós et Santos, 2011*

Genus *Mannophryne* La Marca, 1992

- Mannophryne caquetio* Mijares-Urrutia et Arends, 1999*
Mannophryne collaris (Boulenger, 1912)*
Mannophryne cordilleriana La Marca, 1995*
Mannophryne herminae (Boettger, 1893)*
Mannophryne lamarcai Mijares-Urrutia et Arends, 1999*
Mannophryne larandina (Yústiz, 1991)*
Mannophryne leonardo Manzanilla, La Marca, Jowers, Sánchez,
et García-París, 2007*
Mannophryne neblina (Test, 1956)*
Mannophryne oblitterata (Rivero, 1984)*
Mannophryne orellana Barrio-Amorós, Santos et Molina 2010*
Mannophryne riveroi (Donoso-Barros, 1965)*
Mannophryne speeri La Marca, 2009*
Mannophryne trujillensis Vargas et La Marca, 2007*
Mannophryne urticans Barrio-Amorós, Santos et Molina 2010*
Mannophryne venezuelensis Manzanilla, Jowers, La Marca et
García-París, 2007*
Mannophryne vulcano Barrio-Amorós, Santos et Molina 2010*
Mannophryne yustizi (La Marca, 1989)*

Subfamily **Dendrobatinae** Cope 1865

Genus *Ameerega* Bauer 1986

- Ameerega picta* (Bibron In Tschudi, 1838)
Ameerega trivittata (Spix, 1824)

Genus *Dendrobates* Wagler 1830

- Dendrobates leucomelas* Fitzinger in Steindachner, 1864
Dendrobates steyermarki (Rivero, 1971)*

(Incertae sedis)

Genus *Prostherapis* Cope, 1868

“*Prostherapis*” *dunni* Rivero, 1961*

¹I use the Latin conjunction et instead and or & when more than one author: e. g. Mijares-Urrutia et Arends, 1999, as it should be the proper conjunction used in systematics.

²The *Allobates aff. marchesianus* identified by Morales (1994) must be the same *A. aff. brunneus* cited by La Marca (1997), as both come from the same main locality. We retain both until further studies clarify the situation.