DIVERSITY AND PHYLOGEOGRAPHY OF EASTERN

GUIANA SHIELD FROGS

A thesis submitted in partial fulfilment of the requirements for the Degree

of Doctor of Philosophy in Biology

in the University of Canterbury

by Antoine Fouquet

University of Canterbury

2008

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Abstract

The Guiana Shield is a sub-region of Amazonia, one of the richest areas on earth in terms of species number. It is also one of the most pristine areas and is still largely unexplored. Species number, distribution, boundaries and their evolutionary histories remain at least unclear but most of the time largely unknown. This is the case for most Anurans, a group which is recognized as threatened globally and is disappearing even from pristine tropical forests. Given the pace of forest destruction and the growing concerns about climate change it is urgently necessary to obtain a better estimate of regional biodiversity in Amazonian frogs as well as a better understanding of the origin and distribution of Anuran diversity. Furthermore, given their sensitivity to climatic conditions, amphibians are a good model to investigate the influence of paleoclimatic events on Neotropical diversification which was supposedly the driving force on biotic evolution during Pleistocene in the Guiana Shield.

I first test species boundaries in two species *Scinax ruber* and *Rhinella margaritifera*. These species are widely distributed, abundant and largely recognized as species complexes. I used an original species delineation method based on the combined use of mitochondrial and nuclear DNA in phylogenetic and phylogeographic analyses. Phylogenetic analyses demonstrated the polyphyly of *Scinax ruber* and *Rhinella margaritifera*. These species consist of multiple lineages that may all merit species status. Conflicting signals of mitochondrial and nuclear markers indicated the possibility of ongoing hybridization processes. Phylogeographic analyses added further information in support of the specific status of these lineages. Our results highlight the utility of combining phylogenetic and phylogeographic methods, as well as the use of both mitochondrial and nuclear markers within one study. This approach helped to better understand the evolutionary history of taxonomically complex groups of species. The assessment of the geographic distribution of genetic diversity in tropical amphibian communities can lead to conclusions that differ strongly from prior analyses based on the occurrence of currently recognized species alone. Such studies, therefore, hold the potential to contribute to a more objective assessment of amphibian conservation priorities in tropical areas.

Subsequently, I tested if these first results on cryptic species are generalisable, questioning what would potentially be a minimum estimate of the number of cryptic frog species in Amazonia and the Guiana Shield, using mtDNA with multiple complementary approaches. I also combined isolation by distance, phylogenetic analyses, and comparison of

molecular distances to evaluate threshold values for the identification of candidate species among these frogs. In most cases, geographically distant populations belong to genetically highly distinct lineages that could be considered as candidate new species. This was not universal among the taxa studied and thus widespread species of Neotropical frogs really do exist, *contra* to previous assumptions. Moreover, the many instances of paraphyly and the wide overlap between distributions of inter- and intra-specific distances reinforce the hypothesis that many cryptic species remain to be described. In our data set, pairwise genetic distances below 0.02 are strongly correlated with geographical distances. This correlation remains statistically significant until genetic distance is 0.05, with no such relation thereafter. This suggests that for higher genetic distances allopatric and sympatric cryptic species prevail. Based on our analyses, we propose a more inclusive pairwise genetic distance of 0.03 between taxa to target lineages that could correspond to candidate species. Using this approach, we identify 129 candidate species, two-fold greater than the 60 species included in the current study. This leads to estimates of around 170 to 460 frog taxa unrecognized in Amazonia-Guianas. As a consequence the global amphibian decline detected especially in the Neotropics may be worse than realised.

The *Rhinella margaritifera* complex is characterisized by the presence of many cryptic species throughout its wide distribution, ranging from Panama to Bolivia and almost entire Amazonia. French Guiana has long been thought to harbor two species of this group, though molecular data analysed in previous chapters indicated as many as five lineages. I tested whether morphological measurements are correlated or not with genetic data using discriminant analysis and if diagnostic characteristics among the previously determined lineages can be used to describe these new species. This is a novel integrative method which can lead to a facilitation of the description of cryptic species that have been detected by phylogenetic and/or phylogeographic studies. These analyses, combined with published data of other *Rhinella* species, indicated that two of these lineages represent previously unnamed species. Two of the remaining are allocable to *R. margaritifera* while the status of the fifth is still unclear because so far it is morphologically indistinguishable from *R. castaneotica*.

Determining if codistributed species responded to climate change in an independent or concerted manner is a basic objective of comparative phylogeography. Species boundaries, histories, ecologies and their geographical ranges are still to be explored in the Guiana Shield. According to the refugia hypothesis this region was supposed to host a forest refugium during climatic oscillations of the Pleistocene but the causes and timing for this have been criticized. We investigated patterns of genetic structure within 18 frog species in the eastern Guiana

Shield to explore species boundaries and their evolutionary history. We used mtDNA and nuclear DNA and complementary methods to compare the genetic diversity spatially and temporally. With one exception all the species studied diversified repeatedly within the eastern Guiana Shield during the last 4 million years. Instead of one Pleistocene forest refugium the Guiana Shield has probably hosted multiple refugia during late Pliocene and Pleistocene. Most of these Pleistocene refugia were probably situated on the coast of French Guiana, Amapà, Suriname and Guyana. This diversification likely resulted from forest fragmentation. Many species deserve taxonomic revisions and their ranges to be reconsidered. The local endemism of the Anuran fauna of the Guiana Shield is likely to be much higher and some areas consequently deserve more conservation efforts. Specifically I questioned whether major intraspecific diversification started before the Pleistocene and occurred within the Guiana Shield or ex situ. According to ecological characteristics of the species involved I will test different diversification hypotheses. The consequences on the diversity and the endemism of the Guiana Shield will be explored.

My results demonstrate that we have been grossly underestimating local biological diversity in the Guiana Shield but also in Amazonia in general. The order of magnitude for potential species richness means that the eastern Guiana Shield hosts one of the richest frog fauna on earth. In most of the species studied high levels of mtDNA differentiation between populations call for a reassessment of the taxonomic status of what is being recognised as single species. Most species display deep divergence between eastern Guiana Shield populations and Amazonian ones. This emphasizes that the local endemism in the Guiana Shield of these zones is higher than previously recognized and must be prioritised elements taken into account in conservation planning. Nevertheless, a few other species appear widely distributed showing that widespread species do exist. This underlines the fact that some species have efficient dispersal abilities and that the frog fauna of the eastern Guiana Shield is a mixture of old Guianan endemic lineages that diversified in situ mostly during late Pliocene and Pleistocene and more recently exchanged lineages with the rest of Amazonia. Recognizing this strong historical component is necessary and timely for local conservation as these zones are likely to be irremediably modified in the near future.

Acknowledgments

This dissertation symbolises the end of a long process. During these three years that I worked in the lab, in front of computers or in the field, I was rarely alone. I have been helped by so many people that these acknowledgments will be long and probably not even long enough to thank everyone.

Chapter 1:

General Introduction

1. Measuring biodiversity

Biodiversity is unevenly distributed on earth (Gaston, 2000). Tropical forests shelter 50 to 70% of the species richness in the world and neotropical forests harbour the majority of these species (Gaston and Williams, 1996; Myers et al., 2000; Wilson, 1992). This is particularly true for amphibians with a higher density of species (36% of all species (Young, et al., 2004)) species in the tropical forests of South America than anywhere on Earth even in African and Asian tropical forests (Duellman, 1999) (Fig. 1.1).

However, species richness is not the only component of the biodiversity. This concept actually encompasses the whole variety of life that could be considered on three levels: ecosystems, the species that occupy those ecosystems and the genes of those species (Wilson, 1992). The definition of biodiversity is indeed more complicated than it seems (Purvis and Hector, 2000) and quantifying it requires multiple facets to be accounted. Understanding patterns of biodiversity distribution is essential to conservation strategies (Gaston, 2000), but severe data constraints make surrogate measures necessary (Rodrigues and Brooks, 2007; Margules and Pressey, 2000) especially in the tropics. The species richness and the endemism of a site are of course the basic data most frequently used as surrogates to estimate the degree of biodiversity and its loss (Ennos et al., 2005; Lamoreux et al., 2006). The major biodiversity hotspots (Myers et al., 2000), the wilderness areas (Mittermeier et al., 2003) and most protected areas have been designed upon these measures. Global patterns of species richness are highly correlated among vertebrate groups as are endemism patterns (Lamoreux et al., 2006) but there is controversy that they are sufficient representation of biodiversity in general (Rodrigues and Brooks, 2007; Warman et al., 2004). Consequently, we must keep its potential caveats in mind.

One key point is that these all rely on good estimation of species number and their range. However, most species still remain undescribed. To date, around 1.75 million species have been described, but these may only represent 10% of the currently existing species (Hawksworth and Kalin-Arroyo, 1995). Entire groups, such as bacteria, are still mostly uncharacterized (Horner-Devine et al., 2004; Stackebrandt, 2004; Whitman et al., 1998). Adding to the problem, the species concept remains ambiguous (Agapow et al., 2004), with authors such as Lherminer and Solignac (2000) numerating no less than 92 definitions of this concept. Despite this uncertainty in definition, the controversy has actually focused more on

the criteria that should be used to recognize species rather than on what a species is (Wiens, 2007). De Queiroz (1998; 2007) argued that nearly all contemporary biologists accept that species are segments of population-level evolutionary lineages. However, even in the relatively well known groups like vertebrates, species boundaries are often blurred (Sites and Marshall, 2003) and we are increasingly realising the prevalence of cryptic species (Bickford et al., 2007). Finally, the information regarding the range of described as well as undescribed species, which is necessary to estimate endemism, is largely lacking (Lomolino, 2004; Raven and Wilson, 1992).

Reciprocally, below the species level, populations are defined as entities between which limited gene flow occurs. The genetic diversity among populations also contributes to biodiversity, plays an important role in species evolution (Hoskin et al., 2005), and is a primordial parameter for conservation biology (Narain, 2000; Neel and Cummings, 2003). If populations are considered as the operational entities which should be used to estimate biodiversity, the task appears even vaster. It has been estimated that between 1.1 to 6.6 billion populations exist (Hughes et al., 1997), of which only a negligible portion have been studied.

Additionally, above the species level, an additional component of the biodiversity of a clade or an area can be estimated in terms of its evolutionary history (Faith, 1992; Faith et al., 2004). Phylogenetic diversity (PD) measures the length of evolutionary pathways that connect a given set of taxa. This index takes into account that old clades and deeply rooted relictual species or lineages hold the testimony of unique evolutionary histories that may deserve conservation priorities (Hartmann and Steel, 2006; Weitzman, 1998). This important component of biodiversity is not necessarily taken into account when only the number of species and endemism is considered. However, while the use of PD allows one to side-step current debates about what is or is not a "species", the Tree of Life is far from being resolved yet and the lack of knowledge about most species has so far hampered its use (Mace et al., 2003).

Even if 300 new species are described each year, sometimes resulting in new families or even new *phyla,* 27,000 species are predicted to disappear each year (Hawksworth and Kalin-Arroyo, 1995). The crux of the biodiversity crisis is consequently emphasized by the extinction of numerous species that are still unknown (Purvis and Hector, 2000). Recent technological advances in producing DNA sequences led Hebert et al. (2003) to propose a method to boost the documentation of biodiversity. This so called "DNA barcoding" initiative provides recent opportunities and challenges. Pairwise divergences among sequences are calculated, and if these are above a previously defined threshold, the two sequences

potentially belong to different species. If one of the sequences differs from all known species by a divergence above the threshold, it can be flagged as a "candidate species" (Vences et al., 2005). However, because species-formation is a continuous process and the distinctive key characters (e.g., factors for prezygotic or postzygotic isolation) can evolve either early or late in this process (de Queiroz, 1999), there necessarily are a number of very young (and hence genetically poorly differentiated) species that will be missed by the threshold-based estimates (false negatives). Again, because of introgression or incomplete lineage sorting, quite divergent lineages may not represent different species (false positives) (Funk and Omland, 2003; Meyer and Paulay, 2005). Despite these pitfalls, a few studies on the distribution of the genetic diversity using mitochondrial DNA in different groups have shown that a gap exists between intraspecific and interspecific genetic diversity in some taxonomic groups (e.g. Ekrem et al., 2007; Vences et al., 2005; Hebert et al., 2004). Threshold values therefore should be set high enough to ignore, as much as possible, intraspecific divergence, but low enough to ensure detection of as many incipient or newly emergent species as possible.

2. Biodiversity crisis and the Amphibian decline

Rates of biodiversity loss are accelerating (Pimm et al., 1995) as human dominance of Earth's natural systems increases (Vitousek et al., 1997). Amphibians are particularly threatened by this crisis because they are sensitive to a wide variety of environmental perturbations and are widely considered as "bio-indicators" of ecosystem health (Roy, 2002). This is why they are often cited as the ecological "canaries in the coal mine". In fact, it is already known that amphibians are declining worldwide (Blaustein and Dobson; 2006; Houlahan, et al., 2000; Mendelson et al., 2006; Pechmann and Wilbur, 1994; Stuart, et al., 2004) and the study of this decline has become one of the most active research areas in conservation biology. More than 1856 species are threatened with extinction and many have already disappeared (Young, et al., 2004). Since the early 1990s declining amphibian populations have attracted special attention because of three distinctive features: (1) recent increases in reports of population declines and species' extinctions; (2) cause(s) seemed to be occurring simultaneously and over great distances; and (3) amphibian populations in protected, natural areas were declining. The latter was alarming because it meant that habitat protection, perhaps the best way to ensure a species' survival, was failing in the case of some amphibians. Neotropical frog species show one of the most concerning decline (Stuart, et al., 2004). A famous example is the extinction of almost 20 species, including the golden toad

("*Bufo*" *periglenes*), in the pristine natural reserve of Monteverde in Costa Rica between 1987 and 1990 (Pounds, et al., 1997).

While there is a general consensus on the decline itself, there is much less agreement on the causes. The major hypothesised causes of decline can be sorted in two classes (Collins and Storfer, 2003). Class I hypotheses comprise alien species, over-exploitation and land use change and class II hypotheses comprise global change (including UV radiation and global climate change), contaminants and emerging infectious diseases. The class I causes are the major threats over biodiversity in general and their effects are straightforward and well documented. However, it must be noted that compared to many groups, amphibians have low capacity for dispersal and habitat fragmentation quickly halts genetic exchange between populations threatening the long term survival of populations (Blaustein, et al., 1994). The class II causes are complex and often subtle interactions that connect global change or emerging infectious diseases with amphibian population trends. Emerging infectious diseases caused by chytrid fungus have particularly retained attention (Blaustein and Dobson, 2006; Pounds et al., 2006, Mendelson et al., 2006) as it is the likely cause of population decline and extinction in pristine tropical areas in Australia (Hero and Morisson, 2004) and Central America (Lips et al., 2004; Young et al., 2001). However, the global pattern of the phenomenon indicates associated factors may be involved (Blaustein and Wake, 1995; Pounds, 2001; Pounds, et al., 1999; Young, et al., 2004)

Despite the numerous threats upon the Anuran fauna of the remaining tropical wilderness areas there is a fundamental lack of knowledge in South America. For example, most lowland regions in Amazonia are so remote and so largely unexplored that it is not surprising that amphibian population decline has yet to be documented there. Moreover, a major lack of knowledge also involves the evolutionary and geographical boundaries of Amphibian species. This poses a major problem for efficient conservation planning because a significant proportion of amphibian biodiversity may vanish before even having been described and studied.

3. The Neotropics

The South American continent extends from 56°S at Cape Virgenes in Patagonia to 12°N in Venezuela and hosts an amazingly vast variety of biota. The diversity of habitats ranges from the pampas to the temperate forests of Chile, the Cerrados to the Atacama Desert, the highlands of the Andes to, of course, the immensity of the Amazonian Forest. This incredible diversity of habitat makes South America host to the greatest species richness on

earth for many living groups, such as frogs (Fig. 1.1). The faunal and floral originality is the result of 50 millions years (my) of isolation, after its separation from the rest of Gondwana, prior to its reconnection with North America via a restricted land bridge only 3 my ago (Duellman, 1979). The tropical forests of South America are particularly diverse (Gaston and Williams, 1996; Myers et al., 2000; Wilson, 1992) and the origin of this incredible diversity has intrigued naturalists, beginning with Wallace (1852) and Bates (1863), for more than a century. However, two interrelated questions are still debated today: (1) the extent and (2) the origin of this diversity.

3.1. The extent of Neotropical diversity

The question of the extent of Neotropical biodiversity is of primary interest to evolutionary and conservation biology because we need the basic data to understand how today`s diversity originated and how it is distributed to better conserve it. Much progress has been made to decipher the relationships and ages of higher clades (e.g. Frost et al., 2006, Roelants et al., 2007), but a lot of work is still needed at the species level, and the bulk of work on the genetic diversity within species has yet to be tackled. What if our present definitions of these species result in serious underestimates of the actual diversity? What if many species in Amazonia possess deep genetic divisions that reflect millions of years of evolutionary history but remain largely unrecognized? This may just be the case. Until now, only glimpses of the patterns of genetic diversity within species in the region have been revealed. Advances in genetic knowledge and molecular technology have enabled us to closely examine the complexity of genetic diversity. With the high rate of environmental destruction (Da Silva et al., 2005; Laurance, 2007; Laurance et al., 2002; Lyles, 1988) and the threat of climate change (Bush et al., 2004; Rull and Vegas-Vilarrubia, 2006), this new research comes not a moment too soon as we seek to understand one of the richest species assemblages ever to evolve before it is irrevocably degraded.

3.2. The origin of the diversity

Neotropical diversity has long been thought to originate in an environment dominated by stable warm and wet climate conditions (Ashton, 1969; Fisher, 1960; Richards, 1952; Schwabe, 1969) which would have sustained evergreen rainforests for eons. This stability may have facilitated the accumulation of species and the reduction of extinction rates (Connell and Orians, 1964; Darlington, 1957; Sanders, 1969; Schwabe, 1969). However, this view is challenged by palynological (Flenley, 1979; Livingstone, 1962; Van der Hammen and

Gonzales, 1960) and glaciological (Mercer and Palacios, 1977) evidence, which demonstrates that the climate fluctuations responsible for ice-ages in the Northern Hemisphere have also disturbed tropical biota. In addition, the geologically turbulent history of South America has continuously shaped its landscapes potentially creating barriers to dispersal (Hoorn, 1994; Hoorn et al., 1995). Many hypotheses about the diversification process in the Neotropics have subsequently arisen without any current consensus (Haffer, 1997; Moritz et al., 2000). These hypotheses share the idea that historical and geographically pervasive barriers to gene flow have facilitated speciation in allopatry across much of Amazonia but obviously differ with respect to the identity, location, time and duration of these barriers. Again, recent advances in DNA analysis provide the means to examine the temporal and spatial characteristics of biological diversification of Neotropical organisms and to test the various hypotheses about the factors that have resulted in the biotic diversification observed.

4. The Amazonia and the Guiana Shield

Biodiversity is unevenly distributed also across the Neotropics. First, the South American tropical forests can be divided in five main regions (Duellman, 1999) (Fig. 1.2): The Chocò (Trans-Andean forest) on the Pacific coast, the steep slopes of the Andes, the Caribbean coastal forest; the Atlantic forest of Brazil and the (Cis-Andean) Amazonian forest. These regions are all characterized by high degrees of endemism (Duellman, 1999). Covering an area of about 6×10^6 km², Amazonia itself is not a uniform forest as it is often portrayed. Tree diversity is highly variable depending on soils, precipitation and flooding regime, conditions that vary greatly across the region.

The Amazonian lowland (<600m) forest is considered as an assemblage of sub-regions comprising western Amazonia (Upper Amazon), the Brazilian Shield and the Guiana Shield (Fig. 1.3). The Guiana Shield is one of the three cratons of the South American Plate, a 1.7 billion years old Precambrian geological formation. It is little known and extremely rich biologically. It is bound on the west by the Rio Orinoco and Rio Negro, and in the South by the lower reaches of the Amazon. Hammond (2005) described it as "the land of old rocks, poor soil, much water, extensive forest and few people". It is indeed the most intact (80 to 90% of its area), least inhabited (0.6–0.8 people/km^2) and largest continuous tract of tropical rainforest in the world (Huber and Foster, 2003). Since these areas are now threatened by increased resource extraction and climate change, it is important to gain an understanding of its flora and fauna so that decisions can be made on critical areas that represent high priorities for conservation.

Within the Guiana Shield itself two distinct areas can be segregated, the Tepuis in Venezuela and Guyana on the west, which inspired Conan Doyle's Lost World, and the eastern Guiana Shield (Fig. 1.3). Rupununi savannas areas of the Essequibo-Rio Branco (Guyana-Brazil Roraima) depression separate these two portions of the Guiana Shield. The eastern region, on which this work will focus, is comprised of French Guiana, Suriname, lowlands of Guyana, a portion of Parà and Amazonas states north of the Rio Amazonas and the Amapà state. This region is of low altitude rarely exceeding 400m asl, and is covered by rainforest. The rainfall is concentrated on northeastern Suriname, northern French Guiana and Amapà. Patches of savanna occur in the relatively dry interior zone (e.g. Sipaliwini) and on the coastal strip.

5. Neotropical and Guiana Shield frogs

Despite the drastic global decline that amphibians are undergoing (Beebee, 1992; Mendelson et al., 2006), the number of species known to science has increased exponentially for the last 30 years (Fig. 1.4) (Dubois, 2005; Glaw and Köhler, 1998; Hanken, 1999; Köhler et al., 2005). This remarkable rise (Glaw and Köhler, 1998) does not reflect taxonomic inflation in which known subspecies or variants are elevated to species status but is due to true first-hand discoveries (Köhler et al., 2005; De la Riva, 2007). However, describing amphibian diversity and inferring their evolutionary histories remains a difficult task because there are few diagnostic morphological characters either because morphology is extremely conserved or constrained (Cherry et al., 1977; 1978; Emerson, 1986; Shubin and Jenkins, 1995) or is plagued with homoplasy (Bossuyt and Milinkovitch, 2000; Parra-Olea and Wake, 2001; Wake, 1991). Consequently, it is probable that a large proportion of amphibian diversity still remains to be discovered (Glaw and Köhler, 1998, Vences et al., 2005).

The Neotropics shelter the highest number of frog species on earth with more than 2000 species (Duellman, 1999; Young et al., 2004), with more than 400 frog species thought to be distributed throughout the lowlands of Amazonian forest (source Global Amphibian Assessment). The Guiana Shield is considered an independent biogeographical entity due to the relative high endemism observed in the region. Although, while the endemism of the Guiana highlands (western Guiana Shield) is very high, more than half of the 115 currently recognised frog species in the eastern Guiana Shield occur elsewhere in Amazonia (Lescure and Marty, 2000; Duellman, 1999; Lima et al., 2006, pers. data), but the idea that so many species have such widespread distributions is at odds with (1) the low vagility and high philopatry observed in most amphibian taxa, characteristics that should promote

differentiation and ultimately speciation (Berven and Grudzien, 1990; Duellman, 1982; Gascon et al., 1998; Kusano et al., 1999; Reading et al., 1991) and (2) known historic climatic oscillations and geological events that have likely shaped the ranges of these species and their ancestors (Bush, 1994; Frailey et al., 1989; Haffer, 1969; Moritz et al., 2000; Nores, 1999). Particularly because given their complex life cycles, permeable skin, and exposed eggs, frogs are among the most sensitive vertebrates to climate change. This led Lynch (1979) and Wynn and Heyer (2001) to question respectively how many widespread Amazonian frog species really exist, or if they indeed exist at all.

Lomolino (2004) proposed the terms "Linnaean shortfall" to describe gaps in our taxonomic knowledge, and "Wallacean shortfall" regarding our inability to map species' ranges accurately. Nowhere are these shortfalls more evident than in Amazonia. Indeed, the full distribution of any Amazonian frog species is completely known, much less its fundamental niche. Understanding the biases in our knowledge, and identifying key gaps and filling them, have to be priorities if effective conservation strategies for Amazonia are to be established.

6. PhD goals

It is of primary importance for conservation to obtain accurate regional estimates of species richness and regional endemism in the Guiana Shield and Amazonia in general and particularly for such a threaten group like Anurans. It is also important to evaluate the intraspecific diversity and the depth of species evolutionary histories. Moreover, because of their low vagility and sensitivity to climate change Anurans are also good models to investigate evolutionary history in light of paleoenvironments. The crossover between phylogenetics and the emerging field of comparative phylogeography provides an integrative methodological framework to study the transition from diversity within species to differentiation between species and their interrelationships. Importantly, this framework will provide essential estimates of frog biodiversity and data that will help to decipher a key component of the biogeographic history of the Guiana Shield. For my PhD I focused on the estimation of the eastern Guiana Shield frog diversity and its evolutionary history. The eastern Guiana Shield being intimately, or at least supposedly, linked with Amazonia, this work also deals largely with Amazonian diversity and phylogeography.

The first chapter is an initial proof of concept study to test species boundaries in two species *Scinax ruber* and *Rhinella margaritifera*. These species are widely distributed, abundant and largely recognized as species complexes. I used an original species delineation

method based on the combined use of mitochondrial and nuclear DNA in phylogenetics and phylogeographic analyses. The straightforward use of the phylogenetic species concept can lead to view species not as real evolutionary entities (Goldstein et al., 2005, 2000). As advocated by Frost and Hillis (1990), for amphibians and reptiles, it would be more appropriate to consider amphibian species as monophyletic group of populations that are likely to be on independent phylogenetic trajectories under an evolutionary species concept (Wiley, 1978). In this way, one crucial point in delimiting cryptic species is to distinguish between broad admixture on one hand, and narrow contact zone or restricted hybridization on the other hand (Wake and Jockusch, 2000). That is the interest of combining phylogenetics and phylogeographic analyses. Moreover, diagnostic nucleotide sites of mitochondrial haplotypes in a character-based approach to species delineation (Goldstein et al., 2005) could contradict information from nuclear genes as it has been often found in amphibians (e.g. Garcia-Paris et al., 2003; Kuchta and Tan, 2005; Monsen and Blouin, 2003; Sequeira et al., 2005; Wake and Jockusch, 2000; Zangari et al., 2006). Thus, species borders are better understood using a combination of different kinds of markers as underlined by Moritz (1994a; b). This chapter has been published in Molecular Phylogenetics and Evolution, 43, 567–582 and co-authored by Vences M., Salducci M.-D., Meyer A., Marty C., Blanc M. and Gilles A.

In a second chapter, to test if the first results were generalisable, I questioned what would potentially be a minimum estimate of the number of cryptic frog species in Amazonia and Guiana Shield, using mtDNA with different complementary approaches. I also evaluated previous published threshold values for genetic distances (Vences et al., 2005), and developed another one based on sequences from a large number of taxonomic groups (60 species represented by more than 500 sequences), which can be used to identify candidate species among these frogs. To be accurate, the species delineation needs to use a taxon specific approach (by genus or group of species) using a combination of data from phylogenetic, phylogeographic, morphological and ecological data (Sites and Marshall, 2004). However, considering the enormous number of potential new candidate species it is clear that such analyses would take considerable time. However, biodiversity data are urgently needed to help define conservation priorities. Molecular diversity data may be useful surrogates to evaluate amphibian biodiversity before it vanishes. Even if some of the lineages identified may ultimately be shown not to represent species, while other true species may be missed, the net gain in our understanding of amphibian diversity in regions like the Neotropics makes such a strategy attractive. Ultimately, this can have implications leading to the re-evaluation of the extent of the global amphibian decline. This chapter has been published in PLoS One,

2(10), e1109. doi:10.1371/journal.pone.0001109 and co-authored by Gilles A., Vences M., Marty C., Blanc M. and Gemmell N. J.

The *Rhinella margaritifera* complex is characterisized by the presence of many cryptic species throughout its wide distribution, ranging from Panama to Bolivia and almost entire Amazonia. French Guiana has long been thought to harbor two species of this group (*Rhinella margaritifera* and one unnamed species), though molecular data analysed in previous chapters indicated as many as five lineages. In this third chapter I tested to see whether morphological measurements are correlated or not with genetic data using discriminant analysis and if diagnostic characteristics among the previously determined lineages can be used to describe these new species. This is a new integrative method which can lead to a facilitation of the description of cryptic species that have been detected by phylogenetic and/or phylogeographic studies. This chapter has been published in Zootaxa, 1663, 17–32 and co-authored by Gaucher P., Blanc M. and Velez-Rodriguez C.M.

In a final chapter, congruence among the phylogeographic patterns of 18 frog species was tested to reveal the major patterns of spatial and temporal diversification in the eastern Guiana Shield. Determining if co-distributed species responded to climate change in an independent or concerted manner (e.g. Sullivan et al., 2000) is a basic objective of comparative phylogeography. For all but a handful of taxa, the species boundaries, histories, ecologies and their geographical ranges are still to be explored in the Guiana Shield. Specifically I questioned whether major intraspecific diversification started before Pleistocene or not and occurred within the Guiana Shield or ex situ. The consequences on the diversity and the endemism of the Guiana Shield will be explored. This chapter has been prepared for submission to Systematic Biology and will be co-authored by Noonan B.P., Rodrigues M.T., Pech N., Gilles A. and Gemmell N.J.

References

Ab'Saber, A.N. 1977. Espaços ocupados pela expansão dos climas secos na América do Sul, por ocasião dos períodos glaciais quaternários. *IGEOG-USP – Paleoclimas*, **3**, 1–19.

Agapow, P.M., Bininda-Emonds, O.R.P., Crandall, K.A., Gittleman, J.L., Mace, G.M., Marshall, J.C., Purvis, A. 2004. The impact of species concept on biodiversity studies. *Quarterly Review of Biology*, **79**, 161–179.

Ashton, P.S. 1969. Speciation among tropical forests tree: some deductions in the light of recent evidence. *Biological Journal of the Linnean Society*, **1**, 155–196.

Bates, H.W. 1863-1864. *The naturalist on the river Amazon*. London. John Murray (2 Vol.).

Beebee, T.J.C. 1992. Amphibian Decline. *Nature*, **355**, 120–120.

Berven, K.A., Grudzien, T.A. 1990. Dispersal in the wood frog (*Rana sylvatica*)- implications for genetic population structure. *Evolution*, **44**, 2047–2056.

Bickford, D., Lohman, D.J., Sodhi, N.S., Ng, P.K.L., Meier, R., Winker, K., Ingram, K.K., Das, I. 2007. Cryptic species as a window on diversity and conservation. *Trends in Ecology and Evolution*, **22**, 148–155.

Blaustein, A.R., Dobson, A. 2006. Extinctions: A message from the frogs. *Nature*, **439**, 143–144.

Blaustein, A.R., Wake, D.B. 1995. The puzzle of declining Amphibian populations. *Scientific American*, **272**, 52–57.

Blaustein, A.R., Wake, D.B., Sousa, W.P. 1994. Amphibian declines-judging stability, persistence, and susceptibility of populations to local and global extinctions. *Conservation Biology*, **8**, 60–71.

Bossuyt, F., Milinkovitch, M.C. 2000. Convergent adaptive radiations in Madagascan and Asian ranid frogs reveal covariation between larval and adult traits. *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 6585–6590.

Bush, M.B. 1994. Amazonian speciation - a necessarily complex model. *Journal of Biogeography*, **21**, 5–17.

Bush, M.B., Silman, M.R., Urrego, D.H. 2004. 48,000 years of climate and forest change in a biodiversity hot spot. *Science*, **303**, 827–829.

Cherry, L.M., Case, S.M., Wilson, A.C. 1977. Relative rates of morphological evolution in primates, carnivores and frogs. *American Zoologist*, **17**, 910–910.

Cherry, L.M., Case, S.M., Wilson, A.C. 1978. Frog perspective on morphological difference between Humans and Chimpanzees. *Science*, **200**, 209–211.

Collins, J.P., Storfer, A. 2003. Global amphibian declines: sorting the hypotheses. *Diversity and Distributions*, **9**, 89–98.

Connell, J.H., Orians, E. 1964. The ecological regulation of species diversity. *American Naturalist*, **98**, 399–414.

Da Silva, J.M.C., Rylands, A.B., Da Fonseca, G.A.B., 2005. The fate of the Amazonian areas of endemism. *Conservation Biology*, **19**, 689–694.

Darlington, P.J. 1957. *Zoogeography: the geographical distribution of animals*, New York.

De la Riva, I. 2007. Bolivian frogs of the Genus Phrynopus, with the description of twelve new species (Anura: Brachycephalidae). *Herpetological Monographs*, **21**(1), 241–277.

de Queiroz, K. 1998. The general lineage concept of species, species criteria, and the process of speciation. In: Howard, D.J. and Berlocher, S.H. (eds.). *Endless forms: species and speciation*, Oxford University Press, pp. 57–75.

de Queiroz, K. 1999. The general lineage concept of species, species criteria, and the process of speciation. In: Wilson, R.A. (ed.) *Species: new interdisciplinary essays*, MIT Press, Cambridge, Massachusetts, U.S.A, pp. 49–89

de Queiroz, K. 2007. Species concepts and species delimitation. *Systematic Biolology*, **56**(6), 879–886.

Dixon, J.R. 1979. Reptiles of lowland tropical forests. In: Duellman, W.E. (ed.). *The South American herpetofauna: Its origin, evolution and dispersal*. Monograph of the Museum of Natural History, University of Kansas. pp. 189–215.

Dubois, A. 2005. Developmental pathway, speciation and supraspecific taxonomy in amphibians, 1: Why are so many frog species in Sri Lanka? *Alytes*, **22**, 19–37.

Duellman, W.E. 1979. *The South American herpetofauna: Its origin, evolution, and dispersal*. Museum of Natural History, University of Kansas, Lawrence.

Duellman, W.E. 1982. Quaternary climatic-ecological fluctuations in the lowland tropics: frogs and forests. In: Prance, G.T., (ed.). *Biological diversification in the tropics*, Columbia University Press, pp. 389–402.

Duellman, W.E. 1999. *Patterns of distribution of amphibians: a global perspective*. Baltimore, MD, Johns Hopkins University Press.

Ekrem, T., Willassen, E., Stur, E. 2007. A comprehensive DNA sequence library is essential for identification with DNA barcodes. *Molecular Phylogenetics and Evolution*, **43**(2), 530–542.

Emerson, S.B. 1986. Convergence and morphological constraint in frogs: variation in postcranial morphology. *Fieldiana Zoology*, **43**, 1–19.

Ennos, R.A., French, G.C., Hollingsworth, P.M. 2005. Conserving taxonomic complexity. *Trends in Ecology and Evolution*, **20**, 164–168.

Faith, D.P. 1992. Conservation evaluation and phylogenetic diversity. *Biological Conservation*, **61**, 1–10.

Faith, D.P., Reid, C.A.M., Hunter J. 2004. Integrating phylogenetic diversity, complementarity, and endemism for conservation assessment. *Conservation Biology*, **18**, 255–261.

Fischer, A.G. 1960. Latitudinal variation in organic diversity. *Evolution*, **14**, 64–81.

Flenley, J.R. 1979. *A geological history of tropical rainforest*. Butterworth, London.

Frailey, C.D., Lavina, E.L., Rancy, A., Filho, J.P.S. 1989. A proposed Pleistocene/Holocene lake in the Amazonas basin and its significance to Amazonian geology and biogeography. *Acta Amazonica*, **18**, 119–143.

Frost, D.R., Grant, T., Faivovich, J., Bain, R.H., Haas, A., Haddad, C.F.B., De Sà, R.O., Channing, A., Wilkinson, M., Donnellan, S.C., Raxworthy, C.J., Campbell, J.A., Blotto, B.L., Moler, P., Drewes, R.C., Nussbaum, R.A., Lynch, J.D., Green, D.M., Wheeler, W.C. 2006. The amphibian tree of life. *Bulletin of the American Museum of Natural History*, **297,** 1–370.

Frost, D.R., Hillis, D.M. 1990. Species in concept and practice—herpetological applications. *Herpetologica*, **46**, 87–104.

Funk, D.J., Omland, K.E. 2003. Species-level paraphyly and polyphyly: Frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology Evolution and Systematics,* **34**, 397–423.

Garcia-Paris, M., Alcobendas, M., Buclkey, D., Wake, D.B. 2003. Dispersal of viviparity across contact zones in Iberian populations of fire salamanders (*Salamandra*) inferred from discordance of genetic and morphological traits. *Evolution*, **57**, 129–143.

Gascon, C., Lougheed, S.C., Bogart, J.P. 1998. Patterns of genetic population differentiation in four species of Amazonian frogs: A test of the riverine barrier hypothesis. *Biotropica*, **30**, 104–119.

Gaston, K.J. 2000. Global patterns in biodiversity. *Nature*, **405**, 220–227.

Gaston, K.J., Williams, P.H. 1996. Spatial patterns in taxonomic diversity. In: Gaston, K.J. (ed.), *Biodiversity: A biology of numbers and difference*. Blackwell Science, pp. 202–229.

Glaw, F., Köhler, J. 1998. Amphibian species diversity exceeds that of mammals. *Herpetological Review*, **29**, 11–12.

Goldstein, P., Wyner, K., Doukakis, P., Egan, M.G., Amato, G., Rosenbaum, H., DeSalle, R. 2005. Theory and methods for diagnosing species and populations in conservation. *Annals of the Missouri Botanical Garden*, **92**, 12–27.

Goldstein, P.Z., DeSalle, R., Amato, G., Vogler, A.P. 2000. Conservation genetics at the species boundary. *Conservation Biology*, **14**, 120–131.

Haffer, J. 1969. Speciation in amazonian forest birds. *Science* **165**, 131–137.

Haffer, J. 1997. Alternative models of vertebrate speciation in Amazonia: An overview. *Biodiversity and Conservation*, **6**, 451–476.

Hammond, D.S. 2005. *Tropical Forests of the Guiana Shield*: *Ancient Forests in a Modern World*. CABI publishing. Cambridge, USA. 528 p.

Hanken, J. 1999. Why are there so many new amphibian species when amphibians are declining? *Trends in Ecology and Evolution*, **14**, 7–8.

Hartmann, K., Steel, M. 2006. Maximizing phylogenetic diversity in biodiversity conservation: Greedy solutions to the Noah's Ark Problem. *Systematic Biology*, **55**, 644–651.

Hawksworth, D.L., Kalin-Arroyo, M.T. 1995. Magnitude and distribution of biodiversity. In: Heywood, V.H. (ed.). *Global biodiversity assessment*. Cambridge University Press, pp. 107–191

Hebert, P.D.N., Cywinska, A., Ball, S.L., DeWaard, J.R. 2003. Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **270**, 313–321.

Hebert, P.D.N., Stoeckle, M.Y., Zemlak, T.S., Francis, C.M. 2004. Identification of birds through DNA barcodes. *PLoS Biology*, **2**, 1657–1663.

Hero, J.M., Morrison, C. 2004. Frog declines in Australia: Global implications. *Herpetological Journal*, **14**, 175–186.

Houlahan, J.E., Findlay, C.S., Schmidt, B.R., Meyer, A.H., Kuzmin, S.L. 2000. Quantitative evidence for global amphibian population declines. *Nature*, **404**, 752–755.

Hoorn, C. 1994. Fluvial Paleoenvironments in the Intracratonic Amazonas Basin (Early Miocene - Early Middle Miocene, Colombia). *Palaeogeography, Palaeoclimatology and Palaeoecology*, **109**, 1–54.

Hoorn, C., Guerrero, J., Sarmiento, G.A., Lorente, M.A. 1995. Andean tectonics as a cause for changing drainage patterns in Miocene northern South-America. *Geology*, **23**, 237–240.

Horner-Devine, M.C., Carney, K.M., Bohannan, B.J.M. 2004. An ecological perspective on bacterial biodiversity. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **271**, 113–122.

Hoskin, C.J., Higgie, M., McDonald, K.R., Moritz, C. 2005. Reinforcement drives rapid allopatric speciation. *Nature*, **437**, 1353–1356.

Houlahan, J.E., Findlay, C.S., Schmidt, B.R., Meyer, A.H., Kuzmin, S.L. 2000. Quantitative evidence for global amphibian population declines. *Nature*, **404**, 752–755.

Huber, O., Foster, M.N. 2003. *Conservation priorities for the Guyana Shield*. Washington, D.C. Conservation International.

Hughes, J.B., Daily, G.C., Ehrlich, P.R. 1997. Population diversity: Its extent and extinction. *Science*, **278**, 689–692.

Köhler, J., Vieites, D.R., Bonett, R.M., Garcia, F.H., Glaw, F., Steinke, D., Vences, M. 2005. New amphibians and global conservation: A boost in species discoveries in a highly endangered vertebrate group. *Bioscience*, **55**, 693–696.

Kuchta, S.R., Tan, A.M. 2005. Isolation by distance and post-glacial range expansion in the rough-skinned newt, *Taricha granulosa*. *Molecular Ecology*, **14**, 225–244.

Kusano, T., Maruyama, K., Kanenko, S. 1999. Breeding site fidelity in the Japanese toad, *Bufo japonicus formosus*. *Herpetological Journal*, **9**, 9–13.

Lamoreux, J. F., Morrison, J.C., Ricketts, T.H., Olson, D.M., Dinerstein, E., McKnight, M.W., Shugart H.H. 2006. Global tests of biodiversity concordance and the importance of endemism. *Nature*, **440**, 212–214.

Laurance, W.F. 2007. Have we overstated the tropical biodiversity crisis? *Trends in Ecology and Evolution*, **22**, 65–70.

Laurance, W.F., Albernaz, A.K.M., Schroth, G., Fearnside P.M., Bergen, S., Venticinque, E.M., Da Costa, C. 2002. Predictors of deforestation in the Brazilian Amazon. *Journal of Biogeography*, **29**, 737–748.

Lescure, J., Marty, C. 2000. *Atlas des amphibiens de Guyane*. Muséum National d'Histoire Naturelle. Patrimoines Naturels, **45**. 388 p.

Lherminer, P., Solignac, M. 2000. Species: author definitions. *Comptes Rendus De l`Academie Des Sciences Serie Iii-Sciences De La Vie-Life Sciences*, **323**, 153–165.

Lima, A.P., Magnusson, W.E., Menin, M., Erdtmann, L. K., Rodrigues, D.J., Keller, C., Hödl. W. 2006. *Guide to the frogs of reserva Adolpho Ducke – Guia de sapos da reserva Adolpho Ducke*, Attema design editorial, Manaus, 168 p.

Lips, K.R., Mendelson, J.R., Munoz-Alonso, A., Canseco-Marquez, L., Mulcahy D.G. 2004. Amphibian population declines in montane southern Mexico: resurveys of historical localities. *Biological Conservation*, **119**, 555–564.

Livingstone, D.A. 1962. Age of deglaciation of the Ruwenzori range, Uganda. *Nature*, **194**, 859–860.

Lomolino, M.V. 2004. Conservation biogeography. In: Lomolino, M.V. and Heaney L.R. (eds.), *Frontiers of biogeography: new directions in the geography of nature*. Sinauer Associates, Sunderland, MA, pp. 293–296.

Lyles, L.L. 1988. A long and rocky road to reversing rainforest destruction. *Nature*, **333**, 491–491.

Lynch, J.D. 1979. The amphibians of the lowland tropical forests. In: Duellman, W.E. (ed.) *The South American herpetofauna: Its origin, evolution and dispersal*. Monograph of the Museum of Natural History, University of Kansas. pp. 189–215.

Mace, G.M., Gittleman, J.L., Purvis, A. 2003. Preserving the Tree of Life. *Science*, **300**, 1707–1709.

Margules, C.R., Pressey, R.L. 2000. Systematic conservation planning. *Nature*, **405**, 243–253.

Mendelson, J.R., Lips, K.R., Gagliardo, R.W., Rabb, G.B., Collins, J.P., Diffendorfer, J.E., Daszak, P., Ibanez, R., Zippel, K.C., Lawson, D.P., Wright, K.M., Stuart, S.N., Gascon, C., da Silva, H.R., Burrowes, P.A., Joglar, R.L., La Marca, E., Lotters, S., du Preez, L.H., Weldon, C., Hyatt, A., Rodriguez-Mahecha, J.V., Hunt, S., Robertson, H., Lock, B., Raxworthy, C.J., Frost, D.R., Lacy, R.C., Alford, R.A., Campbell, J.A., Parra-Olea, G., Bolanos, F., Domingo, J.J.C., Halliday, T., Murphy, J.B., Wake, M.H., Coloma, L.A., Kuzmin, S.L., Price, M.S., Howell, K.M., Lau, M., Pethiyagoda, R., Boone, M., Lannoo, M.J., Blaustein, A.R., Dobson, A., Griffiths, R.A., Crump, M.L., Wake, D.B., Brodie, E.D. 2006. Biodiversity - Confronting amphibian declines and extinctions. *Science*, **313**, 48–48.

Mercer, J.H., Palacios, O. 1977. Radiocarbon dating of the last glaciation in Peru. *Geology*, **5**, 600–604.

Meyer, C.P., Paulay, G. 2005. DNA barcoding: Error rates based on comprehensive sampling. *PLoS Biology*, **3**, 2229–2238.

Mittermeier, R.A., Mittermeier, C.G., Brooks, T.M., Pilgrim, J.D., Konstant, W.R., da Fonseca, G.A.B., Kormos, C. 2003. Wilderness and biodiversity conservation. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 10309–10313.

Monsen, K.J., Blouin, M.S. 2003. Genetic structure in a montane ranid frog: restricted gene flow and nuclear-mitochondrial discordance. *Molecular Ecology*, **12**, 3275–3286.

Moritz, C. 1994a. Applications of mitochondrial DNA analysis in conservation—a critical-review. *Molecular Ecology*, **3**, 401–411.

Moritz, C. 1994b. Defining evolutionarily significant units for conservation. *Trends in Ecology and Evolution*, **9**, 373–375.

Moritz, C., Patton, J.L., Schneider, C.J., Smith, T.B., 2000. Diversification of rainforest faunas: An integrated molecular approach. *Annual Review of Ecology and Systematics*, **31**, 533–563.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B., Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

Narain, P. 2000. Genetic diversity - Conservation and assessment. *Current Science*, **79**, 170–175.

Neel, M.C., Cummings, M.P. 2003. Effectiveness of conservation targets in capturing genetic diversity. *Conservation Biology*, **17**, 219–229.

Nores, M. 1999. An alternative hypothesis for the origin of Amazonian bird diversity. *Journal of Biogeography*, **26**, 475–485.

Parra-Olea, G., Wake, D.B. 2001. Extreme morphological and ecological homoplasy in tropical salamanders. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 7888–7891.

Pechmann, J.H.K., Wilbur, H.M. 1994. Putting declining amphibian populations in perspective - Natural fluctuations and human impacts. *Herpetologica*, **50**, 65–84.

Pimm, S.L., Russell, G.J., Gittleman, J.L., Brooks, T.M. 1995. The future of biodiversity. *Science*, **269**, 347–350.

Pounds, J.A. 2001. Climate and amphibian declines. *Nature*, **410**, 639–640.

Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., La Marca, E., Masters, K.L., Merino-Viteri, A., Puschendorf, R., Ron, S.R., Sanchez-Azofeifa, G.A., Still, C.J., Young B.E. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature*, **439**, 161–167.

Pounds, J.A., Fogden, M.P.L., Campbell, J.H. 1999. Biological response to climate change on a tropical mountain. *Nature*, **398**, 611–615.

Pounds, J.A., Fogden, M.P.L., Savage, J.M., Gorman, G.C. 1997. Tests of null models for amphibian declines on a tropical mountain. *Conservation Biology*, **11**, 1307–1322.

Purvis, A., Hector, A. 2000. Getting the measure of biodiversity. *Nature*, **405**, 212–219.

Raven, P.H., Wilson, E.O. 1992. A fifty-year plan for biodiversity surveys. *Science*, **258**, 1099–1100.

Reading, C.J., Loman, J., Madsen, T. 1991. Breeding pond fidelity in the common toad, *Bufo bufo*. *Journal of Zoology*, **225**, 201–211.

Richards, P.W. 1952. *The tropical rain forest: an ecological study*. Cambridge Univ. Press, Cambridge, U.K.

Rodrigues, S.L., Brooks, T.M. 2007. Shortcuts for biodiversity conservation planning. *Annual Review of Ecology, Evolution and Systematics*, **38**, 713–737.

Roelants, K., Gower, D. J., Wilkinson, M., Loader, S.P., Biju, S.D., Guillaume, K., Moriau, L., Bossuyt, F. 2007. Global patterns of diversification in the history of modern amphibians. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 887–892.

Roy, D. 2002. Amphibians as environmental sentinels. *Journal of Biosciences*, **27**, 187–188.

Rull, V., Vegas-Vilarrubia, T., 2006. Unexpected biodiversity loss under global warming in the neotropical Guayana Highlands: a preliminary appraisal. *Global Change Biology*, **12**, 1–9.

Sanders, H.L. 1969. Benthic marine diversity and stability-time hypothesis. *Brookhaven Symposia in Biology*, **22**, 71–81.

Schwabe, G.H. 1969. Towards an ecological characterization of the South American continent. In: Fittkau, E.J., Illies, J., Klinge, H., Schwabe, G.H. and Sioli, H. (eds.), *Biogeography and ecology in South America*. Dr. W. Junk, Dordrecht, The Netherlands, pp. 113–136

Sequeira, F., Alexandrino, J., Rocha, S., Arntzen, J.W., Ferrand, N. 2005. Genetic exchange across a hybrid zone within the Iberian endemic golden-striped salamander, *Chioglossa lusitanica*. *Molecular Ecology*, **14**, 245–254.

Shubin, N.H., Jenkins, F.A. 1995. An Early Jurassic jumping frog. *Nature*, **377**, 49–52.

Sites, J.W., Marshall, J.C. 2003. Delimiting species: a Renaissance issue in systematic biology. *Trends in Ecology and Evolution*, **18**, 462–470.

Sites, J.W., Marshall, J.C. 2004. Operational criteria for delimiting species. *Annual review of ecology, evolution and systematics* , **35** 199–227.

Stackebrandt, E. 2004. Will we ever understand? The undescribable diversity of the prokaryotes. *Acta Microbiologica et Immunologica Hungarica*, **51**, 449–462.

Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L., Waller, R.W. 2004. Status and trends of amphibian declines and extinctions worldwide. *Science*, **306**, 1783–1786.

Sullivan, J., Arellano, E., Rogers, D.S. 2000. Comparative phylogeography of mesoamerican highland rodents: Concerted versus independent response to past climatic fluctuations. *American Naturalist*, **155**, 755–768.

Van der Hammen, T., Gonzales, E. 1960. Upper Pleistocene and Holocene climates and vegetation of the sabana de Bogota (Colombia, South America). *Leidsche Geologische Mededeelingen*, **25**, 126–315.

Vences, M., Thomas, M., Bonett, R.M., Vieites, D.R. 2005. Deciphering amphibian diversity through DNA barcoding: chances and challenges. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **360**, 1859–1868.

Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M. 1997. Human domination of Earth's ecosystems. *Science*, **277**, 494–99.

Wake, D.B. 1991. Homoplasy-the result of natural-selection, or evidence of design limitations. *American Naturalist*, **138**, 543–567.

Wake, D.B., Jockusch, E.L. 2000. Detecting species borders using diverse data sets. In: Bruce, R.C., Jaeger, R.G. and Houck, L.D. (eds.), *The biology of Plethodontid Salamanders*. Kluwer Academic, Plenum Publishers, pp. 95–119.

Wallace, A.R. 1852. The monkeys of the Amazon. *Proceedings of the Zoological Society of London*, **20**, 107–110.

Warman, L.D., Forsyth, D.M., Sinclair, A.R.E., Freemark, K., Moore, H.D., Barrett, T.W., Pressey, R.L., White, D. 2004. Species distributions, surrogacy, and important conservation regions in Canada. *Ecology Letters*, **7**, 374–379.

Weitzman, M.L. 1998. The Noah's ark problem. *Econometrica*, **66**, 1279–1298.

Whitman, W.B., Coleman, D.C., Wiebe, W.J. 1998. Prokaryotes: The unseen majority. *Proceedings of the National Academy of Sciences of the United States of America*, **95**, 6578–6583.

Wiens, J.J. 2007. Species delimitation: New approaches for discovering diversity. *Systematic Biology*, **56**(6), 875–878.

Wiley, E.O. 1978. Evolutionary species concept reconsidered. *Systematic Zoology*, **27**, 17–26.

Wilson, E.O. 1992. *The Diversity of Life*. Belknap Press of Harvard University Press.

Wynn, A., Heyer, W.R. 2001. Do geographically widespread species of tropical amphibians exist? An estimate of genetic relatedness within the Neotropical frog *Leptodactylus fuscus* (Schneider 1799) (Anura, Leptodactylidae). *Tropical Zoology*, **14**, 255–285.

Young, B.E., Stuart, S.N., Chanson, J.S., Cox, N.A., Boucher, T.M. 2004. Disappearing jewels: The status of New World amphibians, *NatureServe*.

Young, B.E., Lips, K.R., Reaser, J.K., Ibanez, R., Salas, A.W., Cedeno, J.R., Coloma, L.A., Ron, S., La Marca, E., Meyer, J.R., Munoz, A., Bolanos, F., Chaves, G. and Romo, D. 2001. Population declines and priorities for amphibian conservation in Latin America. *Conservation Biology*, **15**, 1213–1223.

Zangari, F., Cimmaruta, R., Nascetti, G. 2006. Genetic relationships of the western Mediterranean painted frogs based on allozymes and mitochondrial markers: evolutionary and taxonomic inferences (Amphibia, Anura, Discoglossidae). *Biological Journal of the Linnean Society*, **87**, 515–536.

Chapter 2:

Revealing cryptic diversity using molecular phylogenetics and phylogeography in frogs of the *Scinax ruber* and *Rhinella margaritifera* species groups

Abstract

Few studies to date have examined genetic variability of widespread tropical amphibian species over their distributional range using different kinds of molecular markers. Here, we use genetic data in an attempt to delimit evolutionary entities within two groups of Neotropical frogs, the *Scinax ruber* species group and the *Rhinella margaritifera* species group. We combined mitochondrial and nuclear markers for a phylogenetic (a total of ~2500 bp) and phylogeographic study (~1300 bp) to test the reliability of the currently accepted taxonomic assignments and to explore the geographic structure of their genetic variation, mainly based upon samples from the French Guianan region. Phylogenetic analyses demonstrated the polyphyly of *Scinax ruber* and *Rhinella margaritifera*. *S. ruber* consists of six lineages that may all merit species status. Conflicting signals of mitochondrial and nuclear markers indicated, among some *Scinax* lineages and species, the possibility of ongoing hybridization processes. *R. margaritifera* consisted of 11 lineages which might represent distinct species as well. Phylogeographic analyses added further information in support of the specific status of these lineages. Lineages of low divergence were found in sympatry and were reciprocally monophyletic for mitochondrial as well as nuclear genes, indicating the existence of young lineages that should be awarded species status. Our results highlight the utility of combining phylogenetic and phylogeographic methods, as well as the use of both mitochondrial and nuclear markers within one study. This approach helped to better understand the evolutionary history of taxonomically complex groups of species. The assessment of the geographic distribution of genetic diversity in tropical amphibian communities can lead to conclusions that differ strongly from prior analyses based on the occurrence of currently recognized species alone. Such studies, therefore, hold the potential to contribute to a more objective assessment of amphibian conservation priorities in tropical areas.

Key words: Amphibia; Tyrosinase; 18S rDNA; Mitochondrial genes; Hylidae; *Scinax*; Bufonidae; *Rhinella*; Neotropics.

1. Introduction

The Neotropics are the region of highest species richness in the world (Gaston and Williams, 1996; Myers et al., 2000; Wilson, 1992). Amphibians are one group in which this high species diversity is obvious, with 2750 described species in Central and South America representing 48% of the world's total (Young et al., 2004). The increasing utilization of molecular data has reinforced the conclusion that morphological evolution in amphibians is often cryptic (e.g. Chek et al., 2001; Cherry et al., 1977; Hass et al., 1995; Maxson, 1984; Richards and Moore, 1996; Stuart et al., 2006) and has led to a revitalization of amphibian taxonomy. Many groups of amphibians are morphologically conserved and depauperate in obvious external characters. This and a high degree of convergence led to numerous misinterpretations of anuran phylogeny which were based on morphological traits alone (e.g. Bossuyt and Milinkovitch, 2000; Chiari et al., 2004; Vences et al., 2003). Therefore, and despite important recent advances, amphibian systematics have remained poorly resolved (e.g. Darst and Cannatella, 2004; Faivovich et al., 2005; Frost et al., 2006; Grant et al., 2006; Graybeal, 1997; Ruvinsky and Maxson, 1996; Vences et al., 2003), and amphibian diversity seems to be still largely underestimated in terms of the number of species, and genera as well as families (e.g. Biju and Bossuyt, 2003; Borkin et al., 2004; Bossuyt et al., 2004; De la Riva et al., 2000; Meegaskumbura et al., 2002). Numerous species have recently been described (Duellman, 1999; Glaw and Köhler, 1998; Köhler et al., 2005) and many widely distributed species of frogs are suspected to contain several new species (for the Neotropical region: Chek et al., 2001; De la Riva et al., 2000; Grant et al., 2006; Lescure and Marty, 2000; Lougheed et al., 1999; Vences et al., 2003).

When populations of a taxon are readily sampled and distributions are well known it is possible to study its phylogeographic patterns (Avise, 2000). However, this is rarely the case for the vast majority of amphibians that occur in the tropics. Molecular information for single individuals or single populations of amphibians are therefore of limited value in determining species status. Moreover, population genetic studies of anurans typically discovered very high genetic diversities compared to other vertebrate groups (e.g. Vences et al., 2005a,b). Although high intraspecific genetic divergences certainly occur in many amphibians, the high incidence of such patterns is probably also indicative of taxonomic practice, i.e., the failure to discover cryptic species (Chek et al., 2003; Crawford, 2003; Lougheed et al., 1999). Because most frogs are expected to be of low vagility and highly philopatric (Blaustein et al., 1994; Duellman, 1982), geographical structure and endemism would be expected to be high. However, so little is known of the diversification and age of lineages in Neotropical frog taxa

that current spatial proximity between populations might also be the result of a long history of expansions and contractions of ranges. Geographic and genetic fragmentation is so common in tropical amphibians that Wynn and Heyer (2001) have questioned whether widespread species of tropical amphibians exist at all. Considering the effects of global amphibian declines (Hanken, 1999; Houlahan et al., 2000; Stuart et al., 2004), numerous, still undescribed species are probably vanishing at alarming rates in the Neotropics.

The northeastern part of South America as delimited biogeographically by Hoogmoed (1979) is called the Guianan region. The endemism of frogs in this region is currently considered to be significant, but low compared to the Andes and the Brazilian Atlantic forest (Duellman, 1999) because many frog species are believed to have large ranges in Amazonia as well as the Guianas. Main factors that are thought to have shaped genetic diversity in South America include geological and climatological historical events and changes in the distribution of forested areas (Frailey et al., 1989; Haffer, 1969, 1990, 1997; Nores, 1999; Räsänen et al., 1991, 1990). On a broad scale, French Guiana might be on a borderline segregating east and west assemblages of plants (De Granville, 1982), fishes (Boujard et al., 1997; Jegu and Keith, 1999) and frogs (Lescure and Marty, 2000). On a smaller geographic scale, the central region near Saül, the northeastern area near Cayenne and the northwest region might have played a role as refugium for forest specialists during past climatic oscillations (Charles-Dominique et al., 1998; De Granville, 1988, 1982; Duellman, 1982; Dutech et al., 2003; Ledru et al., 1997). However, genetic studies on tropical trees (Caron et al., 2000; Dutech et al., 2004, 2000, 2003) and rodents (Steiner and Catzeflis, 2003; Van Vuuren et al., 2004) provided preliminary information on the genetic geographical structure of species within French Guiana that fit only partially with this refugia hypothesis.

The available evidence of usually strong phylogeographic structure in amphibians supports their use as model group to understand patterns of local differentiation and endemism. We tested the hypothesis of high cryptic genetic and species diversity in French Guiana by studying two widely distributed and abundant groups of frog species, the *Scinax ruber* group and the *Rhinella margaritifera* group: the genus *Scinax* is distributed from southern Mexico to eastern Argentina and contains 86 described species of treefrogs (Frost, 2004). Eight previously described species are currently considered to inhabit French Guiana (Table 2.1). *S. ruber*, *S. cruentommus*, and *S. x-signatus* are widely distributed species throughout the Guianas and Amazonia and are suspected to be of unresolved species status throughout their range (De la Riva et al., 2000; Duellman and Wiens, 1993; Frost, 2004; Lescure and Marty, 2000). *Scinax ruber* and *S. boesemani* inhabit open areas whereas *S.*

cruentommus, *S.* sp. 1 and *S. x-signatus* inhabit the rainforest. The *Rhinella margaritifera* group is distributed throughout Amazonia and the Guianas and comprises 14 described species of toads (Frost, 2004) that all inhabit the rainforest floor. Morphological analyses of specimens from all over South America indicated that this complex may contain many undescribed species, most having small, allopatric distributional ranges (Hoogmoed, 1990). De la Riva et al. (2000) citing Hoogmoed (1990) and Hass et al. (1995), suggests that four species could exist in Bolivia alone, while Vélez-Rodríguez (2004) hypothesizes that no less than 15 species occur in Colombia. Hass et al. (1995) and recently Pramuk (2006) revealed the existence of a multitude of genetic lineages in this group. Hass et al. (1995) used quantitative immunological techniques and confirmed the presence of two different species in French Guiana: one with pronounced cranial crests (*R. margaritifera sensu stricto*), and a second one without crests (*Bufo typhonius* group sp.1 in Lescure and Marty (2000)). Hoogmoed (1990) further suggested that a third species, of smaller size and with a sharper nose and different call inhabits French Guiana (Lescure and Marty, 2000). More recently, Haas (2004) suggested the occurrence, in the northern part of French Guiana, of three sympatric species of the group, without providing evidence, however.

Here, we apply an integrative phylogenetic and phylogeographic approach using mitochondrial (16S and 12S rDNA) and nuclear data (18S rDNA and tyrosinase) to test whether or not the current species delimitations are consistent with the molecular phylogenetic history. The comparison of the patterns given by these different sets of molecular markers can be meaningful for species delineation and to infer information about their evolutionary history and their relationships.

2. Materials and methods

2.1. Biological samples

Tissue samples (liver or muscle) of 41 *Scinax ruber*, 12 *S. x-signatus*, 10 *S. boesemani*, 21 *S. cruentommus*, 8 *S.* sp. 1, 2 *S. jolyi*, 2 *S. proboscideus*, 3 *S. nebulosus*, 1 *Dendropsophus nanus*, 1 *D. leucophyllatus*, 1 *Sphaenorhynchus lacteus*, 52 *Rhinella margaritifera*, 1 *Rhaebo guttatus*, 1 *Chaunus granulosus*, 1 *Dendrophryniscus minutus*, 1 *Atelopus flavescens*, and 1 *Atelopus barbotini* (see Noonan and Gaucher, 2005) were obtained from different localities of French Guiana (Fig. 2.1; Table S2.1). Sequences of 14 of the hylid samples have already been published in Salducci et al. (2002, 2005). In addition, six *Scinax cruentommus* and five *Rhinella margaritifera* tissue samples were collected by Philippe Gaucher (DIREN Mission Parc French Guiana), four additional samples of *S. ruber* from

Ecuador were sampled by Kathryn Elmer and one was provided by the Netherlands Museum of Natural History. A sample of *Scinax elaeochrous* from Costa Rica was made available from the tissue collection of the Museum of Vertebrate Zoology (Berkeley), and a sample of *S.* sp. 2 from Colombia was provided by Adolfo Amézquita. Further sequences available from GenBank (40 mitochondrial and 26 nuclear sequences) were included as well (Table S2.1).

Identifications of specimens were mainly based on the only available comprehensive reference on anurans of French Guiana (Lescure and Marty, 2000). However, the taxonomy used by these authors may in some aspects be conflicting with the classification used in other parts of the Neotropics. For example, *Scinax x-signatus* is described by many authors (e.g. Bourne and York, 2001; Gorzula and Señaris, 1998; Hoogmoed, 1979) as an inhabitant of open areas that has been often and is still confounded with *S. ruber* (Gorzula and Señaris, 1998). In contrast, in French Guiana, *Scinax x-signatus* is considered to be an explosive breeder restricted to forests. Moreover, Gorzula and Señaris (1998) provide a drawing of this species that does not seem to correspond to the species in French Guiana. Similar doubts exist for the validity of *Scinax cruentommus* for French Guianan populations. We also use the name *Scinax* sp. 1 from Lescure and Marty (2000) for a *Scinax* species that remains to be identified or described. However, these taxonomic uncertainties do not invalidate any of the conclusions from the work presented here.

Based on our personal observations in the field, we used the term "syntopic" for lineages breeding exactly in the same spot or only few meters away from each other, "sympatric" for lineages occurring in at least one shared locality but which have not been observed in the exact same place and "allopatric" for lineages that do not share any locality.

2.2. DNA protocols

Total DNA was extracted with standard phenol–chloroform methods. Two mitochondrial (mt) and two nuclear (nu) DNA fragments were amplified by standard PCR techniques. Primers used for amplification were those described by Salducci et al. (2005) for 16S and 12S, by Bossuyt and Milinkovitch (2000) for tyrosinase, and by Miquelis et al. (2000) for 18S rDNA. The chosen molecular markers previously have been used successfully to assess the relationships among orders, families and species of amphibians (Hay et al., 1995; Ruvinsky and Maxson, 1996; Vences et al., 2000). For nuclear markers it is of foremost importance to ascertain that orthologous and not paralogous genes are analysed. According to Hoegg et al. (2004) only one copy of the tyrosinase gene exists in tetrapods, and we are therefore confident that our analysis is based on orthologous gene fragments for all samples.

PCR was performed as described in Salducci et al. (2005). Furthermore, 66 sequences of 570 bp of the mitochondrial cytochrome *b* gene were obtained for a subset of *Scinax* species to obtain higher support for a conflicting phylogenetic analysis see below; primers used were: MVZ15-L, MVZ18-H, MVZ25-L (Moritz et al., 1992). Sequences were resolved on automated DNA sequencers (ABI 3700).

2.3. Molecular analysis

Preliminary alignment of the sequences was performed with Clustal X (Thompson et al., 1997) with an opening gap cost equal to 6. Each alignment was compared with available secondary structures (12S and 16S) (Van de Peer et al., 1998) as described in Salducci et al. (2002), or with the reading frame (tyrosinase). The analyses were performed on 368 (*Scinax*)-387 (*Rhinella*) aligned bp of the 12S rDNA gene, 413–411 bp of the 16S rDNA gene, 388–539 bp of the tyrosinase gene and 1299–1325 bp of the 18S rDNA gene. We used Gblocks 0.91b (Castresana, 2000) to eliminate poorly aligned positions of the mitochondrial sequences of ambiguous homology for phylogenetic analysis (45 bp for *Scinax* and 34 bp for *Rhinella*). All sequences obtained in this study have been deposited in GenBank (Table S2.1; EF217430–EF372235).

2.3.1. Phylogenetic analyses

To test if analyses of combined DNA sequences of different genes can be conducted, the partition homogeneity test (PHT) (Farris et al., 1994) was used to compare the two mitochondrial genes (12S and 16S) and the two nuclear genes (tyrosinase and 18S), and to compare nuclear with mitochondrial genes.

Saturation plots were constructed in order to determine whether particular positions or classes of substitutions needed to be weighted or excluded prior to phylogenetic analyses (Grant and Kluge, 2003). We visualized the saturation by plotting the distance in transitions and transversions versus the total distance.

Bayesian phylogenetic analysis was performed with MrBayes 3.1 (Ronquist and Huelsenbeck, 2003). Maximum likelihood (ML) trees were calculated using PAUP, version 4.0b10 (Swofford, 2002). The distance matrixes were computed with MEGA 2.1 (Kumar et al., 2001). We used the software Modeltest version 3.6 (Posada and Crandall, 1998) to choose the substitution model that best fits our data using the AIC criterion. These models were subsequently used for Bayesian and ML analyses. Each Bayesian analyses consisted of $2.0*10^7$ generations with a random starting tree and four Markov chains (one cold) sampled

every 1000 generations. Adequate burn-in was determined by examining a plot of the likelihood scores of the heated chain for convergence on stationarity.

Confidence in the phylogenetic grouping for ML was assessed by the bootstrap method (Efron, 1979; Felsenstein, 1985) with 1000 pseudoreplicates with the heuristic search option, tree bisection reconnection branch swapping (TBR) and 10 random taxon addition replicates. Trees were rooted on *D. leucophyllatus*, *D. nanus*, and *S. lacteus* for *Scinax* and on *D. minutus*, *A. flavescens* and *A. barbotini* for *Rhinella*.

The partition homogeneity test did not reject the null hypothesis of congruence between mitochondrial 12S and 16S fragments (*Scinax* $P=0.239$; *Rhinella* $P=0.516$) nor between nuclear tyrosinase and 18S fragments (*Scinax* $P=0.68$; *Rhinella* $P=1$) indicating the possibility for their combined analysis. The test did reject the null hypothesis of congruence of the included mitochondrial vs. nuclear fragments for *Scinax* ($P=0.028$), but not in *Rhinella* ($P=1$).

Consequently, we used the following data partitions:

1. 12S+16S for phylogeny using all the haplotypes without ambiguously aligned positions and for phylogeography using all the individuals and all the positions.

2. Tyrosinase and 18S for phylogeny using only one representative for each clade previously identified in the mitochondrial trees, and because we obtained only a few 18S sequences for each clade.

3. Tyrosinase for phylogeography using all the individuals.

2.3.2. Phylogeography

Statictical parsimony networks were calculated using TCS 1.21 (Clement et al., 2000), with a 95% connection limit, separately on the mitochondrial genes and on the nuclear gene (tyrosinase). Our sampling being heterogeneous and scarce particularly for some remote populations, we considered it to be too premature to infer significance of the phylogeographical patterns observed by statistical tests such as Nested Clade Analyses. Because some haplotypes and haplogroups were not connected to each other with the 95% limit of probability of parsimony as used by TCS, we attempted to connect these haplotypes by decreasing the connection probability up to a minimum of 90%.

3. Results

3.1. Phylogenetic analyses

One hundred and six 16S rDNA and 106 12S rDNA, 100 tyrosinase and 17 18S sequences were available for the analysis of *Scinax* (including outgroups). Sixty-five 16S rDNA and 65 12S rDNA, 55 tyrosinase and nine 18S sequences were available for the *Rhinella margaritifera* group (including outgroups). Of all the samples, only five samples of *Scinax ruber*, two of *S. cruentommus*, three of *R. margaritifera* and *C. granulosus* have not been sequenced for the tyrosinase fragment (Table S2.1).

3.1.1. Phylogenetic analysis of Scinax

Hierarchical likelihood tests implemented in Modeltest (Posada and Crandall, 1998) selected a GTR+I+G substitution model as best fitting the combined mitochondrial data with base frequencies (A=0.3439; C=0.2277; G=0.1858) and substitution matrix (5.1976; 14.8577; 8.7883; 1.3455; 42.3624; 1) estimated from the data, a proportion of invariable sites of P invariant=0.2511 and a gamma distribution shape parameter of α=0.5217. For the combined nuclear data a HKY+I+G substitution model was determined to be the best model with base frequencies (A=0.2291; C=0.2499; G=0.2852), a Tratio=2.1720 estimated from the data, a proportion of invariable sites of P invariant=0.7466 and a gamma distribution shape parameter α=0.9939. Relationships among lineages of the *Scinax ruber* species group were poorly resolved with the mitochondrial data. However, all species previously identified correspond to homophyletic lineages except for *S. ruber*. Indeed, six lineages appeared within this species (Fig. 2.2a): four in French Guiana, one formed by the haplotype from Ecuador and one by the haplotype from Peru. The haplotype from Guyana clustered with one from French Guiana (*S. ruber* C).

The taxon *Scinax ruber* C nested within the *S. ruber* A clade in the tree obtained by Bayesian analyses, although support from posterior probability was low, position of this group was unsupported with ML and displayed a long branch. To solve this uncertainty, we performed an additional analysis adding 570 bp of the cytochrome *b* to a mitochondrial dataset comprising *Scinax ruber* A, B, C, *S. x-signatus* and *S. nasicus*, and rooted with *S. cruentommus* (a partition homogeneity test of cytochrome *b* vs. 12S+ 16S resulted in *P*=1). The best model fitting the combined data following the AIC criterion was TVM+G (base composition (A=0.226; C=0.233; G=0.219); substitution matrix (0.614; 8.512; 2.246; 0.205; 8.512); gamma distribution shape parameter α=0.1796). This combined analysis unambiguously supported the separate position of *S. ruber* C under all methods of tree reconstruction used (Fig. 2.2b).

One individual identified as *Scinax x-signatus* had a haplotype belonging to the lineage of *S. ruber* C (not marked in Fig. 2.2 but see below). *Scinax ruber* E was strongly divergent from the other lineages of *S. ruber* (*p* distances 0.136–0.143) and grouped without ambiguity with *S. fuscovarius*. *Scinax ruber* A emerges as sister taxon of *S. x-signatus* with high support (96/78) (Fig. 2.2b), and with a low genetic distance (pairwise distance between *S. ruber* A and *S. x-signatus* = 0.006; see Table 2.2a). Based on these results, *Scinax ruber* is determined to be a paraphyletic taxon. Furthermore, two distinct lineages can also be distinguished within *S. boesemani* (Fig. 2.2a).

Based on nuclear data, *Scinax x-signatus* is unambiguously placed outside the *S. ruber* A+B clade. Hence, the relative positions of *S. ruber* A, B, C and *S. x-signatus* are incongruent between the nuclear and mitochondrial topologies (Fig. 2.2a–c). A Shimodaira–Hasegawa (Shimodaira and Hasegawa, 1999) test clearly showed significant differences between the likelihoods of these topologies (for the nuclear dataset *p*=0.02 and for the mt dataset *p*=0.003).

3.1.2. Phylogenetic analysis of Rhinella

Modeltest selected a GTR+I+G substitution model as best fitting the combined mitochondrial data with base frequencies (A=0.3208; C=0.2219; G=0.1859) and substitution matrix (8.4255; 34.9686; 26.6056; 0; 121.2654) estimated from the data, a proportion of invariable sites of *P* invariant=0.2919 and a gamma distribution shape parameter of 0.4109. For the combined nuclear data a TrN+I substitution model best fitted the data, with base frequencies (A=0.2368; C=0.2528; G=0.2745) and substitution matrix (1; 2.6127; 1; 1; 5.2347) estimated from the data and a proportion of invariables sites of *P* invariant=0.8306.

The *Rhinella margaritifera* species group + "*Bufo*" *ocellatus* form a monophyletic group ("*B. ocellatus*" is supported as the sister taxon of the *R. margaritifera* species group according to Pramuk (2006)) of 14 divergent lineages (Fig. 2.3a). The most basal lineage, *Rhinella margaritifera* E, corresponds to "*Bufo typhonius*" sp. 1, and *R. margaritifera* A corresponds to *B. margaritifer* of Lescure and Marty (2000). *Rhinella margaritifera* is paraphyletic due to the relative positions of *R. dapsilis*, *R. castaneotica*, "*Bufo*" *ocellatus* and the different lineages of *R. margaritifera*. *Rhinella margaritifera* D has been identified by two of us (CM and MB) as "*Bufo typhonius*" sp. 1 because the individuals lack cranial crests. Except the fact that *Rhinella margaritifera* A, B, and C could not be distinguished based on nuclear markers there was no incongruence between the nuclear and mitochondrial data (Fig. 2.3b).

3.2. Phylogeography

The TCS analysis of the mitochondrial data from the *Scinax ruber* species group produced six unconnected haplotype networks (Fig. 2.4, see also Fig. S2.1). For the lineages *Scinax ruber* A, *S. ruber* B and *S. x-signatus* we performed an independent network reconstruction to estimate which haplotypes are ancestral. Locations of the haplotypes and their connections have been reported on the maps when a geographic structure of genetic variation was obvious, whereas only the distribution of the general lineages is plotted on the maps when no obvious structure could be observed. With nDNA there were three unconnected haplotype networks for the *Scinax ruber* species group (Fig. 2.5). The same analysis of mitochondrial data from the *Rhinella margaritifera* group produced three unconnected haplotype networks (Fig. 2.6) and one with nDNA (Fig. 2.7). Ambiguous sites of the tyrosinase fragment due to heterozygosity, had to be coded as N, which explains the multiple connections seen in the nuclear networks.

Pairwise distances in the mitochondrial rRNA genes between haplotypes of the various major lineages from French Guiana (not considering introgressions) were 1.3–14.3% in *Scinax ruber*, and 1–5.1% in the *Rhinella margaritifera* group (Table 2.2).

3.2.1. Phylogeography of Scinax lineages

3.2.1.1. MtDNA

Sequences of *Scinax ruber* are divided into six clades (Fig. 2.4). The *S. ruber* haplotype from Peru appears to belong to a taxon closer to *S. ruber* B and *S. ruber* A plus *S. x-signatus* (Fig. 2.4). It connected (with a 94% connection limit) with *S. ruber* A by at least 13 mutational steps and by at least 14 mutational steps with both *S. ruber* B and *S. x-signatus*. *S. ruber* C connected with *S. ruber* A (with a 90% connection limit) by at least 22 steps. The haplotype from Guyana connected with *S. ruber* C by at least six mutational steps. *S. boesemani* is divided into two clades separated by ten mutational steps. Geographic structure of mitochondrial haplotypes was found among different sister lineages: *Scinax ruber* A appeared to be mainly distributed in the north-east of French Guiana, *S. ruber* B and *S. ruber* E in the central north near the coast. *Scinax boesemani* G was restricted to the west while *S. boesemani* F was more widespread over the north part of French Guiana (Fig. 2.4).

Within-group variation is geographically structured for *Scinax ruber* A (Fig. 2.4) to the east and along Oyapock River and also for *S. boesemani* F. *Scinax ruber* C has only been

found along major rivers. *S. x-signatus*, *S. ruber* B, and *S. ruber* E are weakly structured (Fig. 2.4) and there is no clear pattern for *S.* sp. 1 and *S. cruentommus* (not shown).

3.2.1.2. Nuclear DNA

The clades here defined as *Scinax ruber* A and B share one haplotype in the nuclear data set and therefore cannot be clustered separately. Similarly, the two individuals constituting *S. boesemani* G are not clearly segregated from *S. boesemani* F even if they have two unique haplotypes. The *S. x-signatus* individual which, by mitochondrial data, is nested within *S. ruber* C was affiliated to *S. x-signatus* in the tyrosinase network (Fig. 2.5). This network clearly shows a position of *S. x-signatus* outside the clade *S. ruber* A+B.

3.2.2. Phylogeography of Rhinella lineages
3.2.2.1. MtDNA

The five clades in the *Rhinella margaritifera* species group occuring in French Guiana, as identified in the phylogenetic analyses, were also retrieved in the haplotype networks. *Rhinella margaritifera* A comprises ten haplotypes (Fig. 2.6). *Rhinella margaritifera* B comprises two individuals separated from RMA by seven mutational steps. *Rhinella margaritifera* C is composed by one haplotype and by two individuals originating from the extreme south of French Guiana (connection to *R. margaritifera* A9 by 15 steps with 92% connection limit). Geographically, *Rhinella margaritifera* A haplotypes show a pattern in which the central, putatively ancestral haplotype (A1) is distributed along the northern strip of French Guiana (Fig. 2.6). In *Rhinella margaritifera* E, the pattern is less clear but the central, putatively ancestral haplotype (E1) seems to be more widely distributed, at least from central to northern French Guiana. However, a clear structure is shown by populations along the Oyapock River.

3.2.2.2. Nuclear DNA

Rhinella margaritifera B shares two different nuclear haplotypes with *R. margaritifera* A (Fig. 2.7). These two nuclear haplotypes correspond to individuals with mt haplotypes of *R. margaritifera* A but sampled in the vicinity of *R. margaritifera* B (near Kaw mountain). *Rhinella margaritifera* C shares the nuclear haplotypes with *R. margaritifera* A, which is its central haplotype. However, one site that is likely heterozygous (C and G) in the tyrosinase sequences of the two individuals constituting *R. margaritifera* C reveals that one allele is only shared by these two individuals.

4. Discussion

4.1. New lineages and new species

A precise and correct delimitation of species is essential as species are basic units of analysis in biogeography, ecology, macroevolution, biodiversity assessment and conservation. Over- or under-resolving species boundaries can lead to wrong interpretations (Sites and Marshall, 2003, 2004).

The straightforward use of the phylogenetic species concept can lead to view species not as real evolutionary entities (Goldstein et al., 2005, 2000). As advocated by Frost and Hillis (1990), for amphibians and reptiles, it would be more appropriate to consider amphibian species as monophyletic group of populations that are likely to be on independent phylogenetic trajectories under an evolutionary species concept (Wiley, 1978). In this way, one crucial point in delimiting cryptic species is to distinguish between broad admixture on one hand, and narrow contact zone or restricted hybridization on the other hand (Wake and Jockusch, 2000). Moreover, diagnostic nucleotide sites of mitochondrial haplotypes in a character-based approach to species delineation (Goldstein et al., 2005) could contradict information from nuclear genes as it has been often found in amphibians (e.g. Garcia- Paris et al., 2003; Kuchta and Tan, 2005; Monsen and Blouin, 2003; Sequeira et al., 2005; Wake and Jockusch, 2000; Zangari et al., 2006). Thus, species borders are better understood using a combination of different kinds of markers as underlined by Moritz (1994a,b).

In the present cases, concordance between the coalescence criterion and the isolation criterion (de Queiroz, 1998) can be employed to assume that several cryptic species are present in *S. ruber* and *R. margaritifera*. Indeed, there is no observed overlap between mitochondrial and nuclear haplotype lineages identified despite sympatry. It is rather between different species that we observed potential gene flow or remains of ancestral polymorphism, as between *S. ruber* C and *S. x-signatus*. Nevertheless, if gene flow exists between the different identified lineages of *Scinax* and *Rhinella*, it appears to be limited. Moreover, the basal position of the mitochondrial haplotype of *Scinax ruber* from Ecuador and the haplotypes of *Rhinella margaritifera* from Brazil, Ecuador and Peru provide evidence that these lineages may be representatives of different species as compared to the ones present in French Guiana.

Rhinella margaritifera D probably corresponds to a species whose existence has already been suggested by Hoogmoed (1990) even if we did not notice any immediate diagnostic characters in morphology or bioacoustics to distinguish it from *R. margaritifera* E.

We note that the morphology of *R. margaritifera* D is close to *R. margaritifera* E with respect to body size and absence of cranial crests, whereas it unambiguously is sister to a clade containing *R. margaritifera* A, B, and C based on molecular data. Thus, the presence of cranial crests in *R. margaritifera* A, B, and C is probably a synapomorphy of these three lineages.

Ambiguity remains whether *Scinax ruber* A and B should be considered different species, and the same applies to *R. margaritifera* A, B, and C. Clear genetic differences exist in mtDNA (distance: seven steps and *d*=0.013 between *S. ruber* A and B, seven steps and *d*=0.01 between *R. margaritifera* A and B, and 15 steps and *d*=0.02 between *R. margaritifera* A and C) which corresponds to different geographical ranges (Fig. 2.6). However, tyrosinase, the nuclear marker, showed no clear divergences (Fig. 2.7). The size of the fragment and the slower rate of evolution of the tyrosinase gene and slower stochastic lineage sorting are the main reasons for the lack of resolution of this nuclear marker compared with mitochondrial data. Given that these lineages present basically similar morphologies (based on external character identification), it seems obvious that they share ancestral polymorphism and retain some features of their ancestor's morphology (Jarman and Elliott, 2000). However, the position of *S. x-signatus*, for which the specific status is clear based on ecology and morphology, as sister taxon of *S. ruber* A (in mtDNA) without overlap in nuclear DNA lineages despite sympatry illustrates that even low genetic distances of mtDNA between groups may separate different species. The same applies for *R. dapsilis* which is the sister taxon of *R. margaritifera* A+B. We should also add that standard haplotypic diversity within species for which there is no ambiguity on their status in French Guiana such as *S. cruentommus* or *R. margaritifera* E "*typhonius*" is not higher than those for each cluster of *S. ruber* A, and B, and *R. margaritifera* A. The similar degree of diversity within these entities tends to indicate that they should be considered on a similar taxonomic status.

Amphibians are often characterized by high genetic differentiation, and intraspecific pairwise divergences of the mitochondrial rRNA (12S and 16S) genes have been found extending up to almost 6% (Vences et al., 2005a,b). However, in most comparisons among conspecific populations values were lower, and divergences of 4–5% usually were indicative of distinct species. Pairwise divergences of around 5% distinguish several of the lineages identified herein, for instance, *Scinax ruber* D from other *S. ruber* lineages, and *Rhinella margaritifera* E from other lineages in the species group. *Scinax ruber* E is even distinguished by divergences around 14% from all other lineages assigned to *S. ruber*. These divergences are therefore at a level that also in other amphibian groups has been observed to characterize

distinct species. Defining new species on the basis of their genetic distances on a single DNA fragment is strongly debated (Meyer and Paulay, 2005) as some species might arise within a very short time frame (as cichlids, e.g. Joyce et al., 2005; Salzburger and Meyer, 2004) and/or hybridize. However, over a threshold, the distances between lineages can certainly be used as a preliminary indicator to identify candidate species (Vences et al., 2005a).

On the other hand, in our data set, several lineages that are sympatric or even syntopic and show no haplotype sharing in either nuclear or mitochondrial genes have much lower divergences, such as *S. ruber* A compared to *S. x-signatus*. This is one of the most convincing examples demonstrating how recently diverged lineages of amphibians should be considered to be species and co-occur due to ecological differences (occurrence in savanna vs. forest; see below), and cautions once more against the uncritical use of pairwise divergences as sole indicator of species status.

4.2. Geographical considerations

If we interpret the six steps connecting the Guyana haplotype as variation within the same species (*S. ruber* C, Fig. 2.4), the comparison with the Peru haplotype branching outside *S. ruber* A and B and connected by a minimum of 13 steps, suggests further that *S. ruber* C and *S. ruber* A+B have independent biogeographical histories over South America. Additional sampling is also necessary to investigate whether *S. boesemani* might contain two sister species in French Guiana.

The restricted geographical distribution of *S. ruber* B and *S. ruber* E in central-northern French Guiana could indicate that they are lineages endemic to the region. It seems unlikely that they belong to described species of the *S. ruber* species group, which, so far, have remained undetected in French Guiana. The *S. ruber* E lineage has a small range near the towns Cayenne and Kourou, which could be seen as an indication of human introduction. However, the haplotype diversity observed in this lineage suggests a substantially long evolutionary history within French Guiana.

The comparison of the patterns among phylogroups in *S. ruber* and *R. margaritifera* reveals a rough similarity (Fig. 2.1), and the genetic distances between the respective lineages are identical (7 mutational steps, $d \geq 1\%$). The mitochondrial network pattern shown by *R. margaritifera* A is geographically sufficiently clear to suggest an evolutionary scenario. This lineage could have expanded from an ancestral range isolated in the northern part of French Guiana. This could be due to a forest refuge isolated by savannas (De Granville, 1982; Haffer, 1997) or by rising sea level (Nores, 1999) during the Quaternary. The location, in the north-

east of French Guiana, of an undisturbed area that could have acted as a refugium for forest species has been suggested by De Granville (1982). Dutech et al. (2004) found some support for this hypothesis in the genetic structure of the tree *Vouacapoua americana*.

This hypothesis implies survival of many populations of *R. margaritifera* A around the northern part of French Guiana despite perturbations during the Holocene. Scattered distributions of refugial zones could increase structure by genetic drift without erasing the initial footprint generated by a Pleistocene expansion. Patterns of genetic variation are less structured in *R. margaritifera* E, *S. ruber* A, and *S. boesemani* F. Nevertheless, they show a pattern that could be interpreted as an expansion to the east from a central origin for *R. margaritifera* E and *S. ruber* A, and from a northwestern origin for *S. boesemani* F. The patterns follow particularly the Oyapock River to the southeast.

4.3. Hybridization in Scinax

Two types of discordances were discovered in the molecular data set for *Scinax*, patterns that could be explained by past or present hybridization events. The discordance among the nuclear and the mitochondrial genes trees for the position of *S. x-signatus* probably results from a past hybridization event. We assume that the mitochondrial genome of *S. x-signatus* has been introgressed by an ancestor of the current *S. ruber* A lineage relatively recently. After the hybridization event, lineage sorting proceeded in opposite directions for mitochondrial and nuclear molecules. Specimens of *S. x-signatus* sampled here retained (1) the original *S. x-signatus* tyrosinase haplotypes, and (2) the mitochondrial molecules originally from *Scinax ruber* which are today slightly differentiated from the mt haplotypes in *S. ruber* A (3 steps). The high nuclear distance between *S. x-signatus* and the *S. ruber* A, B, and C lineages in the nuclear phylogeny (d=1.6%) is in agreement with its morphological and ecological particularities (explosive forest breeder, bigger in size and different in coloration). Mitochondrial alleles might be expected to introgress faster, on average, than nuclear loci if their persistence in a foreign gene pool is less constrained by linkage to selected loci than are the alleles of nuclear genes (Funk and Omland, 2003; Harrison, 1993). Smaller Ne of mtDNA may facilitate the fixation of an introgressed haplotype such that even low levels of introgression may be sufficient to establish a neutral mitochondrial haplotype in a foreign population (Takahata and Slatkin, 1984). The fact that *S. x-signatus* mitochondrial haplotypic diversity is lower than nuclear diversity (two haplotypes on mtDNA and four haplotypes on nDNA) also supports this scenario. The ranges of *S. ruber* A and *S. xsignatus* overlap at least in northwestern French Guiana around the swamps of Kaw. Here these two species are largely

sympatric and genetically are reciprocally monophyletic in mitochondrial as well as nuclear markers. About their habitat, we know that *S. ruber* inhabits mainly open areas whereas *S. x-signatus* lives mostly in rainforests. In reproductive behavior, according to data from Guyana (Bourne, 1992) and our observations, *S. ruber* has an opportunistic reproductive phenology whereas *S. x-signatus*, in French Guiana, is a rather explosively breeding species. Thus, ecological factors such as habitat and reproductive phenology may prevent current hybridization.

On the other hand, our data possibly indicate ongoing or very recent hybridization between *S. x-signatus* and *S. ruber* C. This was inferred from the specimen *S. x-signatus* X4 that connects respectively to *S. ruber* C1 in the mitochondrial dataset (Fig. 2.4) and to *S. x-signatus* in the nuclear dataset (Fig. 2.5). It is particularly difficult to distinguish between incomplete lineage sorting and introgression between sister taxa. Therefore, incomplete lineage sorting for nuclear alleles is an alternative explanation of this incongruence especially since the nuclear haplotype concerned is unique.

4.4. Hybridization and polyspecificity: two pitfalls for biodiversity estimation

In this study, we detected several instances of polyphyletic species that require taxonomic revision and incongruent patterns between mtDNA and nuDNA phylogenetic signals that might be caused by introgressive hybridization and current hybridization or incomplete lineage sorting.

These examples illustrate a complex evolutionary history as found in studies of other taxa (e.g. Patton and Smith, 1994; Sota and Vogler, 2001). It is also another warning that the exclusive use of mitochondrial data could lead to wrong interpretations because of introgression and differential lineage sorting (Ballard and Whitlock, 2004; Meyer et al., 2006).

On the other hand, the systematics among closely related species requires dense taxonomic and geographic sampling. For example, the two already published mitochondrial sequences of *S. ruber* (from Peru and Guyana; Darst and Cannatella, 2004; Faivovich et al., 2004) correspond to two different lineages, one of which is present in French Guiana (*S. ruber* C) (Fig. 2.4). These examples illustrate a complex evolutionary history probably due to multiple and successive vicariance events in South America as also observed in other taxa (e.g. Patton and Smith, 1994; Sota and Vogler, 2001), demonstrating the importance of sampling multiple localities for related species in a combined phylogenetic/phylogeographic approach (Funk and Omland, 2003).

As stated by Funk and Omland (2003), species level polyphyly and paraphyly are much more common phenomena than generally recognized and partially reflect the inadequacy of taxonomy to represent the underlying genetic structure of populations and species. Based on our data, it seems obvious that the number of actual species has so far been underestimated in Guianan anurans. These results also emphasize that cryptic morphological evolution of these groups is widespread and results in the discordance between morphological identification and evolutionary histories. Anuran biodiversity is more reliably estimated by an integrative approach that includes a routine molecular inventory through DNA barcoding in concert with morphological and bioacoustic techniques (Vences et al., 2005a,b). However, the isolated use of DNA sequences, without knowledge about the ecology, morphology and reproductive biology of the animals, will not allow one to reliably discern how often widespread "species" of amphibians are in fact amalgams of various reproductively isolated species.

5. Conclusion

This study suggests the existence of previously unknown lineages/taxa in French Guiana for the *Scinax ruber* species group and in the *Rhinella margaritifera* species group. The general lack of genetic admixture among lineages both regarding mitochondrial and nuclear genes, with only occasional evidence for introgression, together with the sympatric occurrence of many of the lineages identified, is an indication that some of the genetic lineages correspond to new species under an evolutionary species concept (Wiley, 1978) and even under a biological species concept (Mayr, 1942). The combination of simultaneous phylogeographic analysis of mitochondrial and nuclear data as employed here provides an efficient approach towards a better estimation of the biodiversity within widely distributed Neotropical frogs. With the amphibians of the Guianas being particularly poorly known, Young et al. (2004) stated that it is clear that many more amphibian species remain to be discovered as compared to birds and mammals. Amphibian endemism of the Guianan region might be higher than previously thought and biogeographic interpretations based on species distributions and areas of endemism might need to be reassessed.

Stuart et al. (2004) asserted that the global amphibian decline is particularly worrying for Neotropical species. Given that numerous species still remain undetected, it is alarming to think that the situation could be in fact even worse than thought. If additional studies indicate polyspecificity of many existing species, conservation efforts would need to be reevaluated accordingly.

References

Avise, J.C. 2000. *Phylogeography: The history and formation of species*. Harvard University Press.

Ballard, J.W.O., Whitlock M.C. 2004. The incomplete natural history of mitochondria. *Molecular Ecology*, **13**, 729–744.

Biju, S.D., Bossuyt, F., 2003. New frog family from India reveals an ancient biogeographical link with the Seychelles. *Nature*, **425**, 711–714.

Blaustein, A.R., Wake, D.B., Sousa, W.P. 1994. Amphibian declines—judging stability, persistence, and susceptibility of populations to local and global extinctions. *Conservation Biology*, **8**, 60–71.

Borkin, L.Y., Litvinchuk, S.N., Rozanov, Y.M., Skorinov, D.V. 2004. On cryptic species (from the example of amphibians). *Zoologichesky Zhurnal*, **83**, 936–960.

Bossuyt, F., Meegaskumbura, M., Beenaerts, N., Gower, D.J., Pethiyagoda, R., Roelants, K., Mannaert, A., Wilkinson, M., Bahir, M.M., Manamendra-Arachchi, K., Ng, P.K.L., Schneider, C.J., Oommen, O.V., Milinkovitch, M.C. 2004. Local endemism within the western Ghats—Sri Lanka biodiversity hotspot. *Science*, **306**, 479–481.

Bossuyt, F., Milinkovitch, M.C. 2000. Convergent adaptive radiations in Madagascan and Asian ranid frogs reveal covariation between larval and adult traits. *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 6585–6590.

Boujard, T., Pascal, M., Meunier, J.F., Le Bail, P.Y. 1997. *Poissons de Guyane. Guide ecologique de l'Approuague et de la réserve des Nouragues*. INRA editions, Paris, 219 p.

Bourne, G.R. 1992. Lekking behavior in the Neotropical frog *Ololygon rubra*. *Behavioral Ecology and Sociobiology*, **31**, 173–180.

Bourne, G.R., York, H. 2001. Vocal behaviors are related to non-random structure of anuran breeding assemblages in Guyana. *Ethology Ecology and Evolution*, **13**, 313–329.

Caron, H., Dumas, S., Marque, G., Messier, C., Bandou, E., Petit, R.J., Kremer, A. 2000. Spatial and temporal distribution of chloroplast DNA polymorphism in a tropical tree species. *Molecular Ecology*, **9**, 1089–1098.

Castresana, J. 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution*, **17**, 540–552.

Charles-Dominique, P., Blanc, P., Larpin, D., Ledru, M.P., Riera, B., Sarthou, C., Servant, M., Tardy, C. 1998. Forest perturbations and biodiversity during the last ten thousand

years in French Guiana. *Acta Oecologica, International Journal of Ecology*, **19**, 295–302.

Chek, A.A., Austin, J.D., Lougheed, S.C. 2003. Why is there a tropical temperate disparity in the genetic diversity and taxonomy of species? *Evolutionary Ecology Research*, **5**, 69–77.

Chek, A.A., Lougheed, S.C., Bogart, J.P., Boag, P.T. 2001. Perception and history: molecular phylogeny of a diverse group of neotropical frogs, the 30-chromosome *Hyla* Anura: Hylidae. *Molecular Phylogenetics and Evolution*, **18**, 370–385.

Cherry, L.M., Case, S.M., Wilson, A.C. 1977. Relative rates of morphological evolution in primates, carnivores and frogs. *American Zoologist*, **17**, 910.

Chiari, Y., Vences, M., Vieites, D.R., Rabemananjara, F., Bora, P., Ravoahangimalala, O.R., Meyer, A. 2004. New evidence for parallel evolution of colour patterns in Malagasy poison frogs (*Mantella*). *Molecular Ecology*, **13**, 3763–3774.

Clement, M., Posada, D., Crandall, K.A. 2000. TCS: a computer program to estimate gene genealogies. *Molecular Ecology* **9**, 1657–1659.

Crawford, A.J. 2003. Huge populations and old species of Costa Rican and Panamanian dirt frogs inferred from mitochondrial and nuclear gene sequences. *Molecular Ecology*, **12**, 2525–2540.

Darst, C.R., Cannatella, D.C. 2004. Novel relationships among hyloid frogs inferred from 12S and 16S mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, **31**, 462–475.

De Granville, J.-J. 1988. Phytogeographical characteristics of the Guianan forests. *Taxon*, **37**, 578–594.

De Granville, J.-J. 1982. Rain forest and xeric flora refuges in French Guiana. In: Prance, G.T. (ed.), *Biological diversification in the tropics*. Columbia University Press, pp. 159–181.

De la Riva, I., Köhler, J., Lötters, S., Reichle, S. 2000. Ten years of research on Bolivian amphibians: updated checklist, distribution, taxonomic problems, literature and iconography. *Revista Española de Herpetologìa*, **14,** 19–164.

de Queiroz, K. 1998. The general lineage concept of species, species criteria, and the process of speciation. In: Howard, D.J. and Berlocher, S.H. (eds.), *Endless Forms: Species and Speciation*. Oxford University Press, pp. 57–75.

Duellman, W.E. 1982. Quaternary climatic—ecological fluctuations in the lowland tropics: frogs and forests. In: Prance, G.T. (ed.), *Biological diversification in the tropics*. Columbia University Press, pp. 389–402.

Duellman, W.E. 1999. *Patterns of distribution of Amphibians: A global perspective*. Johns Hopkins University Press.

Duellman, W.E., Wiens, J.J. 1993. Hylid frogs of the genus *Scinax* Wagler 1830, in Amazonian Ecuador and Peru. *Museum of Natural History, the University of Kansas*, **153**, 1–57.

Dutech, C., Joly, H.I., Jarne, P. 2004. Gene flow, historical population dynamics and genetic diversity within French Guianan populations of a rainforest tree species, *Vouacapoua americana*. *Heredity*, **92**, 69–77.

Dutech, C., Maggia, L., Joly, H.I. 2000. Chloroplast diversity in *Vouacapoua americana* (Caesalpiniaceae), a neotropical forest tree. *Molecular Ecology*, **9**, 1427–1432.

Dutech, C., Maggia, L., Tardy, C., Joly, H.I., Jarne, P. 2003. Tracking a genetic signal of extinction-recolonization events in a neotropical tree species: *Vouacapoua americana* Aublet in French Guiana. *Evolution*, **57**, 2753–2764.

Efron, B. 1979. 1977 Rietz Lecture—bootstrap methods—another look at the jackknife. *Annals of Statistics*, **7**, 1–26.

Faivovich, J., García, P.C.A., Ananias, F., Lanari, L., Basso, N.G., Wheeler, W.C. 2004. A molecular perspective on the phylogeny of the *Hyla pulchella* species group (Anura, Hylidae). *Molecular Phylogenetics and Evolution*, **32**, 938–950.

Faivovich, J., Haddad, C.F.B., García, P.C.A., Frost, D.R., Campbell, J.A., Wheeler, W.C. 2005. Systematic review of the frog family hylidae, with special reference to Hylinae: phylogenetic analysis and taxonomic revision. *Bulletin of the American Museum of Natural History*, **294**, 1–240.

Farris, J.S., Kallersjo, M., Kluge, A.G., Bult, C. 1994. Testing Significance of Incongruence. *Cladistics*, **10**, 315–319.

Felsenstein, J. 1985. Confidence limits on phylogenies—an approach using the bootstrap. *Evolution*, **39**, 783–791.

Frailey, C.D., Lavina, E.L., Rancy, A., Filho, J.P.S. 1989. A proposed Pleistocene/Holocene lake in the Amazona basin and its significance to Amazonian geology and biogeography. *Acta Amazonica*, **18**, 119–143.

Frost, D.R. 2004. Amphibian species of the world: an online reference. Version 3.0. New York: American Museum of Natural History. [Electronic Database accessible at <http://research.amnh.org/herpetology/amphibia/index.html/>].

Frost, D.R., Hillis, D.M. 1990. Species in concept and practice—herpetological applications. *Herpetologica*, **46**, 87–104.

Frost, D.R., Grant, T., Faivovich, J., Bain, R.H., Haas, A., Haddad, C.F.B., De Sa, R.O., Channing, A., Wilkinson, M., Donnellan, S.C., Raxworthy, C.J., Campbell, J.A., Blotto, B.L., Moler, P., Drewes, R.C., Nussbaum, R.A., Lynch, J.D., Green, D.M., Wheeler, W.C. 2006. The Amphibian tree of life. *Bulletin of the American Museum of Natural History*, **297**, 1–370.

Funk, D.J., Omland, K.E. 2003. Species-level paraphyly and polyphyly: frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual review of ecology, evolution and systematics*, **34**, 397–423.

Garcia-Paris, M., Alcobendas, M., Buclkey, D., Wake, D.B. 2003. Dispersal of viviparity across contact zones in Iberian populations of fire salamanders (*Salamandra*) inferred from discordance of genetic and morphological traits. *Evolution*, **57**, 129–143.

Gaston, K.J., Williams, P.H. 1996. Spatial patterns in taxonomic diversity. In: Gaston, K.J. (ed.), *Biodiversity: A biology of numbers and difference*. Blackwell Science, pp. 202–229.

Glaw, F., Köhler, J. 1998. Amphibian species diversity exceeds that of mammals. *Herpetological Review*, **29**, 11–12.

Goldstein, P., Wyner, K., Doukakis, P., Egan, M.G., Amato, G., Rosenbaum, H., DeSalle, R. 2005. Theory and methods for diagnosing species and populations in conservation. *Annals of the Missouri Botanical Garden*, **92**, 12–27.

Goldstein, P.Z., DeSalle, R., Amato, G., Vogler, A.P. 2000. Conservation genetics at the species boundary. *Conservation Biology*, **14**, 120–131.

Gorzula, S., Señaris, C. 1998. *Contribution to the herpetofauna of the Venezuelan Guayana I.A data base*, 270 p.

Grant, T., Frost, D.R., Caldwell, J.P., Gagliardo, R., Haddad, C.F.B., Kok, P.J.R., Means, D.B., Noonan, B.P., Schargel, W.E., Wheeler, W.C. 2006. Phylogenetic systematics of dart-poison frogs and their relatives (Amphibia: Athesphatanura: Dendrobatidae). *Bulletin of the American Museum of Natural History*, **299**, 1–262.

Grant, T., Kluge, A.G. 2003. Data exploration in phylogenetic inference: scientific, heuristic, or neither. *Cladistics*, **19**, 379–418.

Graybeal, A. 1997. Phylogenetic relationships of bufonid frogs and tests of alternate macroevolutionary hypotheses characterizing their radiation. *Zoological Journal of the Linnean Society*, **119**, 297–338.

Haffer, J. 1969. Speciation in amazonian forest birds. *Science*, **165**, 131–137.

Haffer, J. 1990. Geoscientific aspects of allopatric speciation. In: Peters, G. and Hutterer, R. (eds.), *Vertebrates in the Tropics*. Museum A. Koenig, pp. 45–60.

Haffer, J. 1997. Alternative models of vertebrate speciation in Amazonia: an overview. *Biodiversity Conservation*, **6**, 451–476.

Hanken, J. 1999. Why are there so many new amphibian species when amphibians are declining? *Trends in Ecology and Evolution*, **14**, 7–8.

Harrison, R.G. 1993. *Hybrid Zones and the Evolutionary Process*. Oxford University Press.

Hass, C.A., Dunski, J.F., Maxson, L.R., Hoogmoed, M.S. 1995. Divergent lineages within the *Bufo margaritifer* complex (Amphibia, Anura, Bufonidae) revealed by albumin immunology. *Biotropica*, **27**, 238–249.

Haas, W. 2004. Beitrag zur Biologie und Verbreitung dreier Vertreter des neotropischen *Bufo typhonius*-Komplexes (Anura: Bufonidae). *Salamandra*, **40**(3/4), 207–216.

Hay, J.M., Ruvinsky, I., Hedges, S.B., Maxson, L.R. 1995. Phylogenetic relationships of amphibian families inferred from DNA sequences of mitochondrial 12s and 16s ribosomal RNA genes. *Molecular Biology and Evolution*, **12**, 928–937.

Hoegg, S., Brinkmann, H., Taylor, J.S., Meyer, A. 2004. Phylogenetic timing of the fish-specific genome duplication correlates with the diversification of teleost fish. *Journal of Molecular Evolution*, **59**, 190–203.

Hoogmoed, M.S. 1979. The herpetofauna of the Guianan region. In: Duellman, W.E. (ed.), *The South American herpetofauna: Its origin, evolution and dispersal.* Museum of Natural History, University of Kansas, pp. 241–279.

Hoogmoed, M.S. 1990. Biosystematics of South American Bufonidae, with special reference to the *Bufo "typhonius* group. In: Peters, G. and Hutterer, R. (eds.), *Vertebrates in the tropics.* Museum Alexander Koenig, pp. 113–123.

Houlahan, J.E., Findlay, C.S., Schmidt, B.R., Meyer, A.H., Kuzmin, S.L. 2000. Quantitative evidence for global amphibian population declines. *Nature*, **404**, 752–755.

Jarman, S.N., Elliott, N.G. 2000. DNA evidence for morphological and cryptic Cenozoic speciations in the Anaspididae, 'living fossils' from the Triassic. *Journal of Evolutionary Biology*, **13**, 624–633.

Jegu, M., Keith, P. 1999. Lower Oyapock River as northern limit for the Western Amazon fish fauna or only a stage in its northward progression. *Comptes rendus de l'Académie des sciences III*, **322**, 1133–1143.

Joyce, D.A., Lunt, D.H., Bills, R., Turner, G.F., Katongo, C., Duftner, N., Sturmbauer, C., Seehausen, O. 2005. An extant cichlid fish radiation emerged in an extinct Pleistocene lake. *Nature*, **435**, 90–95.

Köhler, J., Vieites, D.R., Bonett, R.M., Garcia, F.H., Glaw, F., Steinke, D., Vences, M. 2005. New amphibians and global conservation: a boost in species discoveries in a highly endangered vertebrate group. *Bioscience*, **55**, 693–696.

Kuchta, S.R., Tan, A.M. 2005. Isolation by distance and post-glacial range expansion in the rough-skinned newt, *Taricha granulosa*. *Molecular Ecology*, **14**, 225–244.

Kumar, S., Tamura, K., Jakobsen, I.B., Nei, M. 2001. MEGA2: Molecular Evolutionary Genetics Analysis Software. *Bioinformatics*, **17**, 1244–1245.

Ledru, M.P., Blanc, P., Charles-Dominique, P., Fournier, M., Martin, L., Riera, B., Tardy, C. 1997. Palynological reconstruction of the rain forest in French Guiana during the past 3000 years. *Comptes rendus de l'Académie des sciences II*, **324**, 469–476.

Lescure, J., Marty, C. 2000. *Atlas des Amphibiens de Guyane*. Muséum national d'Histoire naturelle. Patrimoines Naturels, **45**, 388 p.

Lougheed, S.C., Gascon, C., Jones, D.A., Bogart, J.P., Boag, P.T. 1999. Ridges and rivers: a test of competing hypotheses of Amazonian diversification using a dart-poison frog (*Epipedobates femoralis*). *Proceedings of the Royal Society of London Series B-Biological Sciences*, **266**, 1829–1835.

Maxson, L.R. 1984. Molecular probes of phylogeny and biogeography in toads of the widespread genus *Bufo*. *Molecular Biology and Evolution*, **1**, 345–356.

Mayr, E. 1942. *Systematics and the Origin of Species*. Columbia University Press, New York.

Meegaskumbura, M., Bossuyt, F., Pethiyagoda, R., Manamendra-Arachchi, K., Bahir, M., Milinkovitch, M.C., Schneider, C.J. 2002. Sri Lanka: an amphibian hot spot. *Science*, **298**, 379.

Meyer, A., Salzburger, W., Schartl, M. 2006. Hybrid origin of a swordtail species (Teleostei: Xiphophorus clemenciae) driven by sexual selection. *Molecular Ecology*, **15** (3), 721.

Meyer, C.P., Paulay, G. 2005. DNA barcoding: Error rates based on comprehensive sampling. *PLoS Biology*, **3**(12), 1–10.

Miquelis, A., Martin, J.-F., Carson, E.W., Brun, G., Gilles, A. 2000. Performance of 18S rDNA helix E23 for phylogenetic relationships within and between the *Rotifera-Acanthocephala* clades. *Comptes Rendus de l'Académie des Sciences III*, **323**, 925–941.

Monsen, K.J., Blouin, M.S. 2003. Genetic structure in a montane ranid frog: restricted gene flow and nuclear-mitochondrial discordance. *Molecular Ecology*, **12**, 3275–3286.

Moritz, C. 1994a. Applications of mitochondrial DNA analysis in conservation—a critical-review. *Molecular Ecology*, **3**, 401–411.

Moritz, C. 1994b. Defining evolutionarily significant units for conservation. *Trends in Ecology and Evolution*, **9**, 373–375.

Moritz, C., Schneider, C.J., Wake, D.B. 1992. Evolutionary relationships within the *Ensatina eschscholtzii* complex confirm the ring species interpretation. *Systematic Biology*, **41**, 273–291.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B., Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

Noonan, B.P., Gaucher, P. 2005. Phylogeography and demography of Guianan harlequin toads *(Atelopus)*: diversification within a refuge. *Molecular Ecology*, **14**, 3017–3031.

Nores, M. 1999. An alternative hypothesis for the origin of Amazonian bird diversity. *Journal of Biogeography*, **26**, 475–485.

Patton, J.L., Smith, M.F. 1994. Paraphyly, polyphyly, and the nature of species boundaries in pocket gophers (genus *Thomomys*). *Systematic Biology*, **43**, 11–26.

Posada, D., Crandall, K.A. 1998. MODELTEST: testing the model of DNA substitution. *Bioinformatics*, **14**, 817–818.

Pramuk, J.B. 2006. Phylogeny of South American *Bufo* (Anura: Bufonidae) inferred from combined evidence. *Zoological Journal of the Linnean Society*, **146**, 407–452.

Räsänen, M.E., Salo, J.S., Jungner, H. 1991. Holocene floodplain lake sediments in the Amazon—C-14 dating and paleoecological use. *Quaternary Science Reviews*, **10**, 363–372.

Räsänen, M.E., Salo, J.S., Jungner, H., Pittman, L.R. 1990. Evolution of the western Amazon lowland relief: impact of andean foreland dynamics. *Terra Nova*, **2**, 320–332.

Richards, C.M., Moore, W.S. 1996. A phylogeny for the African treefrog family Hyperoliidae based on mitochondrial rDNA. *Molecular Phylogenetics and Evolution*, **5**, 522–532.

Ronquist, F., Huelsenbeck, J.P. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, **19**, 1572–1574.

Ruvinsky, I., Maxson, L.R. 1996. Phylogenetic relationships among bufonoid frogs (Anura: Neobatrachia) inferred from mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, **5**, 533–547.

Salducci, M.-D., Marty, C., Chappaz, R., Gilles, A. 2002. Molecular phylogeny of French Guiana Hylinae: implications for the systematic and biodiversity of the neotropical frogs. *Comptes Rendus Biologies*, **325**, 141–153.

Salducci, M.-D., Marty, C., Fouquet, A., Gilles, A. 2005. Phylogenetic relationships and biodiversity in Hylids (Anura: Hylidae) from French Guiana. *Comptes Rendus Biologies*, **328**, 1009–1024.

Salzburger, W., Meyer, A. 2004. The species flocks of East African cichlid fishes: recent advances in molecular phylogenetics and population genetics. *Naturwissenschaften*, **91**, 277–290.

Sequeira, F., Alexandrino, J., Rocha, S., Arntzen, J.W., Ferrand, N. 2005. Genetic exchange across a hybrid zone within the Iberian endemic golden-striped salamander, *Chioglossa lusitanica*. *Molecular Ecology*, **14**, 245–254.

Shimodaira, H., Hasegawa, M. 1999. Multiple comparison of log-likelihoods with applications to phylogenetic inference. *Molecular Biology and Evolution*, **16**, 1114–1116.

Sites, J.W., Marshall, J.C. 2003. Delimiting species: a Renaissance issue in systematic biology. *Trends in Ecology and Evolution*, **18**, 462–470.

Sites, J.W., Marshall, J.C. 2004. Operational criteria for delimiting species. *Annual review of ecology, evolution and systematics*, **35** 199–227.

Sota, T., Vogler, A.P. 2001. Incongruence of mitochondrial and nuclear gene trees in the carabid beetles *Ohomopterus*. *Systematic Biology*, **50**, 39–59.

Steiner, C., Catzeflis, F.M. 2003. Mitochondrial diversity and morphological variation of *Marmosa murina* (Didelphidae) in French Guiana. *Journal of Mammalogy* **84**, 822–831.

Stuart, B.L., Inger, R.F., Voris, H.K. 2006. High level of cryptic species diversity revealed by sympatric lineages of Southeast Asian forest frogs. *Biology Letters*, **2**, 470–474.

Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L., Waller, R.W. 2004. Status and trends of amphibian declines and extinctions worldwide. *Science*, **306**, 1783–1786.

Swofford, D.L. 2002. PAUP: *Phylogenetic Analysis Using Parsimony, version 4.0b10 [computer program]*. Sunderland (Massachusetts), Sinauer.

Takahata, N., Slatkin, M., 1984. Mitochondrial gene flow. *Proceedings of the National Academy of Sciences of the United States of America*, **81**, 1764–1767.

Thompson, J.D., Gibson, T.J., Plewniak, F., Jeanmougin, F., Higgins, D.G. 1997. The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Res*., **24**, 4876–4882.

Van de Peer, Y., Caers, A., De Rijk, P., De Wachter, R. 1998. Database on the structure of small ribosomal subunit RNA. *Nucleic Acids Research*, **26**, 179–182.

Van Vuuren, B.J., Kinet, S., Chopelet, J., Catzeflis, F. 2004. Geographic patterns of genetic variation in four Neotropical rodents: conservation implications for small game mammals in French Guiana. *Biological Journal of the Linnean Society*, **81**, 203–218.

Vélez-Rodríguez, C.M. 2004. Sistemática de los sapos neotropicales pertenecientes al grupo *Bufo typhonius* (Bufonidae). Tesis Doctoral. Universidad austral de Chile. Valdivia Chile. 159 p.

Vences, M., Kosuch, J., Boistel, R., Haddad, C.F.B., La Marca, E., Lötters, S., Veith, M. 2003. Convergent evolution of aposematic coloration in Neotropical poison frogs: a molecular phylogenetic perspective. *Organisms Diversity and Evolution*, **3**, 215–226.

Vences, M., Kosuch, J., Lötters, S., Widmer, A., Jungfer, K.H., Köhler, J., Veith, M. 2000. Phylogeny and classification of poison frogs (Amphibia: Dendrobatidae), based on mitochondrial 16S and 12S ribosomal RNA gene sequences. *Molecular Phylogenetics and Evolution*, **15**, 34–40.

Vences, M., Thomas, M., Bonett, R.M., Vieites, D.R. 2005a. Deciphering amphibian diversity through DNA barcoding: chances and challenges. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **360**, 1859–1868.

Vences, M., Thomas, M., Van der Meijden, A.Y., Chiari, Y., Vieites, D.R. 2005b. Comparative performance of the 16S rRNA gene in DNA barcoding of amphibians. *Frontiers in Zoology*, **2**.

Wake, D.B., Jockusch, E.L. 2000. Detecting species borders using diverse data sets. In: Bruce, R.C., Jaeger, R.G. and Houck, L.D. (eds.), *The Biology of Plethodontid Salamanders*. Kluwer Academic, Plenum Publishers, pp. 95–119.

Wiley, E.O. 1978. Evolutionary species concept reconsidered. *Systematic Zoology*, **27**, 17–26.

Wilson, E.O. 1992. *The Diversity of Life*. Belknap Press of Harvard University Press.

Wynn, A., Heyer, W.R. 2001. Do geographically widespread species of tropical amphibians exist? An estimate of genetic relatedness within the neotropical frog *Leptodactylus fuscus* (Schneider 1799) (Anura Leptodactylidae). *Tropical Zoology*, **14**, 255–285.

Young, B.E., Stuart, S.N., Chanson, J.S., Cox, N.A., Boucher, T.M. 2004. *Disappearing jewels: The status of New World Amphibians*. Nature-Serve.

Zangari, F., Cimmaruta, R., Nascetti, G. 2006. Genetic relationships of the western Mediterranean painted frogs based on allozymes and mitochondrial markers: evolutionary and taxonomic inferences (Amphibia, Anura, Discoglossidae). *Biological Journal of the Linnean Society*, **87**, 515–536.

Chapter 3:

Underestimation of species richness in Neotropical frogs revealed by mtDNA analyses

Abstract

Amphibians are rapidly vanishing. At the same time, it is most likely that the number of amphibian species is highly underestimated. Recent DNA barcoding work has attempted to define a threshold between intra- and inter-specific genetic distances to help identify candidate species. In groups with high extinction rates and poorly known species boundaries, like amphibians, such tools may provide a way to rapidly evaluate species richness. Here we analyse published and new 16S rDNA sequences from 60 frog species of Amazonia-Guianas to obtain a minimum estimate of the number of undescribed species in this region. We combined isolation by distance, phylogenetic analyses, and comparison of molecular distances to evaluate threshold values for the identification of candidate species among these frogs. In most cases, geographically distant populations belong to genetically highly distinct lineages that could be considered as candidate new species. This was not universal among the taxa studied and thus widespread species of Neotropical frogs really do exist, contra to previous assumptions. Moreover, the many instances of paraphyly and the wide overlap between distributions of inter- and intra-specific distances reinforce the hypothesis that many cryptic species remain to be described. In our data set, pairwise genetic distances below 0.02 are strongly correlated with geographical distances. This correlation remains statistically significant until genetic distance is 0.05, with no such relation thereafter. This suggests that for higher genetic distances allopatric and sympatric cryptic species prevail. Based on our analyses, we propose a more inclusive pairwise genetic distance of 0.03 between taxa to target lineages that could correspond to candidate species. Using this approach, we identify 129 candidate species, two-fold greater than the 60 species included in the current study. This leads to estimates of around 170 to 460 frog taxa unrecognized in Amazonia-Guianas. As a consequence the global amphibian decline detected especially in the Neotropics may be worse than realised.

Key words: Neotropical frogs, 16S rDNA, diversity, Guianas, genetic distances, DNA barcoding.

1. Introduction

Amphibians are undergoing a drastic global decline (Collins and Halliday, 2005; Houlahan et al., 2000; Pechmann and Wilbur, 1994; Pounds et al., 1999; Pounds and Puschendorf, 2004; Roy, 2002; Stuart et al., 2004). Paradoxically, the number of amphibian species known to science is increasing with many new species discovered annually (Dubois, 2005; Glaw and Köhler, 1998; Hanken, 1999; Köhler et al., 2005). These new species descriptions are not the result of changes in theoretical species concepts but rather are a consequence of (1) real first hand discoveries (e.g. phenotypically divergent taxa described using traditional taxonomic practices), particularly due to the exploration of previously poorly known tropical areas (Köhler et al., 2005); (2) diagnoses aided by molecular tools, and (3) the recent appreciation that a combination of slight differences in morphology and ecology (e.g. vocalisation) can be sufficient to characterize new species of amphibians (Campbell and Savage, 2000) under both evolutionary and biological species concepts. However, despite these advances, to describe amphibian diversity and to infer evolutionary history remains a difficult task because their morphological evolution is extremely conserved (Cherry et al., 1977; 1978; Emerson, 1986; Shubin and Jenkins, 1995) and plagued with homoplasy (Bossuyt and Milinkovitch, 2000; Parra-Olea and Wake, 2001; Wake, 1991). Consequently, it is probable that a great proportion of amphibian diversity still remains to be discovered, not only at the species level but also in deeply rooted lineages, and this may be true for many other animal groups as well (Pfenninger and Schwenk, 2007).

The Neotropics shelter the highest number of frog species on earth (Duellman, 1999; Young et al., 2004), and this is also one of the regions where amphibians are most threatened (Stuart et al., 2004). Many Neotropical frog species are thought to be distributed throughout Amazonia and adjacent areas (Duellman, 1999; 2004). For example, although the Guianas are considered a single biogeographical entity due to the relative high endemism observed in the region, more than half of the currently recognised frog species in the Guianas occur elsewhere in Amazonia (Duellman, 1999). However, the idea that so many species have a widespread distribution is at odds with the low vagility and high philopatry observed in most amphibian taxa, characteristics that should promote differentiation and ultimately speciation (Berven and Grudzien, 1990; Blaustein et al., 1994; Duellman, 1982; Gascon et al., 1998; Kusano et al., 1999; Reading et al., 1991). Moreover, the view that so many species have a widespread distribution in the Neotropics conflicts with known historic climatic oscillations and geological events that have likely shaped the ranges of these Neotropical species and their ancestors (Bush, 1994; Frailey et al., 1989; Haffer, 1969; 1990; 1997; Moritz et al., 2000;

Nores, 1999). This led Lynch (1979) and Wynn and Heyer (2001) to question respectively how many widespread frog species really exist, or if they indeed exist at all.

To decipher and fully understand amphibian diversification, an acceleration of comprehensive systematic revisions integrating morphological, bioacoustic and genetic data is needed. However, if the underestimation of species richness in Neotropical frogs observed in many groups by many authors (Roberts et al., 2006) is ubiquitous the conservation implications for this threatened group are severe. Thus, there is an urgent need for an approach that can be used to rapidly obtain minimum estimates of the number of undescribed species in this group, and thereby identify priorities for taxonomic research and conservation actions. It has been argued that DNA sequences provide such a tool (Hebert et al., 2004a; 2004b; Vences, 2005a;b), and for the purpose of taxonomy, they can be analysed using three complementary approaches: phylogenetic analysis, comparison of molecular distances, and inferences from isolation-by-distance (IBD) calculations.

Phylogenetic analysis of DNA sequences can lead to the recognition of paraphyletic or polyphyletic gene lineages within *a priori* species. For mitochondrial DNA, species polyphyly and paraphyly have been found to be taxonomically widespread and far more common than generally recognized (Funk and Omland, 2003). Such heterophyletic species designations are, in most cases, indeed indicative of incomplete taxonomy, which occurs when species names fail to identify the genetic limits of separate evolutionary entities (Funk and Omland, 2003). Hence, the prevalence of species paraphyly or polyphyly can be used as an indicator for the number of yet undescribed species in a lineage. However, the reliability of the method is obscured by the possibility of incomplete lineage sorting, and by introgression that can cause gene heterophyly, especially in mitochondrial genes (Avise, 2000).

Another approach that can provide information on polyphyletic species is based on sequence divergences and thresholds for these distances. Vences et al. (2005a; b) suggested that distance-based DNA barcoding could be a useful tool for documenting amphibian biodiversity. Pairwise divergences among sequences are calculated, and if these are above a previously defined threshold, the two sequences potentially belong to different species. If one of the sequences differs from all known species by a divergence above the threshold, it can be flagged as a "candidate species" and subjected to detailed taxonomic study (Vences et al., 2005a). However, because species-formation is a continuous process and the distinctive key characters (e.g., factors for prezygotic or postzygotic isolation) can evolve either early or late in this process (de Queiroz, 1999), there necessarily are a number of very young (and hence genetically poorly differentiated) species that will be missed by the threshold-based estimates

(false negatives). Again, because of introgression or incomplete lineage sorting, quite divergent lineages may not represent different species (false positives) (Meyer and Paulay, 2005). Despite these pitfalls, a few studies on the distribution of the genetic diversity using mitochondrial DNA in different groups have shown that a gap exists between intraspecific and interspecific genetic diversity in some taxonomic groups. This gap is very clear in North American birds (Hebert et al., 2004b) and limited overlap has been found in Chironomidae (Diptera) (Ekrem et al., 2007), in climbing salamanders (*Aneides*), mantellid frogs (Vences et al., 2005a) and cowries (Meyer and Paulay, 2005). Threshold values therefore should be set high enough to ignore, as much as possible, intraspecific divergence, but low enough to ensure detection of as many incipient or newly emergent species as possible. In amphibians, thresholds of 0.05 (=5%) for a fragment of the 16S rDNA gene and of 0.1 (=10%) for the COI gene have been proposed (Vences et al., 2005a;b).

In a group with low vagility like frogs, the main factor supposedly driving genetic differentiation among conspecific populations is isolation by distance (IBD) (Slatkin, 1993). Moreover, the most common mode of amphibian species formation is supposed to be allopatric speciation (Vences and Wake, 2007). In this scenario, a strong correlation between genetic and geographic distances is expected among populations of the same species (Slatkin, 1993). However, once (allopatric) speciation is completed, secondary contact and overlap among the ranges of sister species is to be expected, decreasing the correlation between genetic and geographical distances (Suatoni et al., 2006; Hebert et al., 2004b). Hence, as long as distances between related populations follow an IBD model they can be considered, with some probability, to be conspecific. In contrast, where differentiation cannot be explained by simple IBD models, it is likely that more than one species is involved.

Here, we use a combination of published and new 16S mitochondrial rDNA sequences from 60 frog species known to occur in French Guiana, most of which are considered to be widely distributed across the Guianan and Amazonian regions, to obtain a minimum estimate of the number of undescribed species of amphibians in this region. We base our analyses on the three methods described above, and furthermore combine the IBD and distance-based analysis to evaluate threshold values for the identification of candidate species in amphibians.

2. Materials and Methods

(Further details about the methods used are available in Text S3.1.)

2.1. Sequences and laboratory protocols

We selected available sequences in GenBank attributed to 60 of the 102 anuran species (28 genera) known to occur in French Guiana (445 sequences) according to Boistel et al. (2006) and Lescure and Marty (2000). To this, we added sequence data from 69 individuals sampled in French Guiana and 25 individuals sampled elsewhere in South America (Table S3.1). Each sequence was attributed to one of 60 currently designated species (two to 38 sequences per species; Table S3.1), most of which (88.7%) are currently considered to be widespread across the Guianan and Amazonian regions.

DNA was extracted using either standard phenol chloroform or lithium chloride methods (Gemmell and Akiyama, 1996). Primers used for amplification are described by Salducci et al. (2005) for 16S rDNA. PCRs were performed in a 25-µl total volume with cycle parameters as described in Salducci et al. (2005). Sequencing was performed using ABI Big Dye V3.1 and resolved on an automated sequencer at Macrogene Inc. (Korea) and the University of Canterbury sequencing service (New Zealand).

Preliminary alignment of sequences was performed with Clustal X (Thompson et al., 1997) with a gap penalty equal to five, with other parameters set at the default settings. Each alignment was verified by eye and compared with secondary structures (16S rDNA) (Van de Peer et al., 1998). Newly determined sequences were deposited in GenBank (Table S3.1).

The final alignment of the 16S rDNA fragment was 420 base pairs, a slightly shorter fragment than that used by Vences et al. (2005b), but containing a high proportion of the polymorphic sites detected in this gene segment. Comparing the pairwise distances of the two fragment sizes employed by this study and the earlier work of Vences et al. (2005b) results in a ratio of 1.2 (R^2=0.99; p=0.0001, df=52) (Fig. S3.1). Thus, the 5% divergence threshold proposed by Vences et al. (2005b) corresponds to a 6% threshold with our fragment size.

We chose to use this fragment for several reasons: (1) It is the most commonly used marker for amphibian systematics and thus the DNA fragment for which the taxonomic sampling is currently the highest (Vences et al., 2005b). (2) It is easy to obtain for a wide array of groups because of highly conserved region (hairpins) flanking more variable region (loops) and also for other reasons detailed by Vences et al (2005a; b). Some authors, arguing against the use of this gene, have suggested that sequence alignment can be problematic due to indels occurring within the highly variable loop regions. This indeed is often the case for deep relationships and it is well known that coding mtDNA such as *COI* displays some advantage due to the conservation of the reading frame which usually provides unambiguous guidance for a global alignment (Smith et al., 2007). However, because our analyses only deal with closely related taxa the alignment is unambiguous and the advantage of the large

sequence set available for 16S rDNA far outweighs those of easier alignment of the more limited *COI* data.

2.2. Assessment of species monophyly

For each of the species studied we selected 16S rDNA sequences as "lineages" that had higher uncorrected pairwise distances than 0.01 (= 1%) from the closest other sequence in the analysis. Previous work in two groups of frogs (*Scinax ruber* and *Rhinella margaritifera*) included in this study showed that intraspecific diversity clusters into haplogroups for which the diversity is circumscribed between 0 and 0.01 (Fouquet et al., 2007; Chapter 2). Multiple representatives of lineages, which we called "populations", were selected only when they occurred at several remote localities (i.e., different states or countries).

To test the monophyly of each species we first selected, from GenBank, all available sequences attributed to putatively closely related species that potentially could nest among the identified lineages of any of our study species. To select these additional species, we (1) selected taxa which displayed a close relationship with the species studied according to previous work (Table S3.1, Text S3.1) and (2) using the BLAST option with all the previously selected sequences of the species studied. We chose the first hit of a heterospecific sequence in each case.

Subsequently, preliminary phylogenetic analyses were performed for each species using Maximum Parsimony implemented in PAUP 4.0 (Swofford, 1997). Confidence in the phylogenetic grouping was assessed by the non-parametric bootstrap method (Efron, 1979; Felsenstein, 1985) with 1000 pseudoreplicates undertaken using the heuristic search option, tree bisection reconnection branch swapping (TBR) and 10 random taxon addition replicates. For each analysis we used all the sequences from conspecific populations, the alternative heterospecific sequences potentially introducing paraphyly and a supposedly closest species as an outgroup. Only the alternative species nesting with strong bootstrap support within already selected species were kept. Subsequently, a Bayesian phylogenetic analysis was performed with MrBayes 3.1 (Ronquist and Huelsenbeck, 2003) on the complete dataset. We used the software Modeltest version 3.6 (Posada and Crandall, 1998) to choose the substitution model that best fits our data using the Akaike Information Criterion (Akaike, 1974). These models (Text S1) were subsequently used for Bayesian analysis on the University of Canterbury Supercomputer. Bayesian analysis consisted of 2 independent runs of 1.0×10^7 generations with random starting trees and four Markov chains (one cold) sampled every 1000 generations. Adequate burn-in (1.0×10^6) was determined by examining a plot of

the likelihood scores of the heated chain for convergence on stationarity. We flagged those nodes which received posterior probabilities >80 as supporting paraphyly.

2.3. Comparisons of intraspecific distances

Sixty of the 102 currently known anuran species in French Guiana (59%, representing 28 of 36 genera) were used in the current study. These species were represented by 539 sequences, of which 221 lineages were identified after discarding 318 redundant sequences that corresponded to sequences belonging to already included lineages and originating from the same or very close localities as those already in the analysis (Table S3.1). We calculated 825 pairwise distances between conspecific lineages; of these, 240 distance values were between lineages sampled within the Guianas representing 43 species, and 246 between Guianan lineages and other South American lineages, representing 33 species.

Using the uncorrected pairwise distances, we constructed a neighbour joining tree using MEGA 4 (Kumar et al., 2001). We then plotted the distribution of these distances in two categories "Guianas against South America" and "within Guianas" to check whether the pattern differs between biogeographical regions.

We calculated how many lineages are separated by the 6% threshold, and repeated this analysis with a 3% threshold as lower limit based on data from Fouquet et al. (2007, Chapter 2) that provided evidence that reproductively isolated cryptic species can be separated by 3.8% (*Rhinella*) and 4.3% (*Scinax*) based on 16S rDNA sequences.

2.4. Interspecific distance distribution: the example of Hylinae

To compare the distributions of intraspecific distances calculated above with a distribution of validated interspecific distances, we used homologous 16S rDNA fragments from the dataset published by Faivovich et al. (2005a) because of its very complete taxon coverage for a group of Neotropical frogs (Hylinae). From this dataset, we chose species that were fully resolved as sister species in the original analysis (Faivovich et al., 2005a) in order to capture the most recent speciation events. We eventually used 108 species (54 pairs) to compute the interspecific distance distribution.

2.5. Isolation by distance and species range data

To test whether the critical levels of the intra- and inter-specific distance distributions that we determined *a priori* fit expectations about IBD, we plotted genetic distances against geographic distances (N=822). A Mantel test is not applicable with these kinds of data, where

pairs of intraspecific lineages are compared and pooled altogether. Thus, we described the relation between geographical distances and pairwise genetic distances using a piecewise linear model (Draper and Smith, 1990). The parameters of the model were estimated by the least squares method. We used the Bayesian information criterion (BIC) to choose the adequate model (i.e. number of pieces, up to 6) that best fit the raw data. This procedure was implemented using R 2.5.0 (R Foundation for Statistical Computing, 2005) and was repeated 10 times with a random start. The best model was kept and 95% confidence intervals were estimated using 500 random resamples. Additionally, genetic distances between pairs were grouped into classes and the means and variance of geographical distances was calculated for each class.

Approximate range sizes of the anuran species occurring in Amazonia-Guianas were estimated from the Global Amphibian Assessment (GAA) database (www.globalamphibians.org). The delimitation of Amazonia followed the Amazonia wilderness area and only species occurring broadly in this area were selected. Subsequently, we removed species occurring fully or partially above 600m, in order to avoid including species restricted to the Andes and the Guiana highlands.

3. Results

3.1. Prevalence of paraphyletic species

DNA sequences were available for only a fraction of taxa potentially related to our target species. Nevertheless we found 13 out of our 60 target species (22%) displaying strongly supported paraphyletic relationships according to the Bayesian analyses (Fig. 3.1, Fig. S3.2, Fig. S3.3). Eight of these had been previously recognized, for example, *Scinax ruber* with respect to *S. fuscovarius* and to *S. x-signatus* (Fouquet et al., 2007; Chapter 2) and *Dendropsophus leucophyllatus* with respect to *D. triangulum* (Chek et al., 2001) and seven were novel. Ten of these 13 species have at least one lineage closer to another species than to the other conspecific lineages, with distances below 0.06 between them. The remaining species (outside the 13 above) formed strongly supported monophyletic groups except three ambiguous cases with low posterior probability: *Leptodactylus fuscus* (*L. longirostris* nested within), *Osteocephalus leprieurii* (*O. cabrerai* and *O. taurinus* nested within) and *Leptodactylus pentadactylus* (*L. knudseni* nested within).

3.2. Patterns of intraspecific distances

Twenty-one out of 60 species (35%) contain lineages that differ from each other by uncorrected distances over 0.06, and 35 species (58.3%) contain lineages differing by more than 0.03 (Fig. 3.2). The 0.06 limit segregates 94 lineages instead of the 60 species (56.7% more) included in this study and the 0.03 limit segregates 129 lineages (115% more).

Despite having been sampled in very distant localities (more than 2000 km), sixteen species display close lineages (less distant than 0.03) and four display very close lineages (less than 0.01) (Fig. 3.1, Fig. 3.2) For example, *Dendropsophus nanus* lineages from French Guiana and Argentina have a divergence of only 0.014 but are more than 3200 km apart (Fig. S3.1). However, our pattern fits with geography in certain aspects. Half (47.3%) of the pairwise distances among Guianan populations were between 0 and 0.03 while only one third (34.3%) of the comparisons between Guianan and other South American populations were under 0.03 (Fig. 2). The very low divergences, considered here as distances within a lineage (between 0 and 0.01), are much more frequent among Guianan populations (15%) than between Guianan and other South American populations (5%) ($P(Chi^2)=4.8x10^{-5}$, ddl=1, N=520). Conversely, distances between 0.03 and 0.06 are found in 14.2% of the among-Guiana comparisons and 35.4% of comparisons between Guianan and other South American populations ($P(Chi^2)=3.6x10^{-8}$, ddl=1, N=520). Indeed, distances below 0.03 are significantly more common among Guianan lineages than between lineages from South American and Guiana ($P(Chi^2)=0.002$, ddl=1, N=520).

In contrast, the proportions of very high distances (>0.06) among conspecific populations are only slightly different between populations within Guianas (39.2%) and Guianas vs. South America (29.3%) (Fig. 3.2). Such incongruence between geography and genetic patterns can also be seen in Fig. 3.1. In 14 species in which at least two lineages occur in French Guiana, one of them is closer to a lineage occurring elsewhere in South America (*H. fasciatus, H multifasciatus, H. geographicus, R. ventrimaculata, A. degranvillei, A. granti, S. ruber, S. boesemani, R. margaritifera, L. longirostris, L. mystaceus, A. andreae, A. hylaedactyla, L. gr. wagneri*). Reciprocally, in 12 species (*L. fuscus, L. pentadactylus, L. palmipes, H. calcaratus, A. hahneli, A. trivittatus, R. ventrimaculata, A. femoralis, C. granulosus, R. margaritifera, S. ruber, P. pipa*) one of the South American lineages is closer to one of the Guianan representatives than at least one other conspecific lineage in the rest of South America (Fig. 3.1).

3.3. Patterns of interspecific distances

The distribution of interspecific p distances using Hylinae widely overlaps with the intraspecific distributions (Fig. 3.2). Indeed, the distribution of the genetic distances between Guianan versus South American populations and the distribution of interspecific pairwise distances are almost similar. More than half (53.7%, 29/54) of the interspecific distances correspond to values below 0.06. Still, 29.6% (16/54) of the apical distances correspond to values below 0.03.

3.4. Isolation by distance

According to the BIC, the selected model explaining the relation between geographical and genetic distances was made up of three linear models (Fig. 3.3). The first one concerns genetic distances between 0 and 0.019 and has a strong positive slope ($2.5x10^5 \pm 0.29x10^5$). The second one concerns the genetic distances between 0.019 and 0.049 and has a three-fold weaker but still positive slope ($9x10^3 \pm 4.4x10^3$). Genetic distances that are over 0.049 are best fitted with a negative slope.

4. Discussion

4.1. Deep polyphyly and paraphyly suggest a high proportion of cryptic species

Our data indicate a high number of potentially new frog species occurring in the Guianan and Amazonian region. This conclusion is supported by (1) the high genetic divergences among lineages within species and (2) by the presence of many paraphyletic species. Depending on the method used, the proportion of candidate species relative to the 60 study species varies from 22–115%.

In Hylinae, most distances between sister species (53.5%) were below 0.06 and one third was even below 0.03. This indicates that divergences corresponding to intraspecific distances over 0.03 can be considered as deep. Indeed the intraspecific and interspecific distances distributions widely overlap. While 53.5% of the interspecific data were below 0.06, this was the case for 61.3–69.3% of the intraspecific data (Fig. 3.2). The number of deeply related intraspecific lineages is very high: 94 lineages are more distant than 0.06 and 129 lineages are more distant than 0.03, giving proportions of 56% and 115% of candidate new species.

The phylogenetic analysis demonstrated paraphyly of lineages within 13 species out of 60. Hence, this approach suggests in 22% of cases current species designations do not adequately represent true species designations. This is a maximum estimate given the data, because in some cases it may represent introgression through recent hybridization, incomplete

lineage sorting, or erroneous phylogenetic reconstruction. On the other hand, few species of Neotropical amphibians have been sequenced for this mtDNA fragment so far (Vences and Köhler, 2006), and thus the potential of the available data to detect paraphyly is small, suggesting that this situation might be much more frequent than it is shown by the data herein. This phenomenon is taxonomically widespread and also corroborated by recent studies for other groups of frogs (e.g. *Pseudae* (Garda and Canatella, 2007); *Chaunus marinus* (Mulcahy et al., 2006), Central American *Brachycephalidae* (Crawford and Smith, 2005) and in other parts of the world (Meegaskumbura et al., 2002; Stuart et al., 2006). In Malagasy mantellids and North American salamanders, the overlap between intra- and inter-specific distances is smaller and allows of setting more clearly a threshold values. We assume that this is because their systematics have been extensively studied and their taxonomy is now better fitting their respective evolutionary histories than is the case for most Neotropical frogs. Indeed, the taxonomic coverage of DNA sequence data is one the highest for Malagasy frogs and North American Caudata while it is one of the lowest for Neotropical frogs (Vences and Köhler, 2006).

4.2. Widespread species of Neotropical frogs do exist

Our analysis suggests that widespread Neotropical frog species do exist (Lynch, 1979; Wynn and Heyer, 2001). Here we have confirmation that conspecific populations (*Osteocephalus cabrerai*, *O. taurinus, Sphaenorhynchus lacteus*, *Lithobates palmipes*, *Pipa pipa, Hypsiboas boans*) are genetically so close that they probably belong to one widespread species which has dispersed over vast areas in South America (Fig. 3.1; S3.2). Nevertheless, it seems that widespread lineages are a minority (in our dataset 16 out of 53; 60 species considered in total less seven species purportedly endemic to the Guianan shield). However, species can be at the same time widely distributed and contain candidate new species: in *Pipa pipa*, even if one lineage was widely distributed, the species was still found to be deeply polyphyletic. Low sampling might mask a similar pattern in other species, and further work to determine this is warranted. It is worth mentioning that most of these widespread species are associated with open areas (*Leptodactylus fuscus*, *Adenomera hylaedactyla*, *Scinax ruber*) or with rivers or large swamps (*Lithobates palmipes*, *Pipa pipa*, *Sphaenorhynchus lacteus*, *Hypsiboas raniceps*, *Dendropsophus nanus*).

4.3. Geographical data also support the idea that deep lineages may be considered as candidate new species.

The comparison between genetic and geographical distances (Fig. 3.3) seems to fit the expectations about the process of speciation by allopatry. The strong association between geographical and genetic distances between 0 and 0.019 is certainly due to intraspecific variation among populations mainly driven by isolation by distance. The absence of strong correlation between genetic and geographical distances for distance values over 0.019 is probably due to the increase of the number of allopatric species displaying no contact or superficial contact/hybrid zones, and sympatric species (Fouquet et al., 2007; Chapter 2). The data over 0.049 probably include a prevalence of sympatric species that are likely to be reproductively isolated from each other (Fouquet et al., 2007; Chapter 2).

Moreover, a series of discordant relationships between geography and genetic distances can be detected: (1) in many species, one of the lineages detected within French Guiana is closer to a population sampled elsewhere in South America; (2) the distribution of the pattern of distances on a small geographical scale (within Guianas) and a large one (between Guianas and South America) is basically the same, suggesting that these lineages could represent different species in contact in French Guiana; (3) in *Scinax ruber*, *Rhinella margaritifera* (Fouquet et al., 2007; Chapter 2), *Leptodactylus* gr. *wagneri*, *Anomaloglossus degranvillei*, *Allobates femoralis* (Grant et al., 2006; Lougheed et al., 1999), *Dendropsophus leucophyllatus* (Chek et al., 2001; Lougheed et al., 2006), *Ameerega hahneli* and *Ameerega trivittata* (Grant et al., 2006; Roberts et al., 2006a), for example, the distributions of some lineages and their relationships are clearly discordant and suggests that some of these lineages could be sympatric (Fig. 3.1).

4.4. A divergence threshold value of 0.03 to identify amphibian candidate species

Based on the isolation by distance analysis, a threshold between 0.019 and 0.049 appears to be appropriate to distinguish between intraspecific and interspecific divergences among Neotropical anurans. Several additional lines of evidence support a threshold around 0.03:

1. Divergences within vs. among regions: In Fig. 3.2 (see also the Chi² analyses), the distances calculated among Guianan populations mainly range between 0 and 0.03 whereas the comparisons between Guianan and other South American populations predominantly yielded distance values between 0.03 and 0.07. This also can be interpreted as a dominance of intraspecific distances mainly driven by isolation by distance between 0 and 0.03 and over that threshold, the predominance of pairwise distances between allopatric species distributed in the Guianas and in other regions of South America, respectively.

2. Concordance with assumed ages of speciation. The genetically and geographically highly distant conspecific populations were likely isolated during the recent geological period of climatic oscillations and geological events and many of them have probably remained isolated since this time. The majority of recent speciation events for amphibians seem to have occurred before the Pleistocene period (Chek et al., 2001; Lougheed et al., 1999). This pattern is also observed in birds, primates and rodents in South America (Collins and Dubach, 2000; Cortes-Ortiz et al., 2003; Grau et al., 2005; Salazar-Bravo et al., 2001). A calibration of 0.0037 to 0.006 divergence per million years for tRNA and 16S rDNA combined by Evans et al. (2004) predicts a divergence of 0.0066 to 0.011 on 16S rDNA between closely related species that last share a common ancestor dating from the boundary between the Pliocene and the Pleistocene (1.8 mya) (similar proportions of substitutions are observed with the mtDNA fragment used by Evans et al. and our smaller fragment size, data not shown). Assuming many lineages emerged at the Plio-Pleistocene boundary, this would again suggest that the 0.03 threshold is a more reasonable predictor of lineages describing potential candidate species than the 0.06 threshold.

3. Concordance with well-sampled datasets. The 0.03 threshold segregates 70% (versus 46% false negative with 0.06) of the terminal divergences in the dataset of Faivovich et al. (2005a). Moreover, some of the species below the 0.03 threshold might actually deserve to be synonymised (false negatives) as it has been the case recently for *Dendrobates azureus* and *D. tinctorius* (Wollenberg et al., 2006). Fouquet et al. (2007; Chapter 2) delimited *Scinax ruber* and *Rhinella margaritifera,* lineages that that correspond to reproductively isolated species with divergences as low as 0.0385 (*R. margaritifera* A versus D). They also found five further lineages of lower divergences that may represent distinct species as well given the positions of *Scinax x-signatus* and *Rhinella dapsilis* which are nested among the lineages with low genetic distances. The pattern obtained for the interspecific distances using the dataset of Faivovich et al. (2005a) data overestimates genetic distances between sister species because distances used are not only between sister species but concern deeper relationships as well. The Hylinae clade is not sampled with sufficient rigour to solely examine distances between sister species. It is therefore likely that some high distances observed are actually between distantly related taxa.

These arguments advocate the use of a 0.03 (3%) threshold to identify candidate species of Neotropical anurans and reject the adequacy of the 0.06 (6%) threshold proposed previously. The 0.3 (3%) threshold is preferred to either higher of lower thresholds because a higher threshold (e.g. 0.06) risks missing many potential species while a lower threshold (e.g.

0.02) will more accurately delimit lineages but risks identifying many conspecific lineages as candidate species.

Genetic diversity has been demonstrated to be higher within tropical species than in the temperate species (Martin and McKay, 2004; Chek et al., 2003; Hackett and Rosenberg, 1990). Indeed, the trend for population differentiation to increase with decreasing latitude was used by Moritz and Cicero (2004) to argue against the broad application of such a DNA distance based metric for delineating biodiversity in the tropics. While we did not observe a strong disjunction between the intraspecific and the interspecific pairwise distance distributions in tropical frogs in our data set, Vences et al. (2005a; b) did observe such a gap. Moreover, the levels of divergence between lineages, populations and even most sister species in temperate areas reside well below the 3% threshold in sequence difference we suggest for 16SrDNA in this study (Fromhage et al., 2003; Lymberakis et al., 2007; Veith et al., 2003). Consequently, we believe that a 3% threshold may prove to be a useful tool to document tropical frog biodiversity in a wide variety of contexts.

5. Conclusions

Our results clearly show that the number of species is highly underestimated in anurans from the Guianan and Amazonian regions. Our approach indicated that up to 115% additional species may be expected among Neotropical amphibians. About 400 anuran species are currently recognised in Amazonia-Guianas, with 37% of these species (about 150) having ranges >1 million km² that can be considered as sufficiently widespread for an extrapolation of the number of potential cryptic species. Extrapolating from our data, the total number of species in this region might easily approach 600 (400-150+(150*215%)). However, even if our analysis comprises the most widespread species inhabiting Amazonia-Guianas (85% of the species included have ranges >1 million km²) this extrapolation is likely to be a minimum estimate. Two reasons may account for this: (1) given the low proportion of most of the ranges sampled in our analysis many more extant lineages may have remained unsampled; (2) many species that are currently considered of restricted range are poorly known and their ranges might be wider. If we apply this extrapolation to the total number of species in Amazonia this would lead to a total number of over 860 (400*215%) and over 4400 (2065*215%) for South America (Young et al., 2004). Of course these estimates are extremely rough, but even the lowest estimate of 22% new species (considering only the paraphyly criterion) leads to almost 490 (400*122%) species for Amazonia-Guianas and

almost 2520 (2065*122%) for South America that are to be expected without considering true first-hand discovering which also are going on at a fast pace.

Species delimitation is essential for conservation of biodiversity, especially in the tropics where indicators such as the species richness or the degree of endemism are simple and efficient indicators of biodiversity that can be monitored for change over time. To be accurate, the species delineation needs to use a taxon specific approach (by genus or group of species) using a combination of data from phylogenetic, phylogeographic, morphological and ecological data (Sites and Marshall, 2004). However, considering the enormous number of new candidate species detected by our analysis it is clear that such analyses would take considerable time. However, biodiversity data are urgently needed to help define conservation priorities. Molecular diversity data may be useful surrogates for evaluate amphibian biodiversity before it vanishes. Even if some of the lineages identified may ultimately be shown not to represent species, while others may be missed, the net gain in amphibian diversity in regions like the Neotropics makes such a strategy attractive.

As a consequence of the underestimation of the number of frog species, the global amphibian decline detected especially in the Neotropics may be worse than so far realised (Köhler et al., 2005; Stuart et al., 2004). Indeed, we cannot know how many "species" instead of "populations" have already disappeared or are disappearing, and the situation is particularly acute in the tropics. The rapid identification and recognition of new species may exacerbate an organism's threat status because it can result in the subdivision of a once widespread species into numerous species, each with a smaller and, hence, a more precarious distribution. Nevertheless, it is obviously better to know the state of biodiversity threat than to be ignorant of the mammoth changes in global amphibian diversity that we are witnessing.

References

Akaike, H. 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, **19**(6), 716–723.

Avise, J.C. 2000. *Phylogeography: The history and formation of species*. Harvard University Press, Cambridge, Massachusetts, 447 p.

Berven, K.A., Grudzien, T.A. 1990. Dispersal in the wood frog (*Rana sylvatica*)- implications for genetic population structure. *Evolution*, **44**, 2047–2056.

Blaustein, A.R., Wake, D.B., Sousa, W.P. 1994. Amphibian declines-judging stability, persistence, and susceptibility of populations to local and global extinctions. *Conservation Biology*, **8**, 60–71.

Boistel, R., de Massary, C., Angulo, A. 2006. Description of a new species of the genus *Adenomera* (Amphibia, Anura, Leptodactylidae) from French Guiana. *Acta Herpetologica*, **1**, 1–14.

Bossuyt, F., Milinkovitch, M.C. 2000. Convergent adaptive radiations in Madagascan and Asian ranid frogs reveal covariation between larval and adult traits. *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 6585–90.

Bush, M.B. 1994. Amazonian speciation - a necessarily complex model. *Journal of Biogeography*, **21**, 5–17.

Campbell, J. A., Savage, J. M. 2000. Taxonomic reconsideration of Middle American frogs of the *Eleutherodactylus rugulosus* group (Anura: Leptodactylidae): A reconnaissance of subtle nuances among frogs. *Herpetological Monographs*, **14**, 186–292.

Chek, A.A., Austin, J.D., Lougheed, S.C. 2003. Why is there a tropical-temperate disparity in the genetic diversity and taxonomy of species? *Evolutionary Ecology Research*, **5**, 69–70

Chek, A.A., Lougheed, S.C., Bogart, J.P., Boag, P.T. 2001. Perception and history: molecular phylogeny of a diverse group of neotropical frogs, the 30-chromosome *Hyla* (Anura: Hylidae). *Molecular Phylogenetics and Evolution*, **18**, 370–85.

Cherry, L.M., Case, S.M., Wilson, A.C. 1977. Relative rates of morphological evolution in primates, carnivores and frogs. *American Zoologist*, **17**, 910–910.

Cherry, L.M., Case, S.M., Wilson, A.C. 1978. Frog Perspective on Morphological Difference between Humans and Chimpanzees. *Science*, **200**, 209–211.

Collins, A.C., Dubach, J.M. 2000. Biogeographic and ecological forces responsible for speciation in *Ateles*. *International Journal of Primatology*, **21**, 421–444.

Collins, J.P., Halliday, T. 2005. Forecasting changes in amphibian biodiversity: aiming at a moving target. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **360**, 309–314.

Cortes-Ortiz, L., Bermingham, E., Rico, C., Rodriguez-Luna, E., Sampaio, I., Ruiz-Garcia, M. 2003. Molecular systematics and biogeography of the Neotropical monkey genus, *Alouatta*. *Molecular Phylogenetics and Evolution*, **26**, 64–81.

Crawford, A.J., Smith, E.N. 2005. Cenozoic biogeography and evolution in direct-developing frogs of Central America (Leptodactylidae: *Eleutherodactylus*) as inferred from a phylogenetic analysis of nuclear and mitochondrial genes. *Molecular Phylogenetics and Evolution*, **35**, 536–555.

de Queiroz, K. 1999. The general lineage concept of species and the defining properties of the species category. In: Wilson, R.A. (ed.): *Species: new interdisciplinary essays*. MIT Press, Cambridge, Massachusetts, U.S.A, pp. 49–89.

Draper, N.R., Smith, H. 1990. *Applied regression Analysis*. Wiley, 736 p.

Dubois, A. 2005. Developmental pathway, speciation and supraspecific taxonomy in amphibians, 1: Why are so many frog species in Sri Lanka. *Alytes*, **22**, 19–37.

Duellman, W.E. 1982. Quaternary climatic-ecological flucuations in the lowland tropics: frogs and forests. In: Prance, G.T. (ed.), *Biological diversification in the tropics*, Columbia University Press, pp. 389–402.

Duellman, W.E. 1999. *Patterns of distribution of amphibians: a global perspective*. Johns Hopkins University Press.

Duellman, W.E. 2004. *Cusco Amazónico: the lives of amphibians and reptiles in an Amazonian rainforest*. Cornell University Press.

Efron, B. 1979. 1977 Rietz Lecture - bootstrap methods - another look at the jackknife. *Annals of Statistics*, **7,** 1–26.

Ekrem, T., Willassen, E., Stur, E. 2007. A comprehensive DNA sequence library is essential for identification with DNA barcodes. *Molecular Phylogenetics and Evolution*, **43**(2), 530–542.

Emerson, S.B. 1986. Convergence and morphological constraint in frogs: variation in postcranial morphology. *Fieldiana Zoology*, **43**, 1–19.

Evans, B.J., Kelley, D.B., Tinsley, R.C., Melnick, D.J., Cannatella, D.C. 2004. A mitochondrial DNA phylogeny of African clawed frogs: phylogeography and implications for polyploid evolution. *Molecular Phylogenetics and Evolution*, **33**(1), 197–213.

Faivovich, J., Haddad, C.F.B., Garcia, P.C.A., Frost, D.R., Campbell, J.A., Wheeler, W.C. 2005. Systematic review of the frog family Hylidae, with special reference to Hylinae: phylogenetic analysis and taxonomic revision. *Bulletin of the American Museum of Natural History*, **294**, 1–240.

Felsenstein, J. 1985. Confidence limits on phylogenies-an approach using the bootstrap. *Evolution*, **39**, 783–791.

Fouquet, A., Vences, M., Salducci, M.-D., Meyer, A., Marty, C., Blanc, M., Gilles A. 2007. Revealing cryptic diversity using molecular phylogenetics and phylogeography in frogs of the *Scinax ruber* and *Rhinella margaritifera* species groups. *Molecular Phylogenetics and Evolution*, **43**(2), 567–582.

Frailey, C.D., Lavina, E.L., Rancy, A., Filho, J.P.S. 1989. A proposed Pleistocene/Holocene lake in the Amazonas basin and its significance to Amazonian geology and biogeography. *Acta Amazonica*, **18**, 119–143.

Fromhage, L., Vences, M., Veith, M. 2003. Testing alternative vicariance scenarios in Western Mediterranean discoglossid frogs. *Molecular Phylogenetics and Evolution*, **31**, 308–322.

Frost, D.R., Grant, T., Faivovich, J., Bain, R.H., Haas, A., Haddad, C.F.B., De Sa, R.O., Channing, A., Wilkinson, M., Donnellan, S.C., Raxworthy, C.J., Campbell, J.A., Blotto, B.L., Moler, P., Drewes, R.C., Nussbaum, R.A., Lynch, J.D., Green, D.M., Wheeler, W.C. 2006. The amphibian tree of life. *Bulletin of the American Museum of Natural History*, **297,** 1–370.

Funk, D.J., Omland, K.E. 2003. Species-level paraphyly and polyphyly: Frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology Evolution and Systematics*, **34**, 397–423.

Garda, A.A., Cannatella, D.C. 2007. Phylogeny and biogeography of paradoxical frogs (Anura, Hylidae, Pseudae) inferred from 12S and 16S mitochondrial DNA. *Molecular Phylogenetics and Evolution*, **44**(1), 104–114.

Gascon, C., Lougheed, S.C., Bogart, J.P. 1998. Patterns of genetic population differentiation in four species of Amazonian frogs: A test of the riverine barrier hypothesis. *Biotropica*, **30**, 104–119.

Gemmell, N.J., Akiyama, S. 1996. An efficient method for the extraction of DNA from vertebrate tissues. *Trends in Genetics*, **12**, 338–339.

Glaw, F., Köhler, J. 1998. Amphibian species diversity exceeds that of mammals. *Herpetological Review*, **29**, 11–12.

Grant, T., Frost, D.R., Caldwell, J.P., Gagliardo, R., Haddad, C.F.B., Kok, P.J.R., Means, D.B., Noonan, B.P., Schargel, W.E., Wheeler, W.C. 2006. Phylogenetic systematics of dart-poison frogs and their relatives (Amphibia: Athesphatanura: Dendrobatidae). *Bulletin of the American Museum of Natural History*, **299**, 1–262.

Grau, E.T., Pereira, S.L., Silveira, L.F., Hofling, E., Wajntal, A. 2005. Molecular phylogenetics and biogeography of Neotropical piping guans (Aves: Galliformes): *Pipile* Bonaparte, 1856 is synonym of *Aburria* Reichenbach, 1853. *Molecular Phylogenetics and Evolution*, **35**, 637–645.

Hackett, S.J., Rosenberg, K.V. 1990. Comparison of phenotypic and genetic differentiation in South American Antwrens (Formicariidae). *The Auk*, **107**, 473–489.

Haffer, J. 1969. Speciation in amazonian forest birds. *Science*, **165,** 131–137.

Haffer, J. 1990. Geoscientific aspects of allopatric speciation. In: Peters, G. and Hutterer, R. (eds.), *Vertebrates in the tropics*. Museum A. koening, pp. 45–60.

Haffer, J. 1997. Alternative models of vertebrate speciation in Amazonia: An overview. *Biodiversity and Conservation*, **6**, 451–476.

Hanken, J. 1999. Why are there so many new amphibian species when amphibians are declining? *Trends in Ecology and Evolution*, **14**, 7–8.

Hebert, P.D.N., Penton, E.H., Burns, J.M., Janzen, D.H., Hallwachs, W. 2004a. Ten species in one: DNA barcoding reveals cryptic species in the Neotropical skipper butterfly *Astraptes fulgerator*. *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 14812–14817.

Hebert, P.D.N., Stoeckle, M.Y., Zemlak, T.S., Francis, C.M. 2004b. Identification of birds through DNA barcodes. *PLoS Biology*, **2**, 1657–1663.

Houlahan, J.E., Findlay, C.S., Schmidt, B.R., Meyer, A.H., Kuzmin, S.L. 2000. Quantitative evidence for global amphibian population declines. *Nature*, **404**, 752–755.

Köhler, J., Vieites, D.R., Bonett, R.M., Garcia, F. H., Glaw, F., Steinke, D., Vences, M. 2005. New amphibians and global conservation: A boost in species discoveries in a highly endangered vertebrate group. *Bioscience*, **55**, 693–696.

Kumar, S., Tamura, K., Jakobsen, I. B., Nei, M. 2001. MEGA2: Molecular Evolutionary Genetics Analysis software. *Bioinformatics*, **17,** 1244–1245.

Kusano, T., Maruyama, K., Kanenko, S. 1999. Breeding site fidelity in the Japanese toad, *Bufo japonicus formosus*. *Herpetological Journal*, **9**, 9–13.

Lescure, J., Marty, C. 2000. *Atlas des amphibiens de Guyane*. Muséum national d'Histoire naturelle. Patrimoines Naturels, **45**, 388 p.

Lougheed, S.C., Austin, J.D., Bogart, J.P., Boag, P.T., Chek, A.A. 2006. Multi-character perspectives on the evolution of intraspecific differentiation in a Neotropical hylid frog. *BMC Evolutionary Biology*, **6,** –.

Lymberakis, P., Poulakakis, N., Manthalou, G., Tsigenopoulos, C.S., Magoulas, A., Mylonas, M. 2007. Mitochondrial phylogeography of *Rana* (Pelophylax) populations in the Eastern Mediterranean region. *Molecular Phylogenetics and Evolution*, **44**, 115–125.

Lynch, J.D. 1979. The amphibians of the lowland tropical forests. In: Duellman, W.E. (ed.), *The South American herpetofauna: Its origin, evolution and dispersal*. Monograph of the Museum of Natural History, University of Kansas, pp. 189–215.

Martin, P.R., McKay, J.K. 2004. Latitudinal variation in genetic divergence ofpopulations and the potential for future speciation. *Evolution*, **58**, 938–945.

Meegaskumbura, M., Bossuyt, F., Pethiyagoda, R., Manamendra-Arachchi, K., Bahir, M., Milinkovitch, M.C., Schneider, C.J. 2002. Sri Lanka: an amphibian hot spot. *Science*, **298**, 379.

Meyer, C.P., Paulay, G. 2005. DNA barcoding: Error rates based on comprehensive sampling. *PLoS Biology*, **3**, 2229–2238.

Moritz, C., Patton, J.L., Schneider, C.J., Smith, T.B. 2000. Diversification of rainforest faunas: An integrated molecular approach. *Annual Review of Ecology and Systematics*, **31**, 533–563.

Moritz, C., Cicero, C. 2004. DNA barcoding: Promise and pitfalls. *PLoS Biology*, **2**(10), e354.

Mueller, R.L. 2006. Evolutionary rates, divergence dates, and the performance of mitochondrial genes in Bayesian phylogenetic analysis. *Systematic Biology*, **55**(2), 289–300.

Mulcahy, D.G., Morrill, B.H., Mendelson, J.R. 2006. Historical biogeography of lowland species of toads (*Bufo*) across the Trans-Mexican Neovolcanic Belt and the Isthmus of Tehuantepec. *Journal of Biogeography*, **33**, 1889–1904.

Noonan, B.P., Gaucher, P. 2005. Phylogeography and demography of Guianan harlequin toads (*Atelopus*): diversification within a refuge. *Molecular Ecology*, **14**, 3017–3031.

Nores, M. 1999. An alternative hypothesis for the origin of Amazonian bird diversity. *Journal of Biogeography*, **26**, 475–485.

Parra-Olea, G., Wake, D.B. 2001. Extreme morphological and ecological homoplasy in tropical salamanders. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 7888–7891.

Pechmann, J.H.K., Wilbur, H.M. 1994. Putting declining amphibian populations in perspective - Natural fluctuations and human impacts. *Herpetologica*, **50**, 65–84.

Pfenninger, M., Schwenk, K. 2007: Cryptic animal species are homogeneously distributed among taxa and biogeographical regions. *BMC Evolutionary Biology*, **7**, 121.

Posada, D., Crandall, K.A. 1998. MODELTEST: testing the model of DNA substitution. *Bioinformatics*, **14**, 817–818.

Pounds, J.A., Fogden, M.P.L., Campbell, J.H. 1999. Biological response to climate change on a tropical mountain. *Nature*, **398**, 611–615.

Pounds, J.A., Puschendorf, R. 2004. Ecology - clouded futures. *Nature*, **427**, 107–109.

Reading, C.J., Loman, J., Madsen, T. 1991. Breeding pond fidelity in the common toad, *Bufo bufo*. *Journal of Zoology*, **225**, 201–211.

Roberts, J.L., Brown, J.L., May, R.V., Arizabal, W., Schulte, R., Summers, K. 2006. Genetic divergence and speciation in lowland and montane Peruvian poison frogs. *Molecular Phylogenetics and Evolution*, **41**(1), 149–164.

Ronquist, F., Huelsenbeck, J.P. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, **19**, 1572–1574.

Roy, D. 2002. Amphibians as environmental sentinels. *Journal of Biosciences*, **27**, 187–188.

Salazar-Bravo, J., Dragoo, J. W., Tinnin, D. S., Yates, T. L. 2001. Phylogeny and evolution of the neotropical rodent genus *Calomys*: Inferences from mitochondrial DNA sequence data. *Molecular Phylogenetics and Evolution*, **20**, 173–184.

Salducci, M.-D., Marty, C., Fouquet, A., Gilles, A. 2005. Phylogenetic relationships and biodiversity in hylids (Anura: Hylidae) from French Guiana. *Comptes Rendus Biologies*, **328**, 1009–1024.

Shubin, N.H., Jenkins, F.A. 1995. An Early Jurassic jumping frog. *Nature*, **377,** 49–52.

Sites, J.W., Marshall, J.C. 2004. Operational criteria for delimiting species. *Annual Review of Ecology Evolution and Systematics*, **35**, 199–227.

Slatkin, M. 1993. Isolation by distance in equilibrium and non-equilibrium populations. *Evolution*, **47**, 264–279.

Smith, M.A., Poyarkov N.A., Hebert P.D.N. 2007. CO1 DNA barcoding amphibians: take the chance, meet the challenge. *Molecular Ecology Resourses*, **8**, 235–246

Stuart, B.L., Inger, R.F., Voris, H.K. 2006. High level of cryptic species diversity revealed by sympatric lineages of Southeast Asian forest frogs. *Biology Letters*, **2**, 470–474.

Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L., Waller, R.W. 2004. Status and trends of amphibian declines and extinctions worldwide. *Science*, **306**, 1783–1786.

Suatoni, E., Vicario, S., Rice, S., Snell, T., Caccone, A. 2006. An analysis of species boundaries and biogeographic patterns in a cryptic species complex: The rotifer-*Brachionus plicatilis*. *Molecular Phylogenetics and Evolution*, **41**(1), 86–98.

Swofford, D. L. 1997. *Test version 4.0.0d64 of PAUP*. Sinauer.

Thompson, J.D., Gibson, T.J., Plewniak, F., Jeanmougin, F., Higgins, D.G. 1997. The CLUSTAL X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research*, **25**, 4876–4882.

Van de Peer, Y., Caers, A., de Rijk, P., de Wachter, R. 1998. Database on the structure of small ribosomal subunit RNA. *Nucleic Acids Research*, **26**, 179–182.

Veith., M, Kosuch, J., Vences, M. 2003. Climatic oscillations triggered post- Messinian speciation of Western Palearctic brown frogs (Amphibia, Ranidae). *Molecular Phylogenetics and Evolution*, **26**, 310–327.

Vences, M., Köhler, J. 2008. Global diversity of amphibians (Amphibia) in freshwater. *Hydrobiologia*, **595**, 569–580.

Vences, M., Köhler, J. 2006. The current status of genetic exploration in amphibians: taxonomic and geographic disparities. In: Vences, M., Köhler, J., Ziegler, T. and Böhme, W. (eds.). *Herpetologia Bonnensis II. Proceedings of the 13th Congress of the Societas Europaea Herpetologica*. Bonn, Zoologisches Forschungsmuseum A. Koenig and Societas Europaea Herpetologica. pp. 193–195.

Vences, M., Thomas, M., Bonett, R.M., Vieites, D.R. 2005a. Deciphering amphibian diversity through DNA barcoding: chances and challenges. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **360**, 1859–1868.

Vences, M., Thomas, M., Van der Meijden, A.Y., Chiari, Y., Vieites, D.R. 2005b. Comparative performance of the 16S rRNA gene in DNA barcoding of amphibians. *Frontiers in Zoology*, **2**.

Vences, M., Wake, D. 2007. Speciation, species boundaries and phylogeography of amphibians. In: Heatwole, H. and Tyler, M. (eds.): *Amphibian Biology, vol. 7. Amphibian Systematics*. Surrey Beatty and Sons, Chipping Norton, Australia, pp. 2613–2971.

Wake, D.B. 1991. Homoplasy-the result of natural-selection, or Evidence of Design Limitations. *American Naturalist*, **138**, 543–567.

Wiens, J.J., Fetzner, J.W., Parkinson, C.L., Reeder, T.W. 2005. Hylid frog phylogeny and sampling strategies for speciose clades. *Systematic Biology*, **54**(5), 778–807.

Wiens, J.J., Graham, C.H., Moen, D.S., Smith, S.A., Reeder, T.W. 2006. Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: Treefrog trees unearth the roots of high tropical diversity. *American Naturalist*, **168**, 579–596.

Wiens, J.J., Penkrot, T.A. 2002. Delimiting species using DNA and morphological variation and discordant species limits in spiny lizards (*Sceloporus*). *Systematic Biology*, **51**, 69–91.

Wollenberg, K.C., Veith, M., Noonan, B.P., Lotters, S. 2006. Polymorphism versus species richness—Systematics of large *Dendrobates* from the eastern Guiana Shield (Amphibia: Dendrobatidae). *Copeia*, 623–629.

Wynn, A., Heyer, W.R. 2001. Do geographically widespread species of tropical amphibians exist? An estimate of genetic relatedness within the Neotropical frog *Leptodactylus fuscus* (Schneider 1799) (Anura, Leptodactylidae). *Tropical Zoology*, **14**, 255–285.

Young, B.E., Stuart, S.N., Chanson, J.S., Cox, N.A., Boucher, T.M. 2004. Disappearing jewels: The status of New World amphibians, *NatureServe*.

Chapter 4:

Description of two new species of *Rhinella* (Anura: Bufonidae) from the lowlands of the Guiana shield.

Abstract

The *Rhinella margaritifera* complex is characterisized by the presence of many cryptic species throughout its wide distribution, ranging from Panama to Bolivia and entire Amazonia. French Guiana has long been thought to harbor two species of this group (*Rhinella margaritifera* and one unnamed species), though a recent survey using molecular data indicated as many as five lineages that may represent cryptic species. At least three of these lineages do not appear to interbreed despite broad sympatry and thus could be easily regarded as distinct species according to both the biological and phylogenetic species concepts. We examined morphological variation of four of these lineages, along with acoustic data to determine whether these characters discriminate these goups. These analyses, combined with published data of other *Rhinella* species, indicated that two of these lineages represent previously unnamed species. The remaining two are allocable to *R. margaritifera* while the status of the fifth remains unclear because so far it is morphologically indistinguishable from *R. castaneotica*.

Key words: Systematics, discriminant analysis, morphology, vocalisation, *Rhinella martyi sp. nov.*, *Rhinella lescurei sp. nov.*

1. Introduction

The *Rhinella margaritifera* complex is a group of bufonid toads supported by two morphological characters (Vélez-Rodriguez, 2004): the depressor mandibulae muscle formed by two slips (the first originating on the posterior region of the otic ramus of the squamosal, and the second originating on the anterior region of the otic ramus of the squamosal and the annulus tympanicus), and the presence of a thickening on the ventrolateral border of the quadratojugal that can be seen as a process on the extreme forms. Frost et al. (2006) proposed to resurrect the name *Rhinella* (Fitzinger, 1826) to group the species of this clade, previously referred to as *Bufo margaritifer* complex or group. In that study *Rhinella margaritifera* was found to be closer to the genus *Rhamphophryne* than any other group of the Bufonidae. This clade includes 12 species: *R. acutirostris* (Spix), *R. alata* (Thominot), *R. castaneotica* (Caldwell), *R. dapsilis* (Myers and Carvalho), *R. hoogmoedi* (Caramaschi and Pombal), *R. magnussoni* (Lima, Menin and de Araùjo)*, R. margaritifera* (Laurenti), *R. sclerocephala* (Mijares-Urrutia and Arends), *R. roqueana* (Melin), and numerous undescribed species, across its distribution, from Panama to northern Bolivia. *R stanlaii* (Lötters and Köhler), *R. proboscidea* (Spix) (see Hoogmoed, 1986) and *R. scitula* (Caramaschi and De Niemeyer) are tentatively included in this group until additional material is available for study. *Rhinella cristinae* (Vélez-Rodriguez and Ruiz-Carranza), *R. sternosignata* (Günther), *R. intermedia* (Günther), *R. iserni* (Jiménez de le Espada) and *R. ceratophrys* (Boulanger) are excluded from this group because they do not possess the proposed synapomorphies (above). The position of *Rhaebo nasicus* (Werner) in Pramuk (2006) also suggests that this species do not belong to this group. Describing new species in this clade is challenging due to the cryptic morphological diversity in the group (similarity between the males, the lack of diagnostic characteristics for females) and the confusion surrounding the names of most of the species due to the poor quality of the type material and some descriptions.

Two species of the *R. margaritifera* complex are known to occur in French Guiana (Lescure and Marty, 2000). One is considered by several authors (Lescure and Marty, 2000; Vélez-Rodriguez, 2004; Hoogmoed, 1990, Hoogmoed and Avila-Pires, 1991) to represent *R. margaritifera* sensu stricto in which females develop hypertrophied supratympanic crests. The other is not assigned to any known species, is smaller than *R. margaritifera*, and lacks the well developed cephalic crest (Hoogmoed and Avila-Pires, 1991; Lescure and Marty, 2000). Recently, Haas (2004) suggested that there are actually three species of the *R. margaritifera* complex in northern French Guiana: *R. margaritifera* and two undescribed species.

During surveys in French Guiana, Suriname and Guyana, toads of the *R. margaritifera* complex were sampled from numerous localities (Fig. 4.1) including vocalization recordings. A previous study using molecular data (Fouquet et al., 2007; Chapter 2) revealed that five lineages (coded A to E) are present in the eastern Guianas and that at least three lineages likely represent largely sympatric species that are reproductively isolated (Fig. 4.1). There is no evidence for the reproductive isolation of lineages A+B and C but the A+B lineage appears to be allopatric to lineage C while genetic data suggest incomplete lineage sorting of nuclear DNA (Chapter 2). The two well known species (A and E) are widely distributed in French Guiana. Among the additional lineages, one (C) is present in the extreme south of French Guiana, Suriname and Guyana (Fouquet et al., 2007; Chapters 2,3,5), one (B) is only known from a single localty in the extreme north of French Guiana and lineage (D) is present in central and southwestern French Guiana. Fouquet et al., (2007; Chapter 2) noted that lineage D is morphologically more similar to E, as it does not have a developed cephalic crest, though it shares a more recent common ancestor with A, B and C than with E.

Following Vélez-Rodriguez (2005) and Hoogmoed (1977, 1986), we have considered that *Rhinella margaritifera* (A) corresponds to the Guianan populations of *Rhinella* with hypertrophied cranial crests. According to these authors this seems a reasonable conjecture given that the type locality of the species initially called *Rana margaritifera* is Brazil, a country where more than one species with this morphological characteristic occurs. However, more than one species also occurs within the Guianas. Thus, we considered the species occuring in French Guianan with the most hypertrophied cephalic crests as *Rhinella margaritifera* sensu stricto and used *R. margaritifera* (A) specimens to compare with specimens of undescribed species.

We compared specimens and vocalizations from four of the Guianan lineages (excluding B) described in Fouquet et al., (2007; Chapter 2) and published data of other *Rhinella* species, to determine whether morphological characters are sufficient to discriminate these species. We use these characters to describe two new species and describe their vocalizations and basic ecological characteristics.

2. Materials and Methods

Measurements of the specimens (lineage A n = 27; C n = 7; D n = 9; E n = 23) were recorded to the nearest 0.1 mm with dial calipers. Sex was determined by observation of the gonads when it was not obvious by sexual dimorphism or calling activity. Measurements follow Vélez-Rodriguez and Ruiz-Carranza (2002) (Snout Vent Length (SVL), Eye Snout

Distance (ESD), Femur Length (FML), Foot Length (FTL), Head Length (HL), Head Width (HW), Tibia Length (TIBL)) except that the paratoid glands were not measured, and that we additionally measured IND (inter nostril distance), UEW (upper eyelid width), IOD (inter orbital distance), EN (eye to nostril distance), ED (eye diameter), ETD (eye tympanum distance), FL1 (first finger length, from distal edge of thenar tubercule to tip of the finger), FL3 (third finger length, from distal edge of thenar tubercule to tip of the finger), TL4 (fourth toe length, from distal edge of metatarsian tubercule to tip of the toe), TD (typanum diameter vertically) and ML (mouth length, from angle of the jaw to the junction of the two mandibules).

All measurements were collected and standardized by dividing through SVL (snout-vent length). We analysed the data using discriminant analyses (XLSTAT-Pro 6.1 for Windows) to identify the key discriminant measures and correlated these with genetic grouping (lineages) and sex groupings.

Specimens collected in French Guiana and Suriname that have been measured were deposited to the Museum National d'Histoire Naturelle de Paris (MNHN). Additional specimens were examined from the Universite Montpellier-2 collection, the Collection of Vertebrates of the University of Texas at Arlington (UTACV), from the Royal Ontario Museum (ROM) and from Brigham Young University (BPN). We used diagnoses and morphological descriptions from Caldwell (1991), Caramaschi and De Niemeyer (2003), Caramaschi and Pombal (2006), Haas (2004), Hoogmoed (1977, 1986, 1990), Hoogmoed and Avila-Pires (1991) Lescure and Marty (2000), Lima et al. (2007), Lötters and Köhler (2000), Melin (1941), Mijares-Urrutia and Arends (2001), Myers and Carvalho (1945), Vélez-Rodriguez and Ruiz-Carranza (2002), Vélez-Rodriguez (2004) and Zimmerman and Bogart (1988). We also used description of acoustic signals from Duellman (2005), Lescure and Marty (2000), Marty and Gaucher (2000), Köhler et al. (1997), Lima et al. (2007) and Zimmerman and Bogart (1988).

Recordings were obtained between 2000 and 2006 in French Guiana and Suriname by AF, Christian Marty and PG. Recording equipment included a Marantz PMD670 solid state recorder (Sampling frequency 44.1 kHz) with a built-in XLR microphone, a Sony MZ-NH 700 (minidisc, Hi-MD) (Sampling frequency 44.1 kHz) with a gunzoom MZ00X microphone or a Sony DAT TCD-D8 (Sampling frequency 48 kHz) with a Sennheiser K6 microphone. Distance between recording position and calling individuals varied from about 1 to 2 meters. Settings of the recording level were done manually. No noise reduction systems were used. Temperature during recording was between 25-26°C. Two calls of two individuals per species

(except for lineage D where only one individual was used) were digitized using Raven 1.2.1 (Charif et al., 2004) at a sample rate of 44.1 kHz with 16-bit. For spectrogram analyses settings were a filter bandwidth of 1.5 kHz, Fast Fourier Transforms with window size = 1024 points and a frequency of 47 Hz, resolution of 0.1 ms (overlap = 97 %) with Hanning window function.

3. Results

Using morphology and morphometry, four groups could be confirmed. They largely correspond with material allocated to clades A-E by Fouquet et al. (2007; Chapter 2). Limited instances of molecular/morphological identification mismatch were observed. Two males of *R. margaritifera* (A) were assigned to males of *R.* sp. (C) based on morphological data (Fig. 4.2), and discrimination among sexes within *R.* sp. (E) and *R.* sp. (D) was not strong.

The first axis (Fig. 4.2) holds 64% of the information and discriminates strongly *R. margaritifera* (A) + *R.* sp. (C) and *R.* sp. (D) + *R.* sp. (E). Males and females of *R. margaritifera* (A) and *R.* sp. (C) are also clearly segregated. The variables that mainly contribute to this axis are: ESD, EN, HW, STCH, ML, ED.

The second axis holds 14% of the information and discriminates *R.* sp. (D) and *R.* sp. (E). Males and females of *R. margaritifera* are also clearly segregated along this axis. The variables that are mainly contributing to this axis are: TIBL, IND, UEW, EN, ED and SOCH.

The third axis holds 10% of the information and discriminates *R. margaritifera* (A) and *R.* sp. (C) as well as sexes within *R. margaritifera* (A). The variables that mainly contribute to this axis are: STCD, SOCH, STCH and IND.

Our analysis further confirmed that two lineages represent previously unnamed species, corresponding with clades (C) and (D) of Fouquet et al. (2007; Chapter 2). They are described as new species in the following.

Previous authors referred to *R.* sp. (E) as *Bufo* sp. "*typhonius*" (Lescure and Marty, 2000) and *Bufo* sp. 2 (Haas, 2004), lacking cephalic crests and referred to as a basal clade by Fouquet et al. (2007; Chapter 2). No morphological differences obviously distinguish it from *R. castaneotica* from central Amazonia (Caldwell, 1991) and the Andean foreland region of Amazonia. Awaiting further revisionary action, we here treat it as *Rhinella* sp. E.

3.1. Rhinella martyi sp. nov.

Holotype.- 2006.2601 MNHN, an adult female (Fig. 4.3), collected 14 January 2006 by Antoine Fouquet and Christian Marty from Brownsberg Nature Park, Suriname, Brokopondo district (4°56'N/55°10'W), 510 m above sea level (see Fig. 4.1: 21).

Paratypes.- 2006.2602 MNHN 2006.2603 MNHN, 2006.2605 MNHN, three females collected in the same time and place.

2006.2604 MNHN, a male collected in the same time and place.

2006.2606 MNHN, 2006.2607 MNHN, collected 10 January 2006 by Antoine Fouquet and Michel Blanc nearby the road to Apura and Goliathberg, Para district, Suriname (5°11'N/55°37'W, 50 m above sea level); UTACV 55742-3, collected 20 and 21 December 2002 by Brice Noonan near the Ellerts de Haan airstrip, Sipaliwini district, Suriname (3°6'N/56°28'W); UTACV 55740-1 collected 13 December 2002 by Brice Noonan at Ralleighvallen, Sipaliwini district, Suriname (4°43'N/56°13'W); BPN 897-904, collected 19 May 2003 by Brice Noonan nearby the road to Apura and Goliathberg, Para district, Suriname (5°11'N/55°39'W); BPN 984, 990-91, collected 26 and 30 May 2003 by Brice Noonan near the Sipaliwini village, Sipaliwini district, Suriname (2°2'N/56°7'W); BPN 1053, 1062, collected 3 and 4 June 2003.by Brice Noonan in the Lely Mountains, Suriname, (4°16'N/54°44'W); UTACV 55744 collected 4 January 2002 by Brice Noonan from the type locality; BPN 42, 59 collected 21 and 23 May 1997 by Brice Noonan near Bartica Cuyuni/Mazaruni region, Guyana, (6°22'N/58°39'W); ROM 20652-20654; collected 11 October 1990 by Ross MacCulloch at Kurupukari, west side of Essequibo River, Potaro-Siparuni District, Guyana (4°40'N/58°39'W, 60 m above sea level); ROM 22813, 22833; collected 24 September and 1 October 1992 by Ross MacCulloch at Baramita, Barima-Waini District (aka Northwest Dist.), Guyana (7°22'N/60°29'W, 100 m above sea level); T3022 (Universite Montpellier-2) collected 10 March 2001 by Philippe Gaucher at Mitaraka, French Guiana (02°16'N/54°31'W).

Diagnosis.-A large species of the *R. margaritifera* group as defined genetically by Fouquet et al. (2007; Chapter 2) and morphologically by Hoogmoed (1990) and Vélez-Rodriguez (2004). It is distinguished from all other species of this complex by the following combination of characters (Fig. 4.3): (1) SVL of 4 females 64.7 ± 3.4mm, of three males 55.3 ± 5.8mm; (2) protruding bony knob at the angle of jaws; (3) *canthus rostralis* with a crest, concave laterally; (4) heel just reaches posterior margin of eye when hindlimbs adpressed; (5) cephalic crests hypertrophied in females and postorbital crests laterally extending very distinct in males; (6) neural spines protruding in females, distinct in males; (7) tympanum large round or ovoid but smaller than eye diameter; (8) parotoid glands relatively small,

triangular, posteriorly elongated; (9) upper eyelid without projections; (10) toes about three-quarters webbed, three phalanges free on toe 4; (11) tarsal fold absent; (12) skin tuberculate on dorsal and dorsolateral surfaces, more spinous on limbs; (13) oblique row of tubercles extending from posterior end of postorbital crest to groin; (14) snout pointed dorsally and acute laterally with small fleshy ridge going from tip of snout to the upper lip; (15) iris golden with black reticulations.

Rhinella martyi (C) is distinguished from *R.* sp. (E), *R. castaneotica*, *R. magnussoni*, *R. proboscidea*, *R. dapsilis, R. scitula* and the other new species described below by larger SVL and the presence of prominent cephalic crests (Fig. 4.3). From *R. stanlaii* it differs by larger SVL, the presence of vertebral apophyses salient on dorsum in females and the absence of dermal projection on the eyelid. From *R. hoogmoedi*, the new species is distinguishable by the presence of vertebral apophyses salient on dorsum and by its slightly larger size. From *R. margaritifera* (A) and *R. alata*, it differs by having a more developed bony knob at the angle of the jaw and the shape of its cephalic crests in females: supratympanic and supraorbital crests less high and distance beween supratympanic crests smaller than in *R. margaritifera* (A). *Rhinella martyi* (C) is larger in SVL and has a proportionately wider and longer head than *R. margaritifera* (Table 1). *Rhinella martyi* can be discriminated from *R. acutirostris* by its angular corner of the jaws and well-developed cephalic crests and from *R. sclerocephala* by neural spines being prominent in females only and the presence of postorbital crests. From *R. roqueana, R. martyi* (C) is distinguished by its smaller size and that the heel does not extend beyond the eye when hind limb carried forward along body.

Description of Holotype (Fig. 4.3).-SVL 66.5 mm; HW 28.0 mm at angle of the jaws; head wider than long, HL 22.0 mm. In dorsal view, snout protruding and rounded laterally, a small, thin vertical fleshy ridge extends from tip of snout to mouth; canthus rostralis concave with crests; top of head flat; cephalic crests well developed; parotoids small, well developed, elongated posteriously; eyelids thick, wide, densely tuberculate; nares slightly protuberant, directed dorsolaterally; corner of mouth with a protruding bony knob; tympanum ovoid, clearly visible. Skin of dorsum and limbs covered with flat tubercules, more numerous and pronounced on limbs, flanks and sides of head, sides with lateral row of large pointed tubercules. Forelimbs slender, relatively long, digits long; tips of digits bulbous; lengths of fingers 4<2<1<3; rudimentary webbing; edges of webbing slighlty tuberculated; thenar (metacarpal) tubercule round, subarticular and supernumerary tubercules present and presence of two tubercules on the second articulation of the finger 3. Hindlimbs slender, inner metatarsal tubercule oval, approximately two times as large as outer; plantar surface with

conical subarticular and many supernumerary tubercules. Length of toes 1<2<5<3<4, with well developed webbing; edges of webbing with numerous sipuculous tubercules.

Coloration: dorsum gray-brown with dark brown small patches; dark brown marks also on legs, tarsa and toes; belly cream slighlty orange with more and more small grey spots going to the flanks; throat light grey; interior suface of the tarsa and feet dark brown (except the webbing); no middorsal stripe.

Variation: This species is highly polymorphic. The coloration of the back varies from dark brown to light gray and sometimes even reddish (Fig. 4.3 a,f). The patterns are also very variable with a variety of leaf like patterns with successive shades of dark to light brown or gray. A whitish middorsal stripe can occur and can be very thin to 5 mm wide.

Vocalization.- The advertisement calls are 295 ms long and composed of approximately 6 groups of pulses on average (Table 4.2, Fig. 4.4). These pulses are usually in pairs except the last pulse group that comprises more pulses (up to six). The frequency (mean=1.17 kHz) increases during the call while the time between pulse groups decreases.

Distribution and Ecology.-This species occurs in most of Suriname including Brownsberg Nature Park, Goliathberg area, Lely mountains, Kaysergebergte, Sipaliwini and Raleighvallen; in southern French Guiana in "Savane layon ouest - Haute Wanapi" and "Sud-Mitaraka", and it is known from Guyana, i.e. Bartica, Kurupukari and Baramita. This species is probably also present in adjacent areas of Brazil and may extend into northeastern Venezuela. No difference in habitat or reproductive behaviour between this species and *R. margaritifera* have been noticed but we know very little about their respective ecologies. This species was observed calling at dawn and during the night in small groups on the road leading to the camp of Brownberg Nature Park after heavy rainfall in January 2006.

Etymology.- The name of the species honors the herpetologist Christian Marty who has study the herpetofauna of French Guiana for decades providing a geat contribution to our current knowledge.

3.2. Rhinella lescurei sp. nov.

Holotype.- 2006.2608 MNHN, an adult male collected 16 April 2004 by Philippe Gaucher from "Saut wanapi", Haute Wanapi, French Guiana (02°30'694"N/53°494'153"W), 170m above sea level (see Fig. 4.1: 18).

Paratypes.- 2006.2609 MNHN, 2006.2610 MNHN, 2006.2612 MNHN, 2006.2613 MNHN, four males collected in the same time and place. 2006.2611 MNHN, a female collected by Corine Sarthou at "layon savane Ouest", a very close site from the above one.

PG 103, PG 104, (Philippe Gaucher personal collection) two males collected 12 December, 2002 by Philippe Gaucher from "Crique Limonade", Saül, French Guiana (03º37'N/53º12'W, 100 m above sea level). T3027 (Universite Montpellier-2), collected 10 March, 2001 by Philippe Gaucher from "Mitaraka-Sud", French Guiana (02°16'N/54°31'W, 170 m above sea level). 112BM (Michel Blanc personal collection), a male collected by Michel Blanc from "Litany", French Guiana (02°26'195"N/54°25'184"W, 30 m above sea level). 121BM (Michel Blanc personal collection), a male collected by Michel Blanc from Saül, French Guiana (03º37'N/53º12'W, 100 m above sea level). 5MC, 5'MC (Christian Marty personal collection) a female and a male collected in amplexus by Christian Marty from "camp sisam", French Guiana (04°11'N/52°22'W, 100 m above sea level).

Diagnosis.-A medium sized species of the *R. margaritifera* species group as defined genetically by Fouquet et al. (2007; Chapter 2) and morphologically by Hoogmoed (1990) and Vélez-Rodriguez (2004). It is distinguished from all other species of this complex by the following combination of characters (Fig. 4.5): (1) SVL of two females 43.7 ± 0.8 mm, of eight males 34.6 ± 4.3 mm; (2) bony knob at angle of jaws absent, corner of mouth angular; (3) *canthus rostralis* smooth, concave laterally, without crests; (4) heel not reaching posterior margin of eye when hindlimbs adpressed; (5) cephalic crests low; (6) neural spines indistinct; (7) tympanum large but smaller than eye diameter, round in males, ovoid in females; (8) paratoid glands relatively small, elongated posteriorly; (9) upper eyelid without projections; (10) toes about three-quarters webbed, three phalanges free on toe 4; (11) tarsal fold absent; (12) skin densely tuberculate, particularly on limbs, less between eyes and center of back in females; tubercules conical with small keratinized spicules; (13) oblique row of tubercules present from posterior corner of pratoid glands to groin; (14) snout pointed with fleshy soft ridge extending to tip of snout; (15) iris golden.

Rhinella lescurei (D) can be distinguished from *R. margaritifera* (A), *R. hoogmoedi, R. martyi* (C), *R. stanlaii*, *R. sclerocephala*, *R. roqueana; R. alata* and all the unnamed *Rhinella* species from Colombia identified by Vélez-Rodriguez (2004) by its smaller SVL, the absence of prominent cranial crests, and the very pointed snout due to the presence of a distinct fleshy ridge (Table 4.1 and see Fig. 4.5). It can be distinguished from *R. proboscidea* (after Hoogmoed 1986) by its smaller SVL, densely tuberculate skin (smooth skin in *R. proboscidea* although see Zimmerman and Bogart, 1988) and distinct paratoids (indistinct in *R. proboscidea*). *Rhinella lescurei* (D) can be distinguished from *R. dapsilis*, by its tuberculate skin and smaller size and from *R. acutirostris* by its smaller SVL, more pointed snout, angular corner of the jaws, and its small supratympanic ridges (in males and females).

From *Rhinella scitula*, it can be mostly distinguished by the poorly distinct cephalic crests, a more pointed snout, and less distinct paratoids. From *R.* sp. E (in sympatry in French Guiana and with which it can be easily confused) and *R. castaneotica*, it can be distinguished by its larger size, the color of the iris (golden vs blue to green in *R.* sp. (E) and greenish yellow in *R. castaneotica*), the presence of a fleshy ridge at the tip of the snout, larger eyelids (UEW), longer tibia (TIBL), by having its nostrils closer to each other (IND), by having a clearly distinct tympanum, the presence of a lateral row of tubercules, and the outer metatarsal tubercule only two times smaller than the inner one (three times in *R. sp.* (E) and *R. castaneotica*). *R. lescurei* (D) is distinguishable from *R. magnussoni* by its slightly smaller size and by the tuberculated margins of the external part of the feet and the toes.

Description of holotype.- 2006.2608 MNHN (Fig. 4.5)

SVL 38.3 mm; HW 14.6 mm at angle of jaws; head shorter than wide, HL 12.8 mm. In dorsal view, snout acuminate, protruding and rounded in lateral view, with pointed vertical fleshy ridge from tip of snout to mouth; canthus rostralis strongly concave, smooth, without crests; top of head flat; cephalic crests poorly developed; paratoid poorly developed, elongated posteriously; eyelid thick, wide, densely tuberculate; nares slightly protuberant, directed dorsolaterally; corner of mouth very angular; tympanum clearly visible, ovoid. Skin of dorsum and limbs covered with high spicules, more numerous on outer edges of limbs, eyelids, and jaws; sides with a lateral row of large tubercules. Forelimbs slender, relatively long, digits long; tips of digits slightly bulbous; lengths of fingers 4<1=2<3; webbing basal; edge of webbing spinulous; thenar (metacarpal) tubercule ovoid, subarticular and supernumerary tubercules present (Fig. 4.5). Hindlimbs slender, inner metatarsal tubercle ovoid, approximately two times as large as outer; plantar surface with conical subarticular and many supernumerary tubercles. Length of toes 1<2<3<5<4, webbing well developed, edges of webbing very spinulose (Fig. 4.5).

Coloration: The dorsum has a leaf like pattern with successive shades of dark to light brown (Fig. 4.5). Dark brown triangular area are present on the head and lighter patches begin occur between the eyes and the middle of the flanks. Another dark brown mark begins at the middle of the flank and ends before the junction with legs; darker marks are also present across suface the limbs and the fingers. A large dorsal cream stripe extends from the tip of the snout to the end of the body. The flanks are dark brown except for a lighter mark under the eye. The throat is black with very smal white dots, and the belly is cream with large black spots.

Variation: This species is also highly polymorphic. The coloration of the back can be uniformly brown to light gray or with a variety of leaf-like patterns (Fig. 4.3 a,f) with successive shades of dark to light brown or gray. A whitish mid-dorsal stripe can occur and can be very thin to 5 mm wide. Flanks are generally darker than the back.

Vocalization.- The calls are long (several seconds) and composed of very short pulse groups that last for 30 ms (Fig. 4.6, Table 2). Pulse groups are spaced out by 97.2 ms and comprise 4.8 pulses / group on average. The peak frequency is 1.16 kHz and the pulses last 3.45 ms on average.

Distribution and Ecology.-*Rhinella lescurei* is only known from French Guiana, i.e. the southwestern (Haute Wanapi and Mitaraka), central (Saül), western (Litany) and northeastern portions (Cisame camp on Approuague river, Pararé station on Aratai river). Localities range from 20 to 170 m above sea level. During the rainy season (from November to January and from March to May), males call during day time within 10 meters of slowly running water. Calling males are usually isolated from each other and perched between 0.3 and 1 m high on a vine, dead trunk or root. Amplexus is axillary. *Rhinella lescurei* probably occurs in southeastern Suriname and Brazilian areas adjacent to French Guiana and Suriname. Preliminary results of an analysis of genetic data spanning the distribution of the *R. margaritifera* group suggest that this taxon could be endemic to the Guiana Shield (Fouquet et al., 2007; Chapter 2+5).

Etymology.-The name of the species honors the herpetologist Jean Lescure who has worked in French Guiana for decades and is considered the most important founder of French Guianan herpetology.

4. Discussion

4.1. Rhinella martyi

Rhinella margaritifer (A) and *R. martyi* (C) are morphologically and genetically close. However, morphological (Fig. 4.2) and genetic differences (Chapter 2) are clear and congruent. These are probably sister species originating in allopatry prior to the Pleistocene according to the high genetic distance between the two lineages (Fouquet et al., 2007; Chapter 2). They are probably in contact in the southern half of French Guiana. A more detailed study using more samples across a greater geographic range would probably reveal additional diagnostic characteristics.

The structure of the vocalizations are only slightly different between *R. margaritifera* (A), *R. martyi* (C), the *R. margaritifera* complex from Bolivia (Köhler et al., 1997), the *R.*

margaritifera complex from Amazonian Peru (Duellman, 2005) and *R.* sp. E (Fig. 4.4; Table 4.2). *Rhinella* sp. (E) can be distiguished by the peak frequency, which is higher (1.4 kHz) than in the three others. The differences between the vocalizations of *R. margaritifera* (A) and *R. martyi* (C) are small and would probably require a much more important sampling to be discriminated. The peak frequency is slightly lower in *R. martyi* (1.17 kHz) than in *R. margaritifera* (A) (1.26 kHz). Bolivian populations referred to the *R. margaritifera* complex displayed longer calls (316 ms, sd = 15), with a lower dominant frequency (1.14 kHz, sd = 0.01) and more pulse groups per call (7.9, sd = 0.6) than any of the French Guianan lineages. Calls described in Lescure and Marty (2000) and available in Marty and Gaucher (2000) as *B. margaritifer* and *B. typhonius* correspond respectively to *R. margaritifera* (A) and *R.* sp. (E).

4.2. Rhinella lescurei

This species shares morphological characteristics with *R. proboscidea* and *R. magnussoni* with which it probably has close relationships. However, there are slight morphological differences and clear acoustic differences with *R. magnussoni* (Lima et al., 2007) and *R. proboscidea* (Zimmerman and Bogart, 1988). Peak frequency in *R. magnussoni* is between 2.14 and 2.26 kHz and between 1.63 and 3.20 kHz in *R. proboscidea* while it is around 1.16 kHz in *R. lescurei*. The structures of the vocalizations are also different because *R. lescurei* produces groups of pulses (Fig. 4.6) while there is only a simple structure in *R. magnussoni* and a different structure in *R. proboscidea* which produces longer notes (0.12 s). The structure of *R. lescurei* calls is the most peculiar of the four species occurring in French Guiana (Fig. 4.6, Table 4.2). The calls are much longer (several seconds) than the three other Guianan lineages and are composed of very short pulse groups that last for 30ms. Pulse groups are more widely spaced (mean 97.2 ms between pulses) and have more pulses per group (mean = 4.8 pulses/group). These pulse groups are more spaced out (mean 97.2 ms) than in the other species. There are also more pulses per pulse group (mean = 4.8 pulses/pulse-group). The peak frequency and duration are much lower than in the other species (duration mean = 3.45 ms).

4.3. Rhinella sp (E)

Phylogeny topology in Fouquet et al. (2007; Chapter 2) suggests that *R.* sp. (E) and *R. castaneotica* are different species, *R.* sp. (E) being the most basal of the group (see also Pramuk (2006), and Vélez-Rodriguez (2004) for *R. castaneotica* phylogenetic position). However, we did not find any obvious character differences between *R.* sp. (E) and *R.*

castaneotica from Parà as described by Caldwell (1991). Moreover, the ecology of *R*. sp. (E) is also similar to that of *R. castaneotica* except that *R*. sp. (E) in French Guiana usually uses stalks of dead palm leaves full of water or small holes in dead trunks instead of the fruit capsules of the Brazil nut tree used for breeding by Brazilian populations. We consequently need further analyses, especially to compare specimens of these two species and different kinds of data (e.g. vocalization, larval morphology, detailed osteology, etc.), to be able to adequately describe this species. This species is also one of the two "undescribed" species in Haas (2004).

4.4. Other undescribed species

The other "undescribed" species (sp. 1) from Kaw Mountain (north of French Guiana), according to Haas (2004) is supposedly smaller than *R. margaritifera*, with indistinct paratoids and lacks hypertrophied cranial crests. We assume that Haas (2004) examined small and probably relatively young *R. margaritifera* individuals in which paratoids and cranial crests are not yet fully developed (pers. obs.). However, one lineage (*R. margaritifera* B) appears to be restricted to the Kaw Mountain (north of French Guiana) as detailed in Fouquet et al. (2007; Chapter 2) but we sampled too few individuals of the lineage to add this group to our morphometric analysis. Nevertheless, we did not notice any obvious morphological differences with *R. margaritifera* (A) (e.g. hypertrophied cephalic crests) and the genetic data indicated that *R. margaritifera* A and B are indeed very close and are unlikely to represent different species. Consequently, it is very unlikely that a species morphologically different from *R. margaritifera* is occuring in this region.

4.5. Rhinella dapsilis

R. dapsilis appears to be genetically very close to *R. margaritifera* (A) in Fouquet et al. (2007; Chapter 2) who used a mitochondrial DNA sequence published by Pramuk (2006). Both are closer to each other than to *R. martyi* (C). However, *R. dapsilis* and *R. margaritifera* are supposedly morphologically different (Myers and Carvalho, 1945). The main differences are that *R. dapsilis* lacks cranial crests and has smooth skin. Moreover, Pramuk (2006) used specimen (QCAZ 3509) sampled near Pichincha which is on the pacific side (trans-Andean) of the Andes while *Rhinella dapsilis* is supposed to be distributed on the Amazonian side (Cis-Andean). To fully elucidate the taxonomic relationship between these entities requires additional work, but we can make several hypotheses: (1) *R. dapsilis* and *R. margaritifera* (A) originated relatively recently from a common ancestor and *R. dapilis* secondarily lost

prominent cranial crests and rough skin. (2) The *R. dapsilis* sequences from Pramuk (2006) come from a misidentified specimen of a close relative of *R. margaritifera* (A) or even from a cross-contamination. In any case, it is interesting to note that the lineage formed by *R. margaritifera* A+B+*R. dapsilis* from Pramuk (2006) could be present from north French Guiana to the other side of the Andes in Ecuador through the Amazon Basin. The second hypothesis is most likely because we re-examined the *R. dapsilis* specimen that Myers and Carvalho (1945) described (an adult female without any cranial crest and smooth skin) and confirmed that *R. dapsilis* is a valid species. However, we have yet to find another female with similar dimensions and characteristics. Moreover, the males that have been identified as *R. dapsilis* from different collections are associated with females having very high crests suggesting probable misidentification (Vélez-Rodriguez pers. obs.).

5. Conclusion

When several kinds of data converge to similar results this provides strong support for independent specific status. Here, even if differences are small between *R. margaritifera* and *R. martyi*, the use of fine analytical tools provide evidence that they belong to different species and help describing them. However, morphometric, acoustic and genetic data are in conflict concerning the relationship between *R. lescurei* and the other lineages occuring in French Guiana. Morphological similarities exist between *R. lescurei* (D) and *R.* sp. (E) (Fig. 4.2), particularly the lack of developed cephalic crests. However, it shares a more recent common ancestor with *R. margaritifera* (A) and *R. martyi* (C) than with *R.* sp. E according to genetic data (Fouquet et al., 2007; Chapter 2) and its vocalizations are considerably different from all other species. Such incongruences are common and underline the cryptic trend in amphibian morphological evolution (Bickford et al., 2007) and the relevance of incorporating multiple types of data like acoustic, genetic and morphometric.

The taxonomy of the *R. margaritifera* species remains confusing, but with the help of additional molecular and ecological data we are confident that it can be resolved in the near future.

References

Bickford, D., Lohman, D.J., Sodhi, N.S., Ng, P.K., Meier, R., Winker, K., Ingram, K.K., Das, I. 2007. Cryptic species as a window on diversity and conservation. *Trends in Ecology and Evolution*, **22**(3), 148–155.

Caldwell, J.P. 1991. A new species of toad in the genus *Bufo* from Pará, Brazil, with an unusual breeding site. *Papéis Avulsos de Zoologia*, **37**, 389–400.

Caramaschi, U., de Niemeyer, H. 2003. Nova espécie do complexo de *Bufo margaritifer* (Laurenti 1768) do estado do Mato Grosso do Sul, Brasil (Amphibia, Anura, Bufonidae). *Boletim do Museu Nacional*, **501**, 1–16.

Caramaschi, U., Pombal, jr. J.P. 2006. A new species of *Rhinella* (Fitzinger, 1826) from the Atlantic rain forest, eastern Brazil (Amphibia, Anura, Bufonidae). *Papéis Avulsos de Zoologia*, **46**(23), 251–259.

Charif, R.A., Clark, C.W., Fristrup, K.M. 2004. *Raven 1.2 User's Manual*. Cornell Laboratory of Ornithology, Ithaca, NY.

Duellman, W.E. 2005. *Cusco Amazónico: the lives of amphibians and reptiles in an Amazonian rainforest*. Cornell University Press, Ithaca and London, 472 p.

Fouquet, A., Vences, M., Salducci, M.–D., Meyer, A., Marty, C., Blanc, M., Gilles, A. 2007. Revealing cryptic diversity using molecular phylogenetics and phylogeography in frogs of the *Scinax ruber* and *Rhinella margaritifera* species groups. *Molecular Phylogenetics and Evolution*, **43**(2), 567–582.

Frost, D.R. 2004. *Amphibian species of the world: an online reference*, American Museum of Natural History, pp. Electronic Database accessible at http://research.amnh.org/herpetology/amphibia/index.html.

Frost, D.R., Grant, T., Faivovich, J., Bain, R.H., Haas, A., Haddad, C.F.B., De Sà, R.O., Channing, A., Wilkinson, M., Donnellan, S.C., Raxworthy, C.J., Campbell, J.A., Blotto, R.L., Moler, P., Drewes, R.C., Nussbaum, R.A., Lynch, J.D., Green, D.M., Wheeler, W. C. (2006). The amphibian tree of life. *Bulletin of the American Museum of Natural History*, **297,** 1–370.

Haas, W. 2004. Beitrag zur biologie und verbreitung dreier vertreter des neotropischen *Bufo typhonius*-komplexes (Anura: Bufonidae). *Salamandra*, **40**(3/4), 207–216.

Hoogmoed, M.S. 1977. On the presence of *Bufo nasicus* (Werner) in Guiana, with a redescription of the species on the basis of recently collected material. *Zoologishe Mededelingen, Leiden*, **51**, 265–275.

Hoogmoed, M.S. 1986. Biosystematic studies of the *Bufo "typhonius"* group: A preliminary progress report. In: Rocek, Z. (ed.), *Studies in Herpetology*. Prague, pp. 147–150.

Hoogmoed, M.S. 1990. Biosystematics of South American Bufonidae, with special reference to the *Bufo "typhonius"* group. In: Peters, G. and Hutterer, R. (eds.), *Vertebrates in the tropics.* Museum Alexander Koenig, pp. 113–123.

Hoogmoed, M.S., Avila-Pires, T.C.S. 1991. Observations on the herpetofauna of Petit-Saut Sinnamary River French Guiana. In: Hallé, F. and Blanc, P. (eds.), *Biologie d'une canopée de forêt équatoriale, Rapport de mission*, pp. 222–228.

Jiménez-de-la-Espada, M. 1875. *Vertebrados del viaje al Pacifico verificado de 1862 a 1865 por una comisión de naturalistas enviada por el Gobierno Español*. Batracios. Imprenta de Miguel Ginesta, Madrid.

Lötters, S., Köhler, J. 2000. A new toad of the *Bufo typhonius* complex from humid montane forests of Bolivia (Amphibia, Anura, Bufonidae). *Spixiana*, **23**, 293–303.

Lescure, J., Marty, C. 2000. *Atlas des amphibiens de Guyane*. Patrimoines naturels, **45**, 388 p.

Lima, A.P., Menin, M., De Araùjo, M.C. 2007. A new species of *Rhinella* (Anura: Bufonidae) from Brazilian Amazon. *Zootaxa*, **1663**, 1–15.

Marty, C., Gaucher, P. 2000. Guide sonore des Amphibiens Anoures de Guyane. Centre de Bioacoustique Alpin.

Melin, D. 1941. Contributions to the knowledge of the Amphibia of South America. *Kungliga. Vetenskaps- och Vitterhets-Samhälles Handlingar, Series B*, **1**(4),1–71.

Mijares-Urrutia, A., Arends, A. 2001. A new toad of the *Bufo margaritifer* complex (Amphibia: Bufonidae) from northwestern Venezuela. *Herpetologica*, **57**, 523–531.

Myers, G.S., de Carvalho, A.L. 1945. Notes on some new or little-known brazilian amphibians, with an examination of the history of the plata salamander, *Ensatina platensis*. *Boletim do Museu Nacional*, **35**, 1–24.

Köhler, J., Reichle, S.; Bonn, G.P. 1997. Advertisement calls of three species of *Bufo* (Amphibia: Anura: Bufonidae) from lowland Bolivia. *Stuttgarter Beiträge zur Natukunde (A)*, **562**, 1–8.

Vélez-Rodriguez, C.M. 2004. *Sitemática de los sapos neotropicales pertenecientes al grupo Bufo typhonius (Bufonidae)*. Tesis Doctoral. Universidad Austral de Chile, Valdivia Chile, 159 p.

Vélez-Rodriguez, C.M., Ruiz-Carranza, P.M. 2002. A new species of *Bufo* (Anura: Bufonidae) from Colombia. *Herpetologica,* **58,** 453–462.

Zimmerman, B.L., Bogart, J.P. 1988. Ecology and calls of four species of Amazonian forest frogs. *Journal of Herpetology*, **22**(1), 97–108.

Chapter 5:

Multiple refuges during Pliocene and Pleistocene in the eastern Guiana Shield revealed by comparative phylogeography among 18 frog species.

Abstract

The Guiana Shield is a sub-region of Amazonia, one of the richest areas on Earth biologically. This is one of the most pristine areas of Amazonia, and is still largely unexplored biologically. For nearly four decades, prevailing theory has indicated that this region served as a forested refuge during periods of increased aridity associated with climatic oscillations (glaciations) during the Pleistocene. However, both the mechanisms of forest fragmentation and the timing of speciation in the neotropics have recently become the subject of much debate. In order to overcome the limitations of studies focusing on a single species or species group, we investigated patterns of genetic structure within 18 species of frogs from the Guiana Shield to test for evolutionary patterns consistent with Pleistocene isolation in a single refugium. We used mitochondrial and nuclear sequence data to compare intraspecific patterns of genetic diversity spatially and temporally. With one exception all species reveal a history of repeated fragmentation/isolation within the eastern Guiana Shield during the last 4 million years. Rather than one Pleistocene forest refugium, the Guiana Shield was repeatedly fragmented into multiple refugia during late Pliocene and Pleistocene. Levels of intraspecific genetic divergence suggest that a number of lineages within the Guiana Shield may merit specific recognition. Thus, the endemism of the Anuran fauna of the Guiana Shield is likely to be much higher than current estimates, a factor that will certainly influence future conservation efforts.

Key words: Guiana Shield, Anura, comparative phylogeography, refugia, Pleistocene.

1.Introduction

As concern grows over the destruction of tropical forests (Da Silva et al., 2005; Laurance, 2007; Laurance et al., 2002; Lyles, 1988; Pounds et al., 1999), the consequences of climate change (Bush et al., 2004; Rull and Vegas-Vilarrubia, 2006) and the global decline of amphibians (Beebee, 1992; Mendelson et al., 2006; Pounds, 2001; Stuart et al., 2004), it is imperative that we understand both the extent and evolutionary history of the biodiversity represented by tropical amphibians. The neotropics are particularly important because they host the greatest number of amphibian species on earth (Duellman, 1999). Though the latitudinal distribution bias in species richness towards the equator has been recognized for decades, the mechanism driving this pattern remains heavily debated (Klicka and Zink, 1997; Smith et al., 2007; Weir, 2006; Weir and Schluter, 2004; Wiens, 2007; Zink et al., 2004).

Two hypotheses, long considered incompatible, are often invoked to explain the global latitudinal gradient of diversity: either the tropics have functioned as a cradle of speciation or as a museum for older lineages (Lomolino et al., 2006; Stebbins, 1974). However, recent studies have shown this to represent a false dichotomy and that the disproportionately high levels of tropical biodiversity are the result of diversification both recent and ancient (Jablonski et al., 2006; Roelants et al., 2007). Studies of the evolutionary histories of particular groups have been complimented by a rapidly increasing understanding of Pleistocene paleoclimatic conditions based on a diverse array of climate proxies, mainly focusing on the Northern Hemisphere (Alexandrino et al., 2002; Emerson and Hewitt, 2005; Fedorov and Stenseth, 2002; Griswold and Baker, 2002; Hewitt, 2004; Hickerson and Ross, 2001; Hoffman and Blouin, 2004; Kotlik et al., 2004; Milot et al., 2000). Although these breakthroughs have greatly enhanced our understanding of the 'when', a great debate of the 'how and where' regarding the complex origins of neotropical biota has emerged (Bush, 1994; Noonan and Wray, 2006).

That global biodiversity has been directly impacted by geological events and frequent climatic fluctuations is widely accepted. Diversification mechanisms related to such changes have dominated the literature of neotropical biogeography since the proposal of the refuge hypothesis by Haffer (1969). Since this time, a great deal of effort has been directed at determining not if, but which climatic factors have influenced biotic diversification. Initially, perceived patterns of biotic distribution in Amazonia led Haffer (1969) to suggest the presence of refugial isolates of moist forest during periods of increased aridity coincident with temperate glacial maxima. Subsequent work (e.g. Bush, 1994; Colinvaux et al., 2000; Colinvaux et al., 1996; Rull, 2004a) examining paleofloral community structure revised this

view in light of the scant evidence for significant changes in precipitation in te region and brought to light what is now believed to be the primary driver of paleodistributional change in the Neotropics, temperature. This work has been tested by examining the historical biogeographic patterns of taxa likely to be influenced by changes in temperature, which has substantiated the role of temperature in driving changes in habitat continuity (Noonan and Gaucher, 2005; 2006).

With the recognition that temperature has a primary influence on the diversification of Neotropical biota, the focus turns to the question of what precipitated these thermal changes and promoted diversification. Early work focused primarily on the influence of temperate glacial cycles during the late Pliocene and Pleistocene. Quaternary glaciations, which began approximately 2.5 million years ago (mya) (Andriessen et al., 1993; Bloemendal and Demenocal, 1989; Hooghiemstra, 1989; Liu and Herbert, 2004; Ravelo et al., 2004; Van der Hammen and Hooghiemstra, 1997), had a demonstrable effect on the diversity and distributions of temperate flora and fauna and predictions based on these observations have been extended by many researchers to the neotropics (see reviews in Haffer, 1997; Moritz et al., 2000). However, paleoclimatic data tend to reject widespread, temporally coincident fragmentation of Amazonian lowland forest during the Pleistocene (Colinvaux et al., 2000; Mayle et al., 2004).

Nevertheless, there are evidences from palynology (see Van der Hammen & Absy, 1994; Hooghiemstra, 1997) and geomorphology (reviewed by Clapperton, 1993) that at least some areas on the periphery of Amazonia were considerably drier during the ice ages, but other areas show signs of a wetter climate in the same period. It is therefore impossible to generalize about past climate for the whole region from the meagre data which is currently available, particularly when there is a paucity of data from central and eastern Amazonia (Pennington et al., 2000). However, patches of savannas occur today on the coast and in the interior of the Guiana Shield due to poor and sandy soils associated with a dry corridor running from Venezuela to North East Brazil (Pennington et al., 2000). This segregates two "wet" blocks of Amazonia, the extreme eastern part of the Guiana Shield and the western half of Amazonia. Recent use of ecological niche modelling (Bonaccorso et al., 2006; Peterson and Nyàri, 2007) led to the prediction of past range fragmentation for forest birds species on each side of this corridor which was probably even drier at the last glacial maximum than today.

The possibility that the influence of climatic cycles on the distribution of neotropical biota might result more from the eccentricities of Earth's orbit than polar glaciation was first

raised by Colinvaux (1993) and expanded upon by Bush (Bush, 1994; Bush, 2005; Bush et al., 2002) and Mayle et al. (2004). This proposal, referred to as the Disturbance-Vicariance hypothesis (DV) by Moritz et al. (2000), suggests that although orbital (Milankovitch) cycles are inextricably linked to temperate glaciations, the various components (precession, obliquity, and eccentricity) of these cycles occur at different time scales and likely supersede temperate glaciations in their influence on tropical climate. The DV hypothesis invokes changes in temperature (±4°C) and atmospheric CO_2 levels associated with precessional cycles as the dominant factor (with reductions in precipitation of perhaps 20%) influencing the historical continuity of Amazonian communities.

However, the predicted effects of the DV hypothesis on lowland species (those occurring continuously between 0 and 600m above sea level (asl)) are less clear than for temperature sensitive species today accociated with highlands. Previous studies specifically testing DV predictions have exclusively targeted highland species (Rull, 2004b; 2005; 2007; Rull and Nogue, 2007) or species that were *a priori* expected to exhibit altitudinal fidelity (an expectation of DV) (Noonan and Gaucher 2005; 2006). While Bush (1994) suggests that Amazonian lowland species may have experienced crowding during cool periods (due to the influx of species adapted to adjacent higher altitudes), there is no explicit expectation for the formation of barriers to gene flow between populations of lowland species. The Guiana Shield is located on the NE coast of South America and is bound on the west by the Rio Orinoco and Rio Negro, and in the south by the lower reaches of Rio Amazonas (Fig. 5.1). Within the Guiana Shield itself two distinct areas can be segregated, the Tepuis of Venezuela and Guyana on the west and the eastern Guiana Shield. Rupununi savannas areas of the Essequibo-Rio Branco (Guyana-Brazil Roraima) depression separate these two portions of the Guiana Shield. The eastern region, on which we will focus, comprises French Guiana, Suriname, eastern Guyana, a portion north of the Rio Amazonas of Pará and Amazonas states and Amapá state. The elevation of the eastern Guiana Shield is mostly below 400m asl with only a few relief above this elevation especially in the interior of the shield.

The predictions of the DV Hypothesis have been investigated by Rull (2004a; b; c; 2005), who examined geographic patterns of plant distributions in the western Guiana Shield highlands (Tepuis); and by Noonan and Gaucher (2005; 2006) who examined the phylogeographic structure of two patchily distributed amphibians associated with topographic elements in the eastern Guiana Shield. The lowlands of the eastern Guiana Shield represent an ideal setting to test for the effects of climatic cycles and differentiate the signal of glaciations from other climatic phenomena. While many other hypotheses have been proposed to explain

tropical diversification, many of which are unrelated to climate, (see Moritz et al., 2000 and Noonan and Wray, 2006 for reviews), all of these (as well as the refuge and the DV for lowland species) have either no direct impact on the eastern Guiana Shield or suggest that this area served as a single, continuous isolate during periods of broad fragmentation. Contrary to these predictions, high levels of intraspecific variation within the eastern Guiana Shield have been reported for a number of terrestrial species (Caron et al., 2000; Fouquet et al., 2007a; b; Chapters 2+3; Noonan and Gaucher, 2005; 2006). Such regionalized genetic variation suggests historical fluctuations in distributional continuity, likely in response to a changing environment (e.g. fragmentation during unfavourable conditions). The presence of multiple lineages within the eastern Guiana Shield suggests either fragmentation with subsequent differentiation within this region or immigration from adjacent regions.

In order to further understand the influence of paleoclimatic variation on tropical diversity, we investigated the genetic structure of 18 Amazonian frog species, focusing on the eastern Guiana Shield. As a result of their biphasic life cycle, permeable skin, and exposed eggs, frogs are particularly sensitive to climate change (Carnaval, 2002; Pounds and Crump, 1994; Pounds et al., 1999). Moreover, they are generally philopatric, have low vagility and thus, constitute important and appropriate model organisms for phylogeographical studies. Specifically, we tested whether allopatric or parapatric intraspecific lineages diversified in situ or ex-situ and estimated when this differentiation occurred. We subsequently tested for spatial and temporal congruence among the diversification patterns observed among species to determine whether these might correlate with intrinsic ecological traits or extrinsic common climatic phenomena. As far as we are aware, this study represents the first attempt to use both mitochondrial and nuclear data to test spatio-temporal patterns of tropical diversification in such a large amount of codistributed species simultaneously.

2. Materials and methods

2.1. Sampling

We used data from 1034 individuals (Table S5.1) attributed to 18 selected species (59 individuals/species on average) belonging to eight genera (2-3 species/genus). For 28 samples the data were exclusively downloaded from Genbank; all other specimens were collected during fieldwork by the authors in Suriname (AF, BPN), Guyana (BPN), French Guiana (AF, BPN) and Brazil (AF, MTR) or from tissue samples obtained from F. Catzeflis, P. Kok, R. Ernst, K. Elmer, A.C. Carnaval, P. Gaucher, M. Blanc, C. Marty and R. Boistel. We also used at least one representative for all the congeneric species occurring in French Guiana and all

available data from other congeneric species available in Genbank (208 species). Forty additional lowland species were used as outgroups (Table S5.2).

The 18 focal species were chosen as they spanned a variety of ecological and distributional characteristics. Nine are restricted to the Guiana Shield and nine are thought to be widespread over Amazonia (Text S5.1, Table S5.2). Twelve are thought to be exclusively inhabiting the forest, three (*Adenomera andreae*, *Leptodactylus mystaceus*, *Dendropsophus leucophyllatus*) are predominantly inhabiting the forest but can be found in open or modified habitat associated with adjacent forest, three (*Adenomera hylaedactyla*, *Scinax boesemani*, *Scinax ruber*) are predominantly from open habitat but generally associated with adjacent forest.

2.2. DNA protocol

Tissue was taken from thigh muscle or liver and preserved in 95% ethanol. Genomic DNA was extracted using either standard phenol chloroform or lithium chloride methods (Gemmell and Akiyama, 1996). Two mitochondrial DNA (mtDNA) and one nuclear DNA (nuDNA) fragments were amplified by standard PCR techniques. Primers used for amplification were those described by Salducci et al. (2005) for 16S and 12S rDNA and by Bossuyt and Milinkovitch (2000) for tyrosinase. For this last fragment we also designed additional primers for most genera (Table S5.3).

Sequencing was performed using ABI Big Dye V3.1 and resolved on an automated sequencer at Macrogene Inc. (Korea) and the University of Canterbury sequencing service (New Zealand). Sequences were edited and aligned with Sequencher 4.1 (Gene Code Corp). Newly determined sequences were deposited in GenBank (Table S5.1).

2.3. Data description

We used DnaSP 4.20 (Rozas et al., 2003) to obtain haplotypic (Hd) and nucleotide (Pi) diversity in each species and for mtDNA and nuDNA. DnaSP cannot take into account sites with alignment gaps in mtDNA or polymorphic sites within individuals in nuDNA. The estimation of the number of unique haplotypes and sequence polymporphism is then different than with network reconstruction (Table S5.2).

Tajima's D, Fu and Li's F and D tests of selection were conducted in each species and for both mtDNA and nuDNA datasets with DnaSP (Rozas et al., 2003).

2.4. Phylogenetic analyses

We collated all the data available for 12S and 16S rDNA (8 datasets) and for tyrosinase (8 datasets) for each Genus. The outgroups were chosen according to Grant et al. (2006) for *Allobates* and *Anomaloglossus*, Pramuk et al. (2007) for *Rhinella*, Heinicke et al. (2007) for Pristimantis, Faivovich et al. (2005) for *Dendropsophus* and *Scinax* and according preliminary analysis and Fouquet et al. (2007a; Chapter 2) for *Adenomera* and *Leptodactylus* (Table S5.2). Alignments of sequences were performed with Clustal X (Thompson et al., 1997) with a gap penalty equal to five, with other parameters set at the default settings. Alignments were verified by eye and obvious misalignments corrected if necessary.

We used the software Modeltest version 3.6 (Posada and Crandall, 1998) to select the substitution models that best fit each of our eight mtDNA datasets (with one sequence for each haplotype) using the Akaike Information Criterion (Akaike, 1981). These models (Table S5.4) were subsequently used for Bayesian analysis performed with MrBayes 3.1 (Huelsenbeck and Ronquist, 2001) on the University of Canterbury Supercomputer (http://www.ucsc.canterbury.ac.nz). Bayesian analysis consisted of 2 independent runs of 2.0×10^7 generations with random starting trees and 10 Markov chains (one cold) sampled every 1000 generations. Adequate burn-in (1.0×10^6) was determined by examining a plot of the likelihood scores in Tracer 1.3 (Rambaut and Drummond, 2003) of the heated chain for convergence on stationarity. We also employed maximum parsimony (MP) with PAUP 4.0b10 (Swofford, 1993). Support for proposed clades was assessed via 1000 nonparametric bootstrap pseudoreplicates (Efron, 1979; Felsenstein, 1985) with the heuristic search option, tree bisection-reconnection (TBR) branch swapping and 10 random taxon addition replicates. We considered relationships with posterior probabilities ≥0.95 and/or bootstrap percentages ≥70% (Hillis and Bull, 1993) to be strongly supported.

2.5. Statistical parsimony networks

Statistical parsimony networks were calculated separately for the nuDNA and mtDNA using TCS 1.21 (Clement et al., 2000), with a 95% connection limit. Because some haplotype groups were not connected to each other with the 95% limit of probability of parsimony as used by TCS, we attempted to connect them by decreasing the connection threshold down to a maximum of 30 steps. The probability threshold is indicated when above 90%. Less probable connections are indicated as <90% on the networks (Fig. S5.9-16).

We subsequently used Nested Clade Phylogeographic Analysis (NCPA) according to the criteria of Templeton (1998) to examine the relation between mtDNA haplotypes and geography. In order to infer geographical associations among haplotype clusters, clade (*D*c)

and nested clade (*D*n) distances were measured as straight-line distances by Geodis 2.2 (Posada et al., 2000). Historical factors influencing the evolutionary history of nested clades that demonstrated a significant association for haplotype and geography were inferred using the key of Templeton ((2004); 14 July 2004 version). Evolutionarily distinct haplotypic groups that were geographically isolated and separated by a large number of missing haplotypes we consider to be distinct lineages. We are aware of the different shortcomings inherent to the NCPA revealed by Panchal and Beaumont (2007) and underlined by Petit (2008). However, we choose to undertake these analyses believing they can provide useful insights about the evolutionary history of the species studied (Templeton, 2008) especially when combined with additional analyses (Garrick et al., 2008), keeping in mind their potential shortcomings.

2.6. Divergence time and rates of molecular evolution estimates

2.6.1. Relaxed Bayesian molecular clock

To obtain an estimate of the time of divergence for basal splits within species and to estimate molecular rates of evolution we used a relaxed Bayesian molecular clock with uncorrelated lognormal rates (Beast 1.4.6; Drummond and Rambaut, 2003). Thirteen divergence estimates from the literature were used to place priors on the age of nodes within our trees (Table S5.5). Eleven calibration points were set as normal distributions and two as upper bounds (Table S5.5). Twenty-three additional species were selected to represent these calibration points within our trees. Clades corresponding to these calibration points and all genera were set as monophyletic with the exception of Leptodactylidae. We used an estimate of 63 mya (±10) for the basal split of Hyloidea (the root of our tree) which is consistent with that used previously by Roelants et al. (2007) and San Mauro et al. (2005). This value can be considered as conservative because other dating have considered this clade to be potentially older (Pramuk et al., 2007; Wiens et al., 2005, Igawa et al., 2008).

Unresolved relationships among haplotypes and intraspecific lineages impact the time estimates and rates of evolution (Won and Renner, 2006). Thus, we collated the mtDNA dataset with all the species studied represented by a reduced number (total of 97 sequences; Table S5.4) of haplotypes and lineages per species to obtain a tree that was as resolved as possible.

The tree prior used the Yule Process (initial value=0.75), with a UPGMA starting tree and the operators were optimized by a preliminary run of 10^6 generations sampled every 1000 generations followed by two independent runs of 10^6 generations sampled every 1000

generations were undertaken. Adequate burn-in was determined by examining a plot of the likelihood scores of the heated chain for convergence on stationarity. We estimated the mtDNA rates of molecular evolution in each species by calculating the mean of the rates provided for each branch.

Due to the reduced size of the datasets used we needed to use other methods to estimate dates of diversification at the population level. To take into account the haplotype variability within species and estimate the of time divergence more precisely we used two other complementary methods described hereafter.

2.6.2. Coalescent-based method

In order to infer current and historical demographic parameters of the different lineages, we implemented the application MDIV (Nielsen and Wakeley, 2001) using CBSU Web Computing Resources (http://cbsuapps.tc.cornell.edu/mdiv.aspx; accessed October 2007). Using this method we were able to simultaneously estimate divergence times and migration rates between two "populations" under the finite sites model (HKY) (Nielsen and Wakeley, 2001). Analyses consisted of runs of 2.0×10^6 generations and burn-in of 50000 and were ran one time (M=5 and T=15) to estimate appropriate parameter values to bound a "well-behaved" posterior distribution and then a second time with appropriate θ, M and T values. We calculated coalescence time between "populations" (*t pop*) and between sequences (*t seq*) using the formula $t = T * \theta/(2u)$, where T (pop), Tmrca (seq) and θ are generated by the program, *u* is the mutation rate for the locus. We used the molecular rates of evolution estimated previously for each species (Relaxed Bayesian molecular clock) including 95% credibility intervals.

We compared all the pairs of lineages recovered with unambiguous relationships according to the mtDNA tree reconstructions. When relationships among clades were uncertain we also used the topologies provided by the trees, networks, and geography to design grouping.

2.6.3. Time of divergence with distance based method

Another method for estimating the time of divergence is to compare the distribution of pairwise distance (mismatch distribution) within each species. With this method the distributions and timing of divergence events are inferred without any phylogenetic prior among haplogroups.

We used PAUP with the optimal model of evolution selected previously for the divergence time estimates of the mtDNA alignment (relaxed Bayesian molecular clock) to obtain corrected pairwise distances between each haplotype. Using the rate of evolution calculated for each species we estimated corresponding time of divergence. We described the distribution using a mixture of normal distributions (Mc Lachlan and Peel, 2000). The parameters of the model were estimated using an expectation-maximization (EM) algorithm. We used the Bayesian information criterion (BIC) to choose the adequate model (i.e. number of components, up to 10) that best fit the pairwise distribution. This procedure was implemented using R 2.5.0 (R Foundation for Statistical Computing, 2005) and was repeated 100 times with a random starting point for each replicate.

Only a few distributions corresponding to the initial diversification within species can be directly compared with tree based estimations. For more recent events, several divergences have close pairwise distance means and overlap in the overall distribution. Consequently, to specifically compare coalescent and distance methods we also calculated the average pairwise distances among the same pairs used in the coalescence based method and used the estimated molecular rates of evolution to obtain time estimates.

2.7. Pattern of timing of divergences

To estimate the distribution of the divergence events we combined the (1) peak values of each pairwise distances normal distributions using a sliding window method (width 0.5 my, shifting each 0.05 my) and we added (2) all the pairwise distances distributions with each distribution with equal weight. We also estimated the distribution of the divergenve time point estimates chosen upon the phylogenetic recontruction (3) from mean corrected pairwise distances t seq (4) and t pop (5) from coalecsence based method. This procedure was implemented using R 2.5.0 (R Foundation for Statistical Computing, 2005).

2.8. Geographical analysis

In order to search for spatial congruence among genetic structures, we first mapped the distribution of each higher clade using MapInfo 7.0 (www.mapinfo.com). Each locality was represented by a delimited circle arbitrarily set as 25 km diameter. We used a classical convex polygon method (Mohr, 1947) to draw the connections between sampled localities to delimit the range of each lineage. The locations where breaks between lineages occur were mapped by drawing lines equidistant from each of the groups of points representing the different lineages. We did not use additional background layers to guide the drawing of these

lines to avoid biasing the results toward expected places, such as intervening valleys. These ranges were circumscribed within the corresponding convex polygon of the species. In the eastern Guiana Shield lineages were geographically near each other (parapatric), but westward and southward of the Guiana Shield the samples were farther apart and consequently caution should be taken interpreting observed patterns. To summarize the spatial pattern of breaks in genetic lineages, we counted the number of breaks crossing each 40km² grid cells across the eastern Guiana Shield.

The number of possible breaks in a given grid cell is influenced by the number of species ranges that cross that cell. For each grid cell we determined the number of species (polygons) intersecting it. Then, for each cell, we divided the total number of breaks by the total number of species to evaluate the spatial pattern of breaks, given the number of possible breaks.

We also mapped the range of each species according to the Global Amphibian Assessment (GAA) database which is the most accurate and updated resource for neotropical Anuran species. For more comprehensive illustration purposes we also mapped the range of some additional congeneric species (see text S1).

3. Results

3.1. Data description

Our study has generated 838 12S rDNA, 703 16S rDNA and 840 nuDNA sequences for the 18 selected species (Table S5.1). Additionally, 110 12S rDNA, 80 16S rDNA and 111 nuDNA sequences have been obtained for the congeneric species. Using additional published data a total of 1016 12S rDNA + 16S rDNA and 936 nuDNA were collated for the selected 18 species (Table S5.1). For the congeneric species a total of 307 12S rDNA + 16S rDNA and 161 nuDNA sequences have been collated.

Resulting alignment, for each genus range from 791 to 866 bp for mtDNA and from 524 to 617 for nuDNA sequences (Table S5.4). All the species display a large number of unique mtDNA haplotypes (mean Hd=0.8718), with the exception of *Dendropsophus leucophyllatus* in which only 5 haplotypes were observed in the 28 individuals examined (Hd=0.328) (Table S5.2a). Maximum haplotypic diversity was observed in *Adenomera andreae* (Hd=0.976) with 69 haplotypes (estimated from network reconstruction) from 91 individuals. The genetic variability of nuDNA is much lower (mean Hd=0.274), ranging from 0.000 in *D. leucophyllatus* to a maximum of 0.726 in *Scinax ruber* (Table S5.2b).

Tests of selection were significant in three cases for the mtDNA (Tajima`s D in *Rhinella castaneotica*, Fu and Li's tests in *Dendropsophus minusculus* and *Scinax ruber* (Table S5.2a). For the nuDNA data the tests were significant in six instances (the three tests were significant in *Adenomera andreae*, *Allobates femoralis*, *Dendropsophus minusculus*, *Scinax boesemani* and only Tajima`s D and Fu and Li's F were significant in *Pristimantis chiastonotus* and *Pristimantis zeuctotylus*; Table S5.2b).

3.2. Phylogenetic trees

All but three (*Leptodactylus mystaceus, Rhinella margaritifera, Scinax ruber*) of the 18 species were monophyletic with respect to the congeners included in our analyses (Fig. 5.2; Fig. S5.1-8). All species exhibited high levels of intraspecific mtDNA differentiation across their ranges, with most genetic structure corresponding to geographic distribution. All but *Dendropsophus leucophyllatus* possess two or more mtDNA lineages in contact or overlapping in the eastern Guiana Shield. In several species, the intraspecific genetic divergence (uncorrected) is very high, exceeding 10% in many instances. Though many of these haplotypes clearly cluster as independent lineages, the support for relationships among them is poor. The three observed instances of paraphyly (above) are strongly supported and include what are widely recognized as species complexes (de Sá et al., 2005; De la Riva et al., 2000; Fouquet et al., 2007a,b; Chapters 2,3; Hoogmoed, 1986; Toledo et al., 2005). Paraphyly is almost certainly due to the inadequate knowledge of the true taxonomy of the ingroup and the likely inclusion of multiple species in the sampling of our target 'taxon'.

The observed mtDNA haplotypic structure is strongly associated with geography in all species. There are however, three instances (*Adenomera hylaedactyla* Fig. 5.2, S5.1, *Rhinella margaritifera* Fig. 5.2, S5.7 and *Scinax ruber* Fig. 5.2, S5.8) in which the phylogenetic placement of a particular lineage comprised entirely of samples originating from western or central Amazonia renders Guiana Shield lineages paraphyletic. The relationships among lineages in *Adenomera andreae* and *Allobates femoralis* are not fully resolved but these species could also potentially display a pattern in which Guianan lineages represent a monophyletic group. In other species for which we have samples from outside the Guiana Shield (*Leptodactylus mystaceus* Fig. 5.2, S5.5 and *Rhinella castaneotica* Fig. 5.2, S5.7), representatives from the Guiana Shield formed a monophyletic lineage relative to all other populations. All other species are either endemic to or unsampled outside of the Guiana Shield.

3.3. Network reconstruction and NCPA

Haplotype network reconstructions of mtDNA data recovered groupings consistent with those identified by phylogenetic analysis (Fig. S5.9-16). Conflicts between network and tree reconstructions were associated only with clades receiving very low levels of support from phylogenetic analysis (e.g. *Adenomera andreae* Fig. 5.2, S5.1, S5.9a, *Allobates femoralis* Fig. 5.2, S5.2, S5.10a and *Anomaloglossus baeobatrachus* Fig. 5.2, S5.3, S5.11a).

The strong association between genetic structure and geography observed in phylogenetic reconstructions was also evident in haplotype networks for all species (Table S5.6). Nearly all higher clades within species correspond to discrete geographic areas with little overlap (Fig. 5.2, S5.17-24). This can be observed on the NCPA results and directly on the maps. This is particularly clear in *Adenomera andreae* (Fig. 5.2, S5.1, S5.9a, S5.17a) and *Anomaloglossus degranvillei* (Fig. 5.2, S5.3, S5.11a, S5.19a) in which only a very few sampled populations share haplotypes (Table S5.1). *Dendropsophus leucophyllatus,* on the other hand (Fig. 5.2, S5.4, S5.12a, S5.20a), displays very little genetic diversity (5 haplotypes) in the sampled Guiana Shield localities. In all but two (*Dendropsophus leucophyllatus* Fig. 5.2, S5.4, S5.12a, S5.20a, *Dendropsophus minusculus* Fig. 5.2, S5.4, S5.12b, S5.20b) of the 18 species examined there are obviously differentiated mtDNA haplogroups restricted to French Guiana, and in most of these instances (10/16) one of those groups is found only in the north of French Guiana (Fig. S5.9-16, S5.17-24). The north east of Suriname (Brownsberg and Lely Mountains) and northern Amapà (Brazil) also harbour unique haplogroups for a number of species.

While the coarse illustration of the geographic distributions of haplogroups (Fig. S5.17-24) suggests some overlap, there are actually few observed instances of occurrence within a single locality. Extensive geographic overlap of haplotype groups was encountered only in *Scinax ruber* (Fig. 5.2, S5.8, S5.16b, S5.24b) and *Anomalloglossus baeobatrachus* (Fig. 5.2, S5.3, S5.11a, S5.19a) of French Guiana.

3.4. Patterns of vicariance and dispersal inferred from NCPA

Despite the frequent inference of 'Inconclusive Outcome' due to low sample sizes for many (~50% of all haplogroups), structure of the mtDNA haplotype networks indicate that patterns of fragmentation (past fragmentation, allopatric fragmentation, and past gradual range expansion followed by fragmentation), dispersal (long distance colonization), and isolation by distance (restricted gene flow with IBD) all contributed to the origin of haplogroups for these lowland anurans. Inferences of fragmentation were the most frequent

(44), followed by expansion (31) and isolation by distance (22). Restricted gene flow and isolation by distance are mostly detected for lower clades. It was only detected in four 3-step clades (Table S5.6).

3.5. Tyrosinase networks

All focal species were recovered as independent nuDNA clusters (Fig. S5.25-33). Higher level intraspecific mitochondrial lineages (3 and 4 step clades) were also recovered in a number of species (e.g. *Allobates granti* Fig. S5.26, *Leptodactylus wagneri* species group Fig. S5.29). However, haplotype sharing between individuals having highly divergent mtDNA lineages was also observed (e.g. *Rhinella castaneotica* and *Rhinella margaritifera* Fig. S5.31)

3.6. Estimation of divergence times

3.6.1. Relaxed Bayesian molecular clock

The tree derived from the relaxed Bayesian molecular clock method is generally well resolved (posterior probabilities >0.95) (Fig. 5.3), the exceptions being varying degrees of ambiguity surrounding the relationships among seven genera and among five intraspecific mtDNA lineages.

The estimated rates of molecular evolution for each branch range from 0.0107 to 0.0026 substitutions/site/my (Fig. 3). Within the 18 target species, these rates range from 0.0086 (*Scinax ruber*) to 0.0035 (*Rhinella castaneotica*) with the mean for each species varying from 0.0061 to 0.0053 (Table S5.2). The estimated time of the earliest divergences within the 18 focal species studied all predate the Pleistocene (1.8 my). Of these earliest splits within the history of each species, only the lower bound of the 95% credibility interval (CI) of one (*Scinax boesemani)* extended into the Pleistocene. In fact, a Miocene date for initiation of intraspecific differentiation was more frequently observed (e.g. *Allobates femoralis*, *Anomaloglossus baeobatrachus)*.

3.6.2. Time of divergence using distance based method

We evaluated the distributions of pairwise distances within species (Fig. 5.4) using the BIC criterion. The patterns of pairwise distance ranged from a single normal distribution in *Dendropsophus leucophyllatus*, up to six modal peaks in *Scinax ruber*. The time of divergence estimations are mostly in concordance with Bayesian molecular clock method results, but in general, estimated dates were younger than those inferred using the Bayesian

relaxed clock method. The initial divergence in a number of taxa were estimated predate the Mio-Pliocene boundary (5.3 my), but the majority of intraspecific divergence events appear to have taken place prior to the Pleistocene (Fig. 5.4). The only exception is *Scinax boesemani* in which initial diversification occurred approximately 1.4 mya, during Pleitocene.

3.6.3. Coalescent-based method

Pairwise estimates (n=83) of divergence among haplotype groups were estimated using the coalescent method of Nielsen and Wakeley (2001) (Table S5.7). Again, the coalescence time of the sequences (*t seq*) predate the Pleistocene in all species (except *Scinax boesemani*) (Fig. 5.2, Table S5.7) but is generally slightly lower than with pairwise distance estimates. However, the coalescence time of the population (*t pop*) is generally much lower. Initial diversification within species predates Pleistocene in only 11 species and corresponds to the Plio-Pleistocene boundary in two additional species.

Gene and species tree are not the same because ancestral polymorphism generally predates the population divergence (Arbogast et al., 2002). This is why *t pop* values are lower than *t seq*. However, *t seq* estimates are expected to be similar to pairwise distances estimates but are in fact lower. This is probably due to a conjugation of reasons that makes the coalescence estimates relatively not precise: 1, the fact that MDIV exclude the indels of the alignment reduces the number of variable sites; 2, the HKY model employed in MDIV is less complex than the model used to estimate pairwise distances and probably underestimate the number of substitutions; 3, the use of single mtDNA marker in a phylogenetic based delimitation of the two "populations" compared have notorious poor resolution and very large credibility intervals (Wakeley and Hey, 1997; Carstens and Knowles, 2007). For these reason we will consider *t pop* estimates as the lower bound to the divergence events.

3.7. Temporal patterns of diversification

We summarized all previously described estimates of divergence times to extract a general pattern using distribution addition of each normal distribution (pairwise distance), a sliding window method on the means of each normal distribution (pairwise distance), the divergence time estimations from pairwise coalescence-based and distance-based methods (Fig. 5.5).

A strong peak in the number of diversification events is present between 4 and 2.3 mya with pairwise distances. This pattern is observed in 11 of our 18 species (*Adenomera andreae*, *A. heyeri*, *A. hylaedactyla*, *Allobates femoralis*, *A. granti*, *Anomaloglossus*

baeobatrachus, *A. degranvillei*, *Dendropsophus minusculus*, *Leptodactylus wagneri* C, *Rhinella margaritifera*, *Scinax ruber*). Almost all of the species endemic to the Guiana Shield (Fig. 5.2; Table S5.2) display a divergence during this period (the exception being the pairwise distance estimates obtained for *Pristimantis* ssp. and *Leptodactylus wagneri* B). This pattern is also observed in widespread species (*Adenomera andreae*, *A. hylaedactyla*, *Rhinella margaritifera* and *Scinax ruber*). In all but two species (*Allobates femoralis* and *Rhinella castaneotica*), at least one of these divergences events are between lineages in contact in the eastern Guiana Shield. A strong decline in the number of diversification events around 2.3 mya was observed, separating most Pliocene from Pleistocene events (Fig. 5.5). Then, from 2 to around 0.8 mya a strong increase in diversification is observed again. This increase in the number of observed haplogroup divergence events is a pattern common to all species except *Dendropsophus minusculus* and *Dendropsophus leucophyllatus* in which the divergences are actually estimated younger than 0.8 mya. These divergences occurred among Guianan lineages in all the species studied and among Amazonia VS Guiana Shield lineages in *Adenomera hylaedactyla*, *Allobates femoralis*, *Rhinella castaneotica*, *Rhinella margaritifera* and *Scinax ruber*.

With the coalescent method, gene divergences estimates strongly increase from 3 mya and steadily increase during the Pleistocene. A similar pattern is observed with population divergences but strongly increases only from 2 mya. There is no bimodal distribution observed in coalescence based estimates.

Also notable is that from 0.8 mya the diversity is not represented in punctual estimates because it corresponds to the timing of divergence among haplotypes of the same lower clades. However, diversity is represented in the distance distributions because the smallest pairwise distances within haplotype groups contribute to the last peaks.

3.8. Global spatial patterns of diversification in the eastern Guiana Shield

At least 72 % of the polygons of sampling of the species considered in the study overlap in French Guiana, Amapà and East of Suriname (Fig. 5.6d). Outside of this area data are more widespread and less abundant. Sampling has been extensive in French Guiana and a few localities in Suriname and Amapà. This allows fairly accurate delimitation of the geographic distribution of lineages occurring in French Guiana (but not for most of the lineages occurring in Suriname, Amapà and further localities). Consequently, it would be hazardous to interpret the patterns displayed by phylogeograpic breaks and uniform areas outside French Guiana. However, we observe that many of the "older" (2 mya or greater)

phylogeographic breaks occur outside this zone in the southern and western part of the Guiana Shield.

3.8.1. Pre Pleistocene

In the north-eastern portion of the eastern Guiana Shield, the earliest phylogeographic breaks are concentrated between Suriname and French Guiana along the North of the Maroni River (Fig. 5.6b: 1). This pattern is observed in all but two of the species for which we have specimens from Suriname (*Dendropsophus minusculus* and *D. leucophyllatus*). These early divergence events are also concentrated in the south-western part of French Guiana (Fig. 5.6b: 3) and between northern Amapà and French Guiana (Fig. 5.6b: 2). Conversely, uniform zones (zones with no or very few breaks) are located in the centre of the northern half of French Guiana (Fig. 5.6b: A and B), the central east region (Fig. 5.6b: C) and the extreme South (Fig. 5.6b: D and E).

3.8.2. Pleistocene

The phylogeographic breaks between lineages diverging during the Pleistocene are concentrated in the northern part of French Guiana, forming a North-South delineation (Fig. 5.6c:1 and 2). This delineation approaches coastal French Guiana around the Kaw swamps in the east. Indeed, a phylogeographic break between lineages diverging between 1 (no detected breaks occurred after) and 1.8 mya occurs in this region in 5 species (*Rhinella margaritifera*, *Leptodactylus mystaceus*, *Adenomera hylaedactyla*, *Allobates femoralis*, *Scinax boesemani*). These breaks are also concentrated between French Guiana and Suriname particularly in the South-East of Suriname (Fig. 5.6c: 3). Uniform zones are located in the center of the coastal region (Fig. 5.6c: A), the west of the central region (Fig. 5.6c: B) and the south region (Fig. 5.6c: C and D).

3.8.3. Total

When combined (Fig. 5.6a), observed phylogeographic breaks appear to be concentrated in two areas; the western border of French Guiana with Suriname (Fig. 6a: 1) and the eastern border with Brazil (Fig. 5.6a: 2). The former follows the course of the Maroni River in the north, but delimits inland areas in the South West of French Guiana and South East of Suriname. This biological break also corresponds to clear limits in ranges of other species such as *Hypsoboas crepitans*, *Dendropsophus marmoratus, Dendropsophus leali, Ameerega trivittata, Engystomops ephipiffer, Chaunus granulosus, Leptodactylus bolivianus*,

that occur exclusively to the west of the Maroni River. Conversely, *Engystomops petersi*, *Ranitomeya ventrimaculata*, *Dendropsophus brevifrons*, *Dendrophryniscus minutus*, *Allobates femoralis* and *Rhinella castaneotica* do not occur west of the Maroni River. Zones of uniformity are again found in the southwest (Fig. 5.6a: E), midwest (Fig. 5.6a: B), central and south east (Fig. 5.6a D and E) and central coastal regions of French Guiana (Figure 5.6a: A).

4. Discussion

Striking commonalities among the phylogeographic patterns of the lowland anuran species examined have been observed. Such splits among multiple species are likely the result of successive past climatic changes that promoted both dispersal and vicariance. However, the patterns observed are temporally and spatially varied and testify to complex evolutionary histories. Indeed, despite ecological and distributional similarities between some species assemblages we did not observe any species with identical phylogeographic patterns. This underlies the fact that all species have independent evolutionary histories driven by multiple factors such as different ecological characteristics, ancestral distributions and dispersal abilities.

It appears that in the Amazonian species studied, the eastern Guiana Shield played a major role in intraspecific diversification. Our data provide evidence that contradict the widely held view that the Guiana Shield was a single Pleistocene refugium (Haffer, 1969). Rather our data reveal a picture of eastern Guiana Shield geing fragmented into multiple refugia at multiple times during the Plio-Pleistocene adding considerable support to the findings of recent studies of eastern Guiana Shield anurans (Noonan and Gaucher, 2005; 2006).

Concordant with previous work (Moritz et al., 2000; Weir, 2006) our results fail to support the Pleistocene climatic fluctuations as the driving force behind the recent accumulation of species diversity in lowland Amazonian fauna. The estimated initial divergence time for all species studied precedes the Pleistocene, as does in many instances, intraspecific divergence between genetic lineages. Nevertheless, these climate fluctuations have had a profound influence on intraspecific diversification.

4.1. Refugia in the Guiana Shield: one or more?

4.1.1. Pliocene events

In nearly all species examined at least two, and in some cases such as *Adenomera andreae* many (Fig. 5.2, S5.8), of the observed phylogroups in the Guiana Shield originated prior to the end of the Pliocene. Because of the confounding effects of Pleistocene climate oscillations and different dispersal abilities, it is difficult to identify the geographic origin of these Pliocene groups. However, if the general lack of presently overlapping distributions of these phylogroups can be taken as evidence, it would seem that refugia were probably situated in northern French Guiana, eastern Suriname, and northeast Amapà.

Intraspecific Pliocene divergence (pairwise distances) was observed in all nine (of 18) species that are endemic (or nearly so) to the Guiana Shield, but also for some of the widespread species such as *Adenomera andreae*, *Rhinella margaritifera* and *Scinax ruber*. Most of these intraspecific splits are between 2.3 and 4 mya and have separated two or more lineages in the eastern Guiana Shield. Some species, however, such as *Scinax boesemani*, *Leptodactylus wagneri* B and *Pristimantis zeuctotylus* exhibit intraspecific divergence beginning only in the late Pliocene (2.3 mya or younger).

4.1.2. Pleistocene events

Successive phases of contraction and expansion of habitat patches within the Guiana Shield probably occurred and produced the current pattern of genetic structure with secondary contacts. Some Pleistocene intraspecific phylogroups exhibiting overlapping or parapatric distributions appear to have diversified in narrowly restricted areas of the Guiana Shield. This suggests that fluctuations in habitat continuity, likely linked to climatic oscillations, greatly impacted anurans populations by repeatedly isolating populations during the Pleistocene. Subsequent secondary contacts led to geographic overlap in few phylogroups, similar to (but rarely as extensive as) the pattern found in *Dendrobates tinctorius* (Noonan and Gaucher, 2006). On the other hand, many species, such as *Allobates granti,* have remained allopatric Pleistocene phylogroups, similar to previous findings for Guiana Shield frogs of the genus *Atelopus* (Noonan and Gaucher, 2005).

4.2. Historical interpretation

Temporal and spatial similarities are detected. The putative locations of refugia could have been either highly variable or recently blurred by different patterns of expansions. Given the apparent synchrony of intraspecific divergence and geographic commonalities we argue that extrinsic environmental factors (rather than intrinsic ecological factors) have successively

restricted the ranges of most lowland anuran species of the Guiana Shield between 4.0 and 0.8 mya.

The onset of temperate glaciation (~2.6 mya) coincides phylogroup origination according to distances and coalescence based estimates. It is clear however that a great deal of intraspecific diversity observed within the Guiana Shield dates to Pleistocene age. This period also coincides with the final upheaval of the northern Andes and the closure of the Panamanian Isthmus between 3.0 and 2.5 mya (see Coates and Obando, 1996; Graham, 1992; Webb, 1985; Webb, 1991). This closure changed both the Atlantic and Pacific water circulation, facilitating the installation of the Arctic polar icecap (Jackson and D'Croz, 2003; Shackleton, 1995; Shackleton et al., 1984). Concomitantly, ice sheet formation was initiated in West Antarctica (Rabassa, 1999). In Patagonia, a major glaciation complex was recorded ca. 2.3 mya (Mörner and Sylwan, 1989). As a consequence, late Pliocene and Pleistocene climates were significantly cooler than those of the Late Miocene, with more marked seasonality and environmental subdivision (Pascual et al., 1996; Potts, 1996). Moreover, no significant geological events (including sea level fluctuations) could have contributed to this pattern within the Guiana Shield. It is therefore likely that the ranges of species that occupied the Guiana Shield severely shrank because of colder and/or drier conditions from 3-2.5 mya to Pleistocene.

One of the major current contact zones between lineages that have diverged during the Pliocene and Pleistocene is along the border of French Guiana and Suriname, which corresponds to the position of the Maroni River. This is also the range limit of many species (see results). Upstream the lineages are mostly found on both sides of the river with patterns of recent dispersal. We interpret this as a consequence of a reduction in the effect of the Maroni River on restricting dispersal and gene flow between populations either side of the river in the upstream reaches. However, rather than being the driving force for diversification we argue that Maroni River acted as secondary barriers to recent expansion from isolated refugia, first because multiple lineages have diversified on both sides of the river and also because populations along this river seem to originate from recent expansion. Moreover, it has been shown that major rivers do not adequately explain the genetic structure found in other amphibian species in Amazonia (Gascon et al., 1998; Lougheed et al., 1999). Given that Guianan rivers are not as wide and fast flowing as major tributaries of the Rio Amazonas, where their efficacy as biotic barriers has been extensively tested, it seems reasonable to propose that they do not act as significant barriers in long term but were enough to restrict recent expansion.

4.3. DV vs. Refuge hypothesis

According to the DV hypothesis cooler Pleistocene temperatures allowed cool adapted species to invade lowlands and expand their ranges significantly (Bush, 1994; Bush, 2005; Colinvaux, 1998; Colinvaux et al., 2000). This hypothesis makes little mention of what patterns might be expected of lowland taxa. However, the signature of this hypothesis is readily differentiable from the refuge hypothesis in the Guiana Shield. The refuge hypothesis explicitly addresses the origin of distinct species and relies on habitat dynamics associated with Quaternary glaciations. Within the Guiana Shield, the refuge hypothesis leads to the expectation of Pleistocene species with little differentiation within the eastern Guiana Shield. And if intraspecific variation was present, it would presumably be the result of ecological factors intrinsic to that particular organism. Common phylogeographic patterns among species within the Guiana Shield are not expected. The DV hypothesis relies on orbital eccentricities that, despite our lack of climate proxy data extending beyond this time frame, were certainly in place prior to the Quaternary. Thus, old (pre-Quaternary) speciation is likely, as are common phylogeographic patterns.

As most of the species studied are dependant on primary forest cover, the current patterns of multiple lineages and strong genetic structure among populations suggest the presence of significant forest throughout the Quaternary. The habitat of some species is restricted to pristine rainforest and many have a shallow ecological valence, such as *Anomaloglossus degranvillei* which inhabits only the beds of rocky streams. Populations of this species could have been fragmented by slight climatic variations. However, even ubiquitous forest generalists like *Adenomera andreae* and *Leptodactylus mystaceus* exhibit evolutionary patterns consistent with restricted gene flow in the Guiana Shield, suggesting significant forest fragmentation within this region. Interestingly, a similar signature of repeated isolation and colonization has been recovered for xeric vegetation of the granitic domes (inselbergs) in French Guiana, suggesting corridors between what are today islands in a sea of humid rainforest (Sarthou et al., 2001). Fauna strictly associated to this xeric vegetation like *Tropidurus* lizards also suggest forest fragmentation and the expansion open habitat (Descamps et al., 1978; Vitt et al., 1996).

The only species not showing clear phylogeographic structure in the Guiana Shield is *Dendropsophus leucophyllatus*. This species is ubiquitous and is probably the most vagile species included in the study, inhabiting all types of forest (it has been observed in the canopy, Lescure and Marty, 2000) and savannas from 0 to 600 m asl (Lougheed et al., 2006).

This species has probably either maintained high gene flow between populations despite forest fragmentation and colder climate periods and/or colonised the region very recently from a remote refugium in western Amazonia.

Evidence for savannas expansion in the Guiana Shield during Pleistocene and Holocene have been found in palynologic records and charcoals (De Toledo and Bush, 2007; Hammond, 2005; Van der Hammen and Hooghiemstra, 2000). Savannas are currently distributed in many patches in the Guiana Shield. During drier/colder conditions it is likely that these savannas expanded, especially on the nutrient poor Guiana Shield soils (Pennington et al., 2000), and became connected. The resulting patches of forest were then isolated within the lowlands of the Guiana Shield. According to the current precipitation pattern in Amazonia two main wet sub-regions can be segregated: the coastal region of eastern Guiana Shield down to Eastern Pará and the western and central Amazonia. A "dry" corridor crosses the Guiana Shield from Venezuela to eastern Brazil which separates these two areas. Wüster et al. (2005) argued that corridor of open vegetation allowed *Crotalus durissus*, a savanna specialist, to colonise to the South of the Amazon during the Pleistocene. Drier conditions along this corridor could consequently be concordant with the different refugia in the Eastern Guiana Shield that were concentrated on the coastal region. Moreover, lineages found in central Guiana Shield seemed to have dispersed recently from more peripheral regions in *Adenomera heyeri*, *Rhinella margaritifera*, *Allobates femoralis*. Additional factors such as colder conditions and the rivers might have acted as supplementary barriers to dispersal and gene flow.

4.4. Old events and endemism of the Guiana Shield anurans

Intraspecific Miocene divergence was observed in eight species (*L. mystaceus*, *L. wagneri* B, *D. leucophyllatus*, *S. ruber*, *A. baeobatrachus*, *A. degranvillei*, *A. femoralis* and *R. margaritifera*) and correspond to geographically distant populations across Amazonia. These basal splits segregate entities that may, in fact, represent different species, many of which are endemic to the Guiana Shield. Of eight species currently though to be endemic to the lowlands of the Guiana Shield, there appear to be a number of unrecognized species. These old divergences testify of the long independent evolutionary history of the Guiana Shield fauna. Although the western portion of the Guiana Shield (Pantepui) is commonly recognized as a centre of anuran endemism (Duellman, 1999), the eastern Guiana Shield is generally geographically lumped with Amazonia. Given the data presented here, the anuran fauna of the Guiana Shield appears to be a mixture of endemic species having a long evolutionary history

in the region and more recent invasions of Amazonian species such as *Allobates femoralis* and *Rhinella castaneotica.*

4.5. Conservation implications

Lomolino (2004) proposed the terms Linnean shortfall to describe gaps in our taxonomic knowledge, and Wallacean shortfall regarding our inability to map species' ranges accurately. Nowhere are these shortfalls more evident than in Amazonia. Indeed, no full Amazonian distribution of any frog species is completely known, much less its fundamental niche, species boundaries and genetic diversity. Understanding the biases in our knowledge, and identifying key gaps and filling them, must be priorities if effective conservation strategies for Amazonia are to be established.

Until recently, species have been diagnosed primarily by phenotypic (morphological) characters. Biogeographic reconstruction and endemism were thus inferred independently of any temporal consideration. However, the use of genetic data has led to the discovery of many morphologically cryptic lineages (Daniels et al., 2003; Highton, 1995; Jockusch et al., 2001; Wake, 1997), some, but not all, of which have been or should be elevated to full species status (Fouquet et al., 2007a-c; Chapter 2-4; Sites and Marshall, 2003). For several reasons, species recognized by existing taxonomic practices will continue to under represent historical lineages, yet this historical component of diversity can be readily recovered and should, therefore, be incorporated into conservation planning (Agapow et al., 2004; Bowen, 1999; Moritz, 2002; Riddle, 1996). In addition, concordant phylogeographic patterns among species help to elucidate the historical processes that have shaped regional patterns of biodiversity (Avise, 2000; Lapointe and Rissler, 2005) and are critically important in developing conservation strategies and selecting regions for conservation that will maintain the processes and overall patterns of diversity (Avise, 1992; Moritz, 2002; Smith et al., 1993).

The prevalence of cryptic species in the Guiana Shield has already been demonstrated by Fouquet et al. (2007a; Chapter 2). The presence of this undocumented diversity has important consequences for biological conservation. The present analyses provide additional insight into the severity of this problem in the eastern Guiana Shield. As this region is the most intact and least inhabited tropical rainforest region in the world (Huber and Foster, 2003), it is alarming that our understanding of the regional biota is so poor. The conservation status of coastal French Guianan lineages is especially worrying given their eminent threat by human activities and the apparently deep, independent evolutionary history of the region.

References

Agapow, P.M., Bininda-Emonds, O.R.P., Crandall, K.A., Gittleman, J.L., Mace, G.M., Marshall, J.C., Purvis, A. 2004. The impact of species concept on biodiversity studies. *Quarterly Review of Biology*, **79**, 161–179.

Akaike, H. 1981. A new look at the statistical-model identification. *Engineering Technology and Applied Sciences*, **19**, 716–723.

Alexandrino, J., Arntzen, J.W., Ferrand, N. 2002. Nested clade analysis and the genetic evidence for population expansion in the phylogeography of the golden-striped salamander, *Chioglossa lusitanica* (Amphibia : Urodela). *Heredity*, **88**, 66–74.

Andriessen, P.A.M., Helmens, K.F., Hooghiemstra, H., Riezebos, P.A., Vanderhammen, T. 1993. Absolute chronology of the Pliocene-Quaternary sediment sequence of the Bogota area, Colombia. *Quaternary Science Reviews*, **12**, 483–501.

Arbogast, B.S., Edwards, S.V., Wakeley, J., Beerli, P., Slowinski, J.B. 2002. Estimating divergence times from molecular data on phylogenetic and population genetic timescales. *Annual Review of Ecology and Systematics*, **33**, 707–740.

Avise, J.C. 1992. Molecular population structure and the biogeographic history of a regional fauna: a case history with lessons for conservation biologists. *Oikos*, **63**, 62–76.

Avise, J.C. 2000. *Phylogeography: The history and formation of species*. Harvard University Press, Cambridge, Massachusetts, pp.447.

Beebee, T.J.C. 1992. Amphibian decline. *Nature*, **355**, p.120.

Bloemendal, J., Demenocal, P. 1989. Evidence for a change in the periodicity of tropical climate cycles at 2.4 Myr from whole-core magnetic-susceptibility measurements. *Nature*, **342**, 897–900.

Bonaccorso, E., Koch, I., Peterson, A.T. 2006. Pleistocene fragmentation of Amazon species' ranges. *Diversity and Distributions*, **12**, 157–164.

Bossuyt, F., Milinkovitch, M.C. 2000. Convergent adaptive radiations in Madagascan and Asian ranid frogs reveal covariation between larval and adult traits. *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 6585–6590.

Bowen, B.W. 1999. Preserving genes, species, or ecosystems? Healing the fractured foundations of conservation policy. *Molecular Ecology*, **8**, S5–S10.

Bush, M.B. 1994. Amazonian speciation - a necessarily complex model. *Journal of Biogeography*, **21**, 5–17.

Bush, M.B. 2005. Of orogeny, precipitation, precession and parrots. *Journal of Biogeography*, **32**, 1301–1302.

Bush, M.B., Miller, M.C., De Oliveira, P.E., Colinvaux, P.A. 2002. Orbital forcing signal in sediments of two Amazonian lakes. *Journal of Paleolimnology*, **27**, 341–352.

Bush, M.B., Silman, M.R., Urrego, D.H. 2004. 48,000 years of climate and forest change in a biodiversity hot spot. *Science*, **303**, 827–829.

Carnaval, A.C.O.Q. 2002. Phylogeography of four frog species in forest fragments of Northeastern Brazil - A preliminary study. *Integrative and Comparative Biology*, **42**, 913–921.

Caron, H., Dumas, S., Marque, G., Messier, C., Bandou, E., Petit, R.J., Kremer, A. 2000. Spatial and temporal distribution of chloroplast DNA polymorphism in a tropical tree species. *Molecular Ecology*, **9**, 1089–1098.

Carstens, B.C., Knowles, L.L. 2007. Shifting distributions and speciation: species divergence during rapid climate change. *Molecular Ecology*, **16**, 619–627.

Clapperton, C.M. 1993. Nature of environmental changes in South America at the Last Glacial Maximum. *Palaeogeography Palaeoclimatology, Palaeoecology*, **101**, 189–208.

Clement, M., Posada, D., Crandall, K.A. 2000. TCS: a computer program to estimate gene genealogies. *Molecular Ecology*, **9**, 1657–1659.

Coates, A.G., Obando, J.A. 1996. The geological evolution of the Central American Isthmus. In: Budd, A.F. and Coates, A.G. (eds.), *Evolution and environment in tropical Americas*. The University of Chicago Press, Chicago. pp. 21–56.

Colinvaux, P.A. 1993. Pleistocene biogeography and diversity in tropical forests of South America. In: Goldblatt, P. (ed.), *Biological relationships between Africa and South America*. Yale University Press, New Haven, Connecticut. pp. 473–499.

Colinvaux, P.A., De Oliveira, P.E., Bush, M.B. 2000. Amazonian and neotropical plant communities on glacial time-scales: The failure of the aridity and refuge hypotheses. *Quaternary Science Reviews*, **19**, 141–169.

Colinvaux, P.A., De Oliveira, P.E., Moreno, J.E., Miller, M.C., Bush, M.B. 1996. A long pollen record from lowland Amazonia: Forest and cooling in glacial times. *Science*, **274**, 85–88.

Da Silva, J.M.C., Rylands, A.B., Da Fonseca, G.A.B., 2005. The fate of the Amazonian areas of endemism. *Conservation Biology*, **19**, 689–694.

Daniels, S.R., Gouws, G., Stewart, B.A., Coke, M. 2003. Molecular and morphometric data demonstrate the presence of cryptic lineages among freshwater crabs (Decapoda: Potamonautidae: Potamonautes) from the Drakensberg Mountains, South Africa. *Biological Journal of the Linnean Society*, **78**, 129–147.

De la Riva, I., Köhler, J., Lötters, S., Reichle, S. 2000. Ten years of research on Bolivian amphibians: updated checklist, distribution, taxonomic problems, literature and iconography. *Revista Española de Herpetologìa*, **14,** 19–164.

de Sá R.O., Heyer W.R., Camargo A. 2005. Are *Leptodactylus didymus* and *L. mystaceus* phylogenetically sibling species (Amphibia, Anura, Leptodactylidae)? In: Ananjeva N. and Tsinenko O., (eds.) Herpetologica Petropolitana-Proceedings of the 12th Ordinary General Meeting of the Societas Europaea Herpetologica, August 12-16, 2003, St. Petersburg, Russia. *Russian Journal of Herpetology*, **12**(Supplement), 90–92.

Descamps, M., Gasc, J.P., Lescure, J., Sastre C., 1978. Étude des écosystemes Guyanais. II. Données biogeographiques sur la partie orientale des Guyanes. *Compte-Rendu des séances de la Société de Biogéographie*, **467**, 55–82.

De Toledo, M.B., Bush, M.B. 2007. A mid-Holocene environmental change in Amazonian savannas. *Journal of Biogeography*, **34**, 1313–1326.

Donnelly, M.A. 1999. Reproductive phenology of *Eleutherodactylus bransfordii* in northeastern Costa Rica. *Journal of Herpetology*, **33**, 624–631.

Drummond, A.J., Rambaut, A. 2003. *BEAST*, version 1.0. (BEAST Website http://beast.bio.ed.ac.uk/Main_Page.)

Duellman, W.E. 1999. *Patterns of Distribution of Amphibians: A Global Perspective*. Johns Hopkins University Press, Baltimore.

Duellman, W.E., Trueb, L. 1986. *Biology of amphibians*. McGraw Hill, New York.

Efron, B. 1979. 1977 Rietz Lecture - bootstrap methods - another look at the jackknife. *Annals of Statistics*, **7,** 1–26.

Emerson, B.C., Hewitt, G.M. 2005. Phylogeography. *Current Biology*, **15**, R367–R371.

Faivovich, J., Haddad, C.F.B., Garcia, P.C.A., Frost, D.R., Campbell, J.A., Wheeler, W.C. 2005. Systematic review of the frog family Hylidae, with special reference to Hylinae: phylogenetic analysis and taxonomic revision. *Bulletin of the American Museum of Natural History*, **294**, 1–240.

Fedorov, V.B., Stenseth, N.C. 2002. Multiple glacial refugia in the North American Arctic: inference from phylogeography of the collared lemming (*Dicrostonyx*

groenlandicus). *Proceedings of the Royal Society of London Series B-Biological Sciences*, **269**, 2071–2077.

Felsenstein, J. 1985. Confidence limits on phylogenies-an approach using the bootstrap. *Evolution*, **39**, 783–791.

Fouquet, A., Vences, M., Salducci, M.-D., Meyer, A., Marty, C., Blanc, M., Gilles A. 2007a. Revealing cryptic diversity using molecular phylogenetics and phylogeography in frogs of the *Scinax ruber* and *Rhinella margaritifera* species groups. *Molecular Phylogenetics and Evolution*, **43**(2), 567–582.

Fouquet, A., Gilles, A., Vences, M., Marty, C., Blanc, M., Gemmell, N.J. 2007b. Underestimation of species richness in neotropical frogs revealed by mtDNA analyses. *PLoS ONE*, **2**, e1109.doi:10.1371/journal.pone.0001109.

Fouquet, A., Gaucher, P., Blanc, M., Velez-Rodriguez, C.M. 2007c. Description of two new species of *Rhinella* (Anura: Bufonidae) from the lowlands of the Guiana shield. *Zootaxa*, **1663**, 17–32.

Galatti, U. 1992. Population biology of the frog *Leptodactylus pentadactylus* in a central Amazonian rain-forest. *Journal of Herpetology*, **26**, 23–31.

Garrick, R.C., Dyer, R.J., Beheregaray, L.B., Sunnucks, P. 2008. Babies and bathwater: a comment on the premature obituary for nested clade phylogeographic analysis. *Molecular Ecology*. doi: 10.1111/j.1365-294X.2008.03675.x.

Gascon, C., Lougheed, S.C., Bogart, J.P. 1998. Patterns of genetic population differentiation in four species of Amazonian frogs: A test of the riverine barrier hypothesis. *Biotropica*, **30**, 104–119.

Gemmell, N.J., Akiyama, S. 1996. An efficient method for the extraction of DNA from vertebrate tissues. *Trends in Genetics*, **12**, 338–339.

Graham, A. 1992. Utilization of the isthmian land-bridge during the Cenozoic - Paleobotanical evidence for timing, and the selective influence of altitudes and climate. *Review of Palaeobotany and Palynology*, **72**, 119–128.

Gramapurohit, N.P., Shanbhag, B.A., Saidapur, S.K. 2004. Growth, sexual maturation and body size dimorphism in the Indian bullfrog, *Hoplobatrachus tigerinus* (Daudin). *Herpetologica*, **60**, 414–419.

Grant, T., Frost, D.R., Caldwell, J.P., Gagliardo, R., Haddad, C.F.B., Kok, P.J.R., Means, D.B., Noonan, B.P., Schargel, W.E., Wheeler, W.C. 2006. Phylogenetic systematics of dart-poison frogs and their relatives (Amphibia: Athesphatanura: Dendrobatidae). *Bulletin of the American Museum of Natural History*, **299**, 1–262.

Griswold, C.K., Baker, A.J. 2002. Time to the most recent common ancestor and divergence times of populations of common chaffinches (*Fringilla coelebs*) in Europe and North Africa: Insights into pleistocene refugia and current levels of migration. *Evolution*, **56**, 143–153.

Haffer, J. 1969. Speciation in amazonian forest birds. *Science*, **165,** 131–137.

Haffer, J. 1997. Alternative models of vertebrate speciation in Amazonia: An overview. *Biodiversity and Conservation*, **6**, 451–476.

Halliday, T.R., Tejedo, M. 1995. Intrasexual selection and alternative mating behaviour. In: Heatwole, H.(ed.), *Amphibian biology*. Surrey Beatty and Sons, Chipping Norton, NSW. pp. 419–468.

Hammond, D.S. 2005. *Tropical Forests of the Guiana Shield*: *Ancient Forests in a Modern World*. CABI publishing. Cambridge, USA. 528 p.

Heinicke, M.P., Duellman, W.E., Hedges, S.B. 2007. Major Caribbean and Central American frog faunas originated by ancient oceanic dispersal. *Proceedings of the National Academy of Sciences of the United States of America*, **104**(24), 10092–10097.

Hewitt, G.M. 2004. Genetic consequences of climatic oscillations in the Quaternary. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **359**, 183–195.

Hickerson, M.J., Ross, J.R.P. 2001. Post-glacial population history and genetic structure of the northern clingfish (*Gobbiesox maeandricus*), revealed from mtDNA analysis. *Marine Biology*, **138**, 407–419.

Highton, R. 1995. Speciation in eastern North American salamanders of the genus *Plethodon*. *Annual Review of Ecology and Systematics*, **26**, 579–600.

Hillis, D.M., Bull, J.J. 1993. An empirical-test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Systematic Biology*, **42**, 182–192.

Hoffman, E.A., Blouin, M.S. 2004. Evolutionary history of the northern leopard frog: Reconstruction of phylogeny, phylogeography, and historical changes in population demography from mitochondrial DNA. *Evolution*, **58**, 145–159.

Hooghiemstra, H. 1989. Quaternary and upper-Pliocene glaciations and forest development in the tropical Andes - Evidence from a long high-resolution pollen record from the sedimentary basin of Bogota, Colombia. *Palaeogeography, Palaeoclimatology and Palaeoecology*, **72**, 11–26.

Hooghiemstra, H. 1997. Tropical rain forest versus savanna; two sides of a precious medal, pp. 32–43. NWO/Huygenslezing (1997), The Hague, NRC Handelsbad, Rotterdam.

Huber, O., Foster, M.N. 2003. *Conservation priorities for the Guyana Shield*. Washington, D.C. Conservation International.Huelsenbeck, J.P., Ronquist, F. 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, **17**, 754–755.

Igawa, T., Kurabayashi, A., Usuki, C., Fujii, T., Sumida, M. 2008. Complete mitochondrial genomes of three neobatrachian anurans: A case study of divergence time estimation using different data and calibration settings. *Gene*, **407**, 116–129.

Jablonski, D., Roy, K., Valentine, J.W. 2006. Out of the tropics: Evolutionary dynamics of the latitudinal diversity gradient. *Science*, **314**, 102–106.

Jackson, J.B.C., D'Croz, L. 2003. El océano se divide. In: Coates, A.G. (ed.), *Paseo Pantera*. Smithsonian Books, Washington DC, pp. 41–79

Jockusch, E.L., Yanev, K.P., Wake, D.B. 2001. Molecular phylogenetic analysis of slender salamanders, genus *Batrachoseps* (Amphibia: Plethodontidae), from central coastal California with descriptions of four new species. *Herpetological Monographs*, **15**, 54–99.

Klicka, J., Zink, R.M. 1997. The importance of recent ice ages in speciation: a failed paradigm. *Science*, **277**, 1666–1669.

Kotlik, P., Bogutskaya, N.G., Ekmekci, F.G. 2004. Circum Black Sea phylogeography of *Barbus* freshwater fishes: divergence in the Pontic glacial refugium. *Molecular Ecology*, **13**, 87–95.

Krajangdara, T., Watanabe, S. 2005. Growth and reproduction of the red frog crab, *Ranina ranina* (Linnaeus, 1758), in the Andaman Sea off Thailand. *Fisheries Science*, **71**, 20–28.

Kumbar, S.M., Pancharatna, K. 2001. Determination of age, longevity and age at reproduction of the frog *Microhyla ornata* by skeletochronology. *Journal of Biosciences*, **26**, 265–270.

Lapointe, F.J., Rissler, L.J. 2005. Congruence, consensus, and the comparative phylogeography of codistributed species in California. *American Naturalist*, **166**, 290–299.

Laurance, W.F. 2007. Have we overstated the tropical biodiversity crisis? *Trends in Ecology and Evolution*, **22**, 65–70.

Laurance, W.F., Albernaz, A.K.M., Schroth, G., Fearnside, P.M., Bergen, S., Venticinque, E.M., Da Costa, C. 2002. Predictors of deforestation in the Brazilian Amazon. *Journal of Biogeography*, **29**, 737–748.

Lescure, J., Marty, C. 2000. *Atlas des amphibiens de Guyane*. Muséum National d'Histoire Naturelle. Patrimoines Naturels, **45**. 388 p.

Liu, Z.H., Herbert, T.D. 2004. High-latitude influence on the eastern equatorial Pacific climate in the early Pleistocene epoch. *Nature*, **427**, 720–723.

Lomolino, M.V. 2004. Conservation biogeography. In: Lomolino, M.V. and Heaney L.R.(eds.), *Frontiers of biogeography: new directions in the geography of nature*., Sinauer Associates, Sunderland, MA, pp. 293–296.

Lomolino, M.V., Riddle, B.R., Brown, J.H., Brown, J.H. 2006. *Biogeography, 3rd edition*. Sinauer Associates, Sunderland, Mass.

Lougheed, S.C., Austin, J.D., Bogart, J.P., Boag, P.T., Chek, A.A. 2006. Multi-character perspectives on the evolution of intraspecific differentiation in a Neotropical hylid frog. *BMC Evolutionary Biology*, **6,** –.

Lougheed, S.C., Gascon, C., Jones, D.A., Bogart, J.P., Boag, P.T. 1999. Ridges and rivers: a test of competing hypotheses of Amazonian diversification using a dart-poison frog (*Epipedobates femoralis*). *Proceedings of the Royal Society of London Series B-Biological Sciences*, **266**, 1829–1835.

Lyles, L.L. 1988. A long and rocky road to reversing rainforest destruction. *Nature*, **333**, 491–491.

Mayle, F.E., Beerling, D.J., Gosling, W.D., Bush, M.B. 2004. Responses of Amazonian ecosystems to climatic and atmospheric carbon dioxide changes since the last glacial maximum. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **359**, 499–514.

Mc Lachlan, G., Peel, D. 2000. *Finite mixture models*. Wiley and sons.

Mendelson, J.R., Lips, K.R., Gagliardo, R.W., Rabb, G.B., Collins, J.P., Diffendorfer, J.E., Daszak, P., Ibanez, R., Zippel, K.C., Lawson, D.P., Wright, K.M., Stuart, S.N., Gascon, C., da Silva, H.R., Burrowes, P.A., Joglar, R.L., La Marca, E., Lotters, S., du Preez, L.H., Weldon, C., Hyatt, A., Rodriguez-Mahecha, J.V., Hunt, S., Robertson, H., Lock, B., Raxworthy, C.J., Frost, D.R., Lacy, R.C., Alford, R.A., Campbell, J.A., Parra-Olea, G., Bolanos, F., Domingo, J.J.C., Halliday, T., Murphy, J.B., Wake, M.H., Coloma, L.A., Kuzmin, S.L., Price, M.S., Howell, K.M., Lau, M., Pethiyagoda, R., Boone, M., Lannoo, M.J., Blaustein, A.R., Dobson, A., Griffiths, R.A., Crump, M.L., Wake, D.B., Brodie, E.D. 2006. Biodiversity - Confronting amphibian declines and extinctions. *Science*, **313**, 48–48.

Milot, E., Gibbs, H.L., Hobson, K.A. 2000. Phylogeography and genetic structure of northern populations of the yellow warbler (*Dendroica petechia*). *Molecular Ecology*, **9**, 667–681.

Mohr, C.O. 1947. Table of equivalent populations of North American mammals. *American Midland Naturalist*, **37**, 223–249.

Moritz, C. 2002. Strategies to protect biological diversity and the evolutionary processes that sustain it. *Systematic Biology*, **51**, 238–254.

Moritz, C., Patton, J.L., Schneider, C.J., Smith, T.B., 2000. Diversification of rainforest faunas: An integrated molecular approach. *Annual Review of Ecology and Systematics*, **31**, 533–563.

Mörner, N.A., Sylwan, C. 1989. Magnetostratigraphy of the Patagonian moraine sequence at Lago Buenos Aires. *Journal of South American Earth Sciences*, **2**, 385–389.

Morrison, C., Hero, J.M. 2003. Geographic variation in life-history characteristics of amphibians: a review. *Journal of Animal Ecology*, **72**, 270–279.

Nielsen, R., Wakeley, J. 2001. Distinguishing migration from isolation: A Markov chain Monte Carlo approach. *Genetics*, **158**, 885–896.

Noonan, B.P., Gaucher, P. 2005. Phylogeography and demography of Guianan harlequin toads (*Atelopus*): diversification within a refuge. *Molecular Ecology*, **14**, 3017–3031.

Noonan, B.P., Gaucher, P. 2006. Refugial isolation and secondary contact in the dyeing poison frog *Dendrobates tinctorius*. *Molecular Ecology*, **15**, 4425–4435.

Noonan, B.P., Wray, K.P. 2006. Neotropical diversification: the effects of a complex history on diversity within the poison frog genus *Dendrobates*. *Journal of Biogeography*, **33**, 1007–1020.

Panchal, M., Beaumont, M.A. 2007. The automation and evaluation of nested clade phylogeographic analysis. *Evolution*, **61**, 1466–1480.

Pascual, R., Ortiz-Jaureguizar, E., Prado, J.L. 1996. Land mammals: paradigm of Cenozoic South American geobiotic evolution. In: Arratia, G. (ed.) *Contribution of Southern South America to Vertebrate Paleontology.* Müncher Geowissenschaftliche Abhandlungen. pp. 265–319

Pennington, R.T., Prado, D.E., Pendry, C.A. 2000. Neotropical seasonally dry forests and Quaternary vegetation changes. *Journal of Biogeography*, **27**, 261–273.

Peterson, A.T., Nyàri, A.S. 2007. Ecological niche conservatism and pleistocene refugia in the thrush-like mourner, *Schiffornis* sp., in the neotropics. *Evolution*, **62**, 173–183.

Petit, R.J. 2008. The coup de grace for the nested clade phylogeographic analysis? *Molecular Ecology*, **17**, 516–518.

Posada, D., Crandall, K.A. 1998. MODELTEST: testing the model of DNA substitution. *Bioinformatics*, **14**, 817–818.

Posada, D., Crandall, K.A., Templeton, A.R. 2000. GeoDis: a program for the cladistic nested analysis of the geographical distribution of genetic haplotypes. *Molecular Ecology*, **9**, 487–488.

Potts, R. 1996. Evolution and climate variability. *Science*, **273**, 922–923.

Pounds, J.A. 2001. Climate and amphibian declines. *Nature*, **410**, 639–640.

Pounds, J.A., Crump, M.L. 1994. Amphibian declines and climate disturbance - the case of the golden toad and the harlequin frog. *Conservation Biology*, **8**, 72–85.

Pounds, J.A., Fogden, M.P.L., Campbell, J.H. 1999. Biological response to climate change on a tropical mountain. *Nature*, **398**, 611–615.

Pramuk, J.B., Robertson, T., Sites, J.W., Noonan, B.P. 2007. Around the world in 10 million years: biogeography of the nearly cosmopolitan true toads (Anura: Bufonidae). *Global Ecology and Biogeography*, **17**, 72–83.

Rabassa, J. 1999. Cuaternario de la cordillera patagónica y Tierra del Fuego. In: Caminos, R. (ed.), *Geología Argentina*. Anales del Instituto de Geología y Recursos Minerales, Buenos Aires, pp. 710–714.

Rambaut, A., Drummond, A. 2003. *Tracer*, version 1.2. (Available from http://evolve.zoo.ox.ac.uk/software.html?id=tracer.)

Ravelo, A.C., Andreasen, D.H., Lyle, M., Lyle, A.O., Wara, M.W. 2004. Regional climate shifts caused by gradual global cooling in the Pliocene epoch. *Nature*, **429**, 263–267.

Reading, C.J., Jofre, G.M. 2003. Reproduction in the nest building vizcacheras frog *Leptodactylus bufonius* in central Argentina. *Amphibia-Reptilia*, **24**, 415–427.

Riddle, B.R. 1996. The molecular phylogeographic bridge between deep and shallow history in continental biotas. *Trends in Ecology and Evolution*, **11**, 207–211.

Roelants, K., Gower, D.J., Wilkinson, M., Loader, S.P., Biju, S.D., Guillaume, K., Moriau, L., Bossuyt, F. 2007. Global patterns of diversification in the history of modern amphibians. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 887–892.

Rozas, J., Sanchez-DelBarrio, J.C., Messeguer, X., Rozas, R. 2003. DnaSP, DNA polymorphism analyses by the coalescent and other methods. *Bioinformatics*, **19**, 2496–2497.

Rull, V. 2004a. Biogeography of the 'Lost World': a palaeoecological perspective. *Earth-Science Reviews*, **67**, 125–137.

Rull, V. 2004b. An evaluation of the lost world and vertical displacement hypotheses in the Chimanta massif, venezuelan Guayana. *Global Ecology and Biogeography*, **13**, 141–148.

Rull, V. 2004c. Is the 'Lost World' really lost? Palaeoecological insights into the origin of the peculiar flora of the Guayana Highlands. *Naturwissenschaften*, **91**, 139–142.

Rull, V. 2005. Biotic diversification in the Guayana Highlands: a proposal. *Journal of Biogeography*, **32**, 921–927.

Rull, V. 2007. Holocene global warming and the origin of the Neotropical Gran Sabana in the Venezuelan Guayana. *Journal of Biogeography*, **34**, 279–288.

Rull, V., Nogue, S. 2007. Potential migration routes and barriers for vascular plants of the Neotropical Guyana Highlands during the quaternary. *Journal of Biogeography*, **34**, 1327–1341.

Rull, V., Vegas-Vilarrubia, T. 2006. Unexpected biodiversity loss under global warming in the neotropical Guayana Highlands: a preliminary appraisal. *Global Change Biology*, **12**, 1–9.

Salducci, M.-D., Marty, C., Fouquet, A., Gilles, A. 2005. Phylogenetic relationships and biodiversity in hylids (Anura: Hylidae) from French Guiana. *Comptes Rendus Biologies*, **328**, 1009–1024.

San Mauro, D., Vences, M., Alcobendas, M., Zardoya, R., Meyer, A. 2005. Initial diversification of living amphibians predated the breakup of Pangaea. *American Naturalist*, **165**, 590–599.

Sarthou, C., Samadi, S., Boisselier-Dubayle, M.C. 2001. Genetic structure of the saxicole *Pitcairnia geyskesii* (Bromeliaceae) on inselbergs in French Guiana. *American Journal of Botany*, **88**, 861–868.

Shackleton, N.J. 1995. New data on the evolution of Pliocene climate variability. In: Vrba, E.S., Denton, G.H., Patridge, T.C. and Burckle, L.H. (eds.), *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven, pp. 242–248.

Shackleton, N.J., Backman, J., Zimmerman, H., Kent, D.V., Hall, M.A., Roberts, D.G., Schnitker, D., Baldauf, J.G., Desprairies, A., Homrighausen, R., Huddlestun, P., Keene, J.B., Kaltenback, A.J., Krumsiek, K.A.O., Morton, A.C., Murray, J.W.,

Westbergsmith, J. 1984. Oxygen isotope calibration of the onset of ice-rafting and history of glaciation in the North-Atlantic region. *Nature*, **307**, 620–623.

Sites, J.W., Marshall, J.C. 2003. Delimiting species: a Renaissance issue in systematic biology. *Trends in Ecology and Evolution*, **18**, 462–470.

Smith, S.A., Nieto Montes de Oca, A., Reeder, T.W., Wiens, J.J. 2007. A phylogenetic perspective on elevational species richness patterns in Middle American treefrogs: why so few species in lowland tropical rainforests? *Evolution*, **61**, 1188–1207.

Smith, T.B., Bruford, M.W., Wayne, R.K. 1993. The preservation of process: the missing element of conservation programs. *Biodiversity Letters*, **1**, 164–167.

Stebbins, G.L. 1974. *Flowering plants: evolution above the species level*. Belknap Press of Harvard University Press, Cambridge, Mass.

Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L., Waller, R.W. 2004. Status and trends of amphibian declines and extinctions worldwide. *Science*, **306**, 1783–1786.

Swofford, D.L. 1993. Paup - a computer-program for phylogenetic inference using maximum parsimony. *Journal of General Physiology*, **102**, A9–A9.

Templeton, A.R. 1998. Nested clade analyses of phylogeographic data: testing hypotheses about gene flow and population history. *Molecular Ecology*, **7**, 381–397.

Templeton, A.R. 2004. Statistical phylogeography: methods of evaluating and minimizing inference errors. *Molecular Ecology*, **13**, 789–809.

Templeton, A.R. 2008. Nested clade analysis: an extensively validated method for strong phylogeographic inference-a reply to Petit 2008. *Molecular Ecology*, doi: 10.1111/j.1365-294X.2008.03731.x

Thompson, J.D., Gibson, T.J., Plewniak, F., Jeanmougin, F., Higgins, D.G. 1997. The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research*, **25**, 4876–4882.

Toledo, L.F., Castanho, L.M., Haddad, C.F.B. 2005. Recognition and distribution of *Leptodactylus mystaceus* (Anura; Leptodactylidae) in the state of São Paulo, Southeastern Brazil. *Biota Neotropica*, 5(1), http://www.biotaneotropica.org.br/v5n1/pt/abstract?article+BN00505012005.

Van der Hammen, T., Absy, M.L. 1994. Amazonia during the last glacial. *Palaeogeography Palaeoclimatology and Palaeoecology*, **109**, 247–261.

Van der Hammen, T., Hooghiemstra, H. 1997. Chronostratigraphy and correlation of the Pliocene and Quaternary of Colombia. *Quaternary International*, **40**, 81–91.

Van der Hammen, T., Hooghiemstra, H. 2000. Neogene and Quaternary history of vegetation, climate, and plant diversity in Amazonia. *Quaternary Science Reviews*, **19**, 725–742.

Vitt, L.J., Zani, P.A., Caldwell, J.P. 1996. Behaviour ecology of *Tropidurus hispidus* on isolated rock outcrops in Amazonia. *Journal of Tropical Ecology*, **12**, 747–747.

Wake, D.B. 1997. Incipient species formation in salamanders of the *Ensatina* complex. *Proceedings of the National Academy of Sciences of the United States of America*, **94**, 7761–7767.

Wakeley, J., Hey J. 1997. Estimating ancestral population parameters. *Genetics*, **145**, 847–855.

Webb, S.D. 1985. Late Cenozoic mammal dispersals between the Americas. In: Stheli, F. and Webb, S.D. (eds.), *The great American biotic interchange*. Plenum Press, New York, pp. 357–386.

Webb, S.D. 1991. Ecogeography and the Great American Interchange. *Paleobiology*, **17**, 266–280.

Weir, J.T. 2006. Divergent timing and patterns of species accumulation in lowland and highland neotropical birds. *Evolution*, **60**, 842–855.

Weir, J.T., Schluter, D. 2004. Ice sheets promote speciation in boreal birds. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **271**, 1881–1887.

Wiens, J.J. 2007. Global patterns of species richness and diversification in amphibians. *American Naturalist*, **170**, S86–S106.

Wiens, J.J., Fetzner, J.W., Parkinson, C.L., Reeder, T.W. 2005. Hylid frog phylogeny and sampling strategies for speciose clades. *Systematic Biology*, **54**(5), 778–807

Won, H., Renner, S.S. 2006. Dating dispersal and radiation in the gymnosperm Gnetum (Gnetales) - Clock calibration when outgroup relationships are uncertain. *Systematic Biology*, **55**, 610–622.

Wüster, W., Ferguson, J.E., Quijada-Mascarenas, J.A., Pook, C.E., Salomao, M.D., Thorpe, R.S. 2005. Tracing an invasion: landbridges, refugia, and the phylogeography of the Neotropical rattlesnake (Serpentes: Viperidae: *Crotalus durissus*). *Molecular Ecology*, **14**, 1095–1108.

Zink, R.M., Klicka, J., Barber, B.R. 2004. The tempo of avian diversification during the Quaternary. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences,* **359**, 215–220.

Chapter 6:
General Conclusions

1. The extent of the Guiana Shield diversity

Globally, we have been grossly underestimating the biological diversity of frogs at the species level, the so-called "Linnean shortfall" (Lomolino, 2004). This is true across a wide range of locales, including the Guiana Shield, but also Amazonia in general. While 115 described frog species are recognized in the eastern Guiana Shield I identified at least 16 potentially undescribed species either detected by morphological characters (Lescure and Marty, 2000; pers. obs.) and/or by very old phylogenetic divergence (pre-Pliocene) (Chapters 3,5). If the lineages diverging before the Pleistocene described in Chapters 3 and 5 are considered as cryptic species, this would add 30 species to those so far described for a total of at least 161. For example, in French Guiana alone there are currently 95 species described but we know of at least 14 potentially undescribed species (Lescure and Marty, 2000; pers. obs.) and 15 additional cryptic species (Chapters 3 and 5). Thus, the total number of frog species occurring in French Guiana is at least 124. Given the proportion of species groups readily investigated and the poor sampling in the Guianan part of Parà and Amazonas and outside the Guiana Shield, the actual number of putative species is likely to be much higher. From the rates of cryptic species estimated in Chapter 3, the total number might actually exceed 200 in the eastern Guiana Shield. For example, in Centrolenidae, a family not investigated in this work, the actual number of species occurring in French Guiana could be as high as nine instead of the of the three species currently considered (Michel Blanc pers. com.). My thesis work has not addressed the issue of how many species are in the eastern Guiana Shield with great precision but nevertheless it gives a significant improvement of the estimated number of frog species in the region. This level of species richness (>200 species) means that, behind the Andes with more than 750 species and the Atlantic forest with more than 330 species (Duellman, 1999), the eastern Guiana Shield hosts one of the richest Anuran fauna on earth.

In most of the species studied high levels of mtDNA differentiation between populations call for a reassessment of the taxonomic status of what is being recognized as single widespread species. Comprehensive reviews based on molecular, morphological, and call data (Chapters 2 and 4) will certainly change the way we view the status and the evolution of amphibian diversity in Amazonia. Frog taxonomy is mainly based on morphological characters. Under this approach, morphological differences may be viewed as surrogates for taxonomic distinctiveness. However, the level of genetic and morphological

differences reflected in taxonomy is often discordant among taxa (Salducci et al., 2005). Thus, it is likely that because species taxonomy is based on morphological characters, a bias is induced in the delineation of frog species. For example, there is a striking contrast in the species boundaries between the aposematic and diurnal species, such as *Dendrobates* ssp. and *Atelopus* ssp. and the dull coloured morphologically cryptic groups like *Scinax ruber* and *Rhinella margaritifera*. In the former ones, obvious regional variation exists in morphology especially in the colouration (Noonan and Gaucher, 2005; 2006). These variants are sometimes considered as independent species while they are genetically very similar entities. This was the case of *Dendrobates azureus* and *D. tinctorius*, which were recently synonymized (Wollenberg et al., 2006), and still the case for *Atelopus flavescens*, *A. franciscus* and *A. spumarius* (Noonan and Gaucher, 2005). In contrast, the dull coloured cryptic groups are frequently amalgams of old lineages that should be considered as different species but there is a lack of obvious external characters to allow an easy discrimination (Chapter 2-5). In diurnal and aposematic species, coloration is known to evolve quickly as has been showed in Dendrobatids (Darst and Cummings, 2006; Darst et al., 2006; 2005; Roberts et al., 2006). However, more typical frog species have dull colouration which may produce fewer obvious characters to allow segregation of close species. Indeed, a characteristic trend in amphibians is that their morphological characters are highly conserved (Cherry et al., 1977; 1978; Shubin and Jenkins, 1995). Most anuran groups share the same basic morphology, which appears to originate from the Jurassic period (Roelants and Bossuyt, 2005). Recent drastic improvements have been done in Anuran higher level taxonomy by Faivovich et al. (2005), Grant et al. (2006), Frost et al. (2006) and Roelants et al. (2007), using molecular data. However, at lower levels, this trend of low resolution of morphological characters seems to be true as well, and cryptic species are more the rule than the exception as assumed by Hebert et al. (2004) for Neotropical fauna in general.

Moreover, methods for delimiting species with morphological data remain understudied (Wiens, 2007). This is paradoxical in that many recent papers that have raised the problems of "DNA taxonomy" seem to assume that species delimitation with morphology is simple and straightforward. Wiens and Servedio (2000) examined the sample sizes needed to have statistical confidence that a given diagnostic character is truly fixed within a species and showed that being reasonably certain that a trait is truly fixed within a species is basically impossible despite huge sampling. Other approaches to delimit species with morphology, for example using phylogenetic analyses, remain largely unexplored (e.g. Wiens and Penkrot, 2002). Furthermore, the few studies that have compared the results of this approach to those

using diagnostic morphological characters found these methods can give quite different species limits in some cases (e.g. Wiens and Penkrot, 2002; Doan and Castoe, 2003).

Large scale sequencing of 16S rDNA for example is today easy and straightforward and I argue that such a snapshot of the existing diversity would be a giant step forward as Vences (2005) and Smith et al. (2007) are advocating. If equivalent datasets to the one presented herein for eastern Guiana Shield anurans are available from other regions of Amazonia or from the neotropics in general, current biodiversity could be better estimated and fertile comparisons could be made. Of course morphological, ecological and distributional data will always be necessary to discriminate species, describe them and also necessary to understand their natural history, their evolution and for efficient conservation purposes. However, in an emergency situation like the current one, information given by short DNA sequences is the most efficient way to obtain a snapshot of the existing diversity of amphibians.

2. Distribution of the Guiana Shield diversity

The present work also provides significant updates of the geographical distributions of many species (Chapter 5), underlining the extent of the lack of knowledge on the distribution of frog species in Amazonia, the so-called "Wallacean shortfall" (Lomolino, 2004). Some species appeared to be more widespread than previously recognized like the recently described *Adenomera heyeri* which extend up to Guyana while it was known only from French Guiana and *Allobates granti* which occurs in most of Suriname as well as French Guiana (Chapter 5). However, some other species appeared circumscribed to restricted areas like "*Anomaloglossus baeobatrachus* 2" only found on Brownsberg Mountain and "*Anomalloglossus degranvillei* 2" only found in the northern and central part of French Guiana (Chapter 5). Moreover, most species display deep divergences between eastern Guiana Shield populations and those elsewhere in Amazonia. This emphasizes that the local endemism in the Guiana Shield of these zones is higher than previously recognized. Consequently, this endemism represents the testimony of unique evolutionary history and must be a prioritized element taken into account in conservation planning. Nevertheless, a few other species like the ones corresponding to one of the lineages in *Scinax ruber* and *Adenomera hylaedactyla* appear widely distributed showing that widespread species do exist (Chapter 3 and 5). This underlines the fact that some species have strong dispersal abilities and that the frog fauna of the eastern Guiana Shield is a mixture of old Guianan endemic lineages and lineages more recently exchanged with the rest of Amazonia (see Chapter 5 Fig.

1). For these reasons the present work also contributes in improving significantly our knowledge of the distribution of species and confirmed that the Guiana Shield hosts an immense and unique natural heritage and that it is a singular biogeographical region.

The considerable genetic diversity observed in the focal frog species is highly structured geographically and the distributions of these phylogroups are relatively concordant among each other (Chapter 5). Some of the intraspecific lineages could potentially be elevated to specific rank. They are mostly allopatric (without overlap or parapatric when limited overlap occurs). Consequently, if considered as different species, they would not account for an increase of the alpha diversity (diversity of a locality) but it would increase significantly the estimation of the diversity harboured at a larger scale like the national scale and even more at the scale of the Guiana Shield or Amazonia. Thus, many local protected areas would be more efficient than only a few large ones to preserve a greater proportion of the anuran diversity as suggested by Duellman (1999) and (Zimmerman and Bierregaard, 1986). Of course, what is true for frogs might not be true for all organisms, especially large mammals or birds and also because of complex interactions among ecosystem components (Laurance, 2005). This result also underlines that efficient conservation strategies would need multinational collaborations and synergetic efforts.

3. The origin of the Guiana Shield diversity

An improved understanding of the extent of the diversity and its distribution provides the opportunity for investigating its origin. Patterns and levels of genetic diversity observed among conspecific populations in the eastern Guiana Shield are heavily influenced by taxon-specific habitat requirements. The observed patterns were so variable that it reflects the complex histories and the diversity in the ecologies of these species. However, many divergences are spatially and temporally congruent and are likely the consequences of the events leading to multiple forest refugia (Chapter 5 Fig. 5). If diversification started during late Pliocene, well before the supposedly most intense climatic fluctuations, divergences of most populations fall within the Pleistocene period, when a presumably colder and drier environment could have lead to isolation of demes and subsequent genetic differentiation. Also contradicting the view that the eastern Guiana Shield hosted one single refuge, I showed that there were many refugia that were distributed in many different places in the eastern Guiana Shield but particularly in the northern half of French Guiana, Suriname and Amapà (Chapter 5 Fig. 5). Recognizing this strong historical component is necessary and timely for local conservation planning as these zones are also the most inhabited and the most likely to

be irremediably modified in the near future. We still do not know precisely enough the distribution of the species to be able to calculate the geographical distribution of the Phylogenetic Diversity (PD) on a large scale. However, given the results in Chapter 5, one would expect the PD to be maximised on the main contact zones or phylogeographic breaks because several lineages occur on the same area or hypothetically very close. However, these are probably recent secondary contact zones between lineages likely to be highly modified in case of climate change. On the contrary, forest refugia might be the places where the habitat is most likely to remain relatively stable in case of disruption.

We are still in the infancy of Amazonian phylogeography. This work demonstrates that much is yet to be learned at all levels from population genetic parameters, to species taxonomy, and up to phylogenetic relationships among these frogs. However, my findings should recommend to biologists studying intraspecific diversity especially in Amazonia that they must sample at a broad geographic scale to fully encompass all phyletic diversity, and that even at the finest geographic scales intensive geographic sampling may be required to accurately capture local diversity. A political reality for research in South America, and particularly in the Guiana Shield where five different official languages are spoken, is that studies will often be restricted by political boundaries that do not reflect biogeographic ones. The peculiar political situation of French Guiana, which is a department of France and consequently a part of the European Union nested in South America, brings challenges and opportunities for conservation. One of the challenges is the isolation of the research and conservation program because of political boundaries whereas on the other hand the European Union has a great responsibility toward the conservation of its only "Amazonian Forest".

Nonetheless, thorough sampling should be a major goal. Further, my results caution against the common phylogenetic practice of sampling a single individual when inferring evolutionary relationships. The present state of knowledge about Neotropical amphibians is far too sparse to support that methodology, because cryptic diversity appears to be the rule in Neotropical anurans, and incomplete lineage sorting, could result in spurious conclusions.

4. Future directions

It is both exciting and frustrating to do graduate work on almost completely unstudied species in an area with many logistical and political challenges to fieldwork. As I suspect is common, my dissertation has produced more questions than it has answered. Though this is often simply the nature of scientific research, the conclusions of my dissertation leave some

difficult unanswered questions about species delimitation and historical events. These will hopefully be the source of future research.

Of course the picture drawn is still incomplete but it is increasingly feasible to quickly obtain DNA sequences from a large number of tissue samples from unidentified specimens and even tadpoles. If this could be achieved for a large number of localities from Amazonia this would allow us to encompass the full supposed range of the species, estimate accurately the diversity of frogs and the geographic ranges of lineages. It would be especially valuable to obtain samples in the rest of the eastern Guiana Shield (especially central, southern and western Suriname, upper Trombetas, Acarai mountains, North of Obidos, upper Rio Jari) and in Amazonia (Brazilian Shield, Bolivia, Belem, Colombian lowlands). Ultimately, once sufficient data are available comparisons could be made across subregions using phylogenetic diversity, endemism etc… More genetic data (mtDNA and nuDNA) would also be worth obtaining to clarify those relationships that remain ambiguous among some mtDNA lineages, to determine the dates of divergence and the degree of reproductive isolation between lineages.

The study of microevolutionary processes, the improvement of ecological characterisation of the species would also bring important information to better understand the mechanisms of evolution in the neotropics. Population genetic studies of *Adenomera andreae* for example, which display an important level of genetic structure, would clarify the level of gene flow, connectivity among populations and their demographic history. This can ultimately lead to fertile comparisons among species, and paleoclimatic reconstruction. The emerging field of ecological niche modelling (Peterson and Nyari, 2008; Rissler et al., 2006; Graham et al., 2006) is particularly promising in this context.

Much is left to be done and I wish to be able to dig more deeply in these promising new directions over the coming years.

References

Cherry, L.M., Case, S.M., Wilson, A.C. 1977. Relative rates of morphological evolution in primates, carnivores and frogs. *American Zoologist*, **17**, 910–910.

Cherry, L.M., Case, S.M., Wilson, A.C. 1978. Frog Perspective on Morphological Difference between Humans and Chimpanzees. *Science*, **200**, 209–211.

Darst, C.R., Cummings, M.E. 2006. Predator learning favours mimicry of a less-toxic model in poison frogs. *Nature*, **440**, 208–211.

Darst, C.R., Cummings, M.E., Cannatella, D.C. 2006. A mechanism for diversity in warning signals: Conspicuousness versus toxicity in poison frogs. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 5852–5857.

Darst, C.R., Menendez-Guerrero, P.A., Coloma, L.A., Cannatella, D.C. 2005. Evolution of dietary specialization and chemical defense in poison frogs (Dendrobatidae): A comparative analysis. *American Naturalist*, **165**, 56–69.

Doan, T.M., Castoe, T.A. 2003. Using morphological and molecular evidence to infer species boundaries within *Proctoporus bolivianus* Werner (Squamata: Gymnophthalmidae). *Herpetologica*, **59**, 433–450.

Duellman, W.E. 1999. *Patterns of distribution of amphibians: a global perspective*. Johns Hopkins University Press.

Faivovich, J., Haddad, C.F.B., Garcia, P.C.A., Frost, D.R., Campbell, J.A., Wheeler, W.C. 2005. Systematic review of the frog family Hylidae, with special reference to Hylinae: phylogenetic analysis and taxonomic revision. *Bulletin of the American Museum of Natural History*, **294**, 1–240.

Frost, D.R., Grant, T., Faivovich, J., Bain, R.H., Haas, A., Haddad, C.F.B., de Sá, R.O., Channing, A., Wilkinson, M., Donnellan, S.C., Raxworthy, C.J., Campbell, J.A., Blotto, B.L., Moler, P., Drewes, R.C., Nussbaum, R.A., Lynch, J.D., Green, D.M., Wheeler, W.C. 2006. The amphibian tree of life. *Bulletin of the American Museum of Natural History*, **297**, 1–370.

Noonan, B.P., Gaucher, P. 2005. Phylogeography and demography of Guianan harlequin toads (*Atelopus*): diversification within a refuge. *Molecular Ecology*, **14**, 3017–3031.

Noonan, B.P., Gaucher, P. 2006. Refugial isolation and secondary contact in the dyeing poison frog *Dendrobates tinctorius*. *Molecular Ecology*, **15**, 4425–4435.

Graham, C. H., C. Moritz, and S. E. Williams. 2006. Habitat history improves prediction of biodiversity in rainforest fauna. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 632–636.

Grant, T., Frost, D.R., Caldwell, J.P., Gagliardo, R., Haddad, C.F.B., Kok, P.J.R., Means, D.B., Noonan, B.P., Schargel, W.E., Wheeler, W.C. 2006. Phylogenetic systematics of dart-poison frogs and their relatives (Amphibia: Athesphatanura: Dendrobatidae). *Bulletin of the American Museum of Natural History*, **299**, pp. 262.

Laurance, W.F. 2005. When bigger is better: the need for Amazonian mega-reserves. *Trends in Ecology and Evolution*, **20**, 645–648.

Lescure, J., Marty, C. 2000. *Atlas des amphibiens de Guyane*. Muséum National d'Histoire Naturelle. Patrimoines Naturels, **45**. 388 p.

Lomolino, M.V. 2004. Conservation biogeography. In: Lomolino, M.V. and Heaney, L.R. (eds.), *Frontiers of biogeography: new directions in the geography of nature*. Sinauer Associates, Sunderland, MA, pp. 293–296.

Hebert, P.D.N., Penton, E.H., Burns, J.M., Janzen, D.H., Hallwachs, W. 2004. Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly Astraptes fulgerator. *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 14812–14817.

Peterson, T.A., Nyari, S.A. 2007. Ecological niche conservatism and Pleistocene refugia in the trush-like mourner, *Schiffornis* sp., in the Neotropics. *Evolution*, **62**(1), 173–183.

Rissler, L.J., Hijmans, R.J., Graham, C.H., Moritz, C., Wake, D.B. 2006. Phylogeographic lineages and species comparisons in conservation analyses: A case study of california herpetofauna. *American Naturalist*, **167**, 655–666.

Roberts, J.L., Brown, J.L., Schutle, R., Wilfredo, A., Summers, K. 2006. Rapid diversification of colouration among populations of a poison frog isolated on sky peninsulas in the central cordilleras of Peru. *Journal of Biogeography*, **34**(3), 417–426.

Roelants, K., Bossuyt, F. 2005. Archaeobatrachian paraphyly and pangaean diversification of crown-group frogs. *Systematic Biology*, **54**, 111–126.

Roelants, K., Gower, D.J., Wilkinson, M., Loader, S.P., Biju, S.D., Guillaume, K., Moriau, L., Bossuyt, F. 2007. Global patterns of diversification in the history of modern amphibians. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 887–892.

Salducci, M.-D., Marty, C., Fouquet, A., Gilles, A. 2005. Phylogenetic relationships and biodiversity in Hylids (Anura: Hylidae) from French Guiana. *Comptes Rendus Biologies*, **328**, 1009–1024.

Shubin, N.H., Jenkins, F.A. 1995. An Early Jurassic jumping frog. *Nature*, **377**, 49–52.

Smith, M.A., Poyarkov N.A., Hebert P.D.N. 2007. CO1 DNA barcoding amphibians: take the chance, meet the challenge. *Molecular Ecology Resources*, **8**, 235–246.

Vences, M., Thomas, M., Bonett, R.M., Vieites, D.R. 2005. Deciphering amphibian diversity through DNA barcoding: chances and challenges. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **360**, 1859–1868.Wiens, J.J. 2007. Species delimitation: new approaches for discovering diversity. *Systematic Biology*, **56**, 875–878.

Wiens, J.J., Penkrot, T.A. 2002. Delimiting species using DNA and morphological variation and discordant species limits in spiny lizards (*Sceloporus*). *Systematic Biology*, **51**, 69–91.

Wiens, J.J., Servedio, M.R. 2000. Species delimitation in systematics: inferring diagnostic differences between species. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **267**, 631–636.

Wollenberg, K.C., Veith, M., Noonan, B.P., Lotters, S. 2006. Polymorphism versus species richness—Systematics of large *Dendrobates* from the eastern Guiana Shield (Amphibia: Dendrobatidae). *Copeia*, 623–629.

Zimmerman, B.L., Bierregaard, R.O. 1986. Relevance of the equilibrium-theory of island biogeography and species area relations to conservation with a case from Amazonia. *Journal of Biogeography*, **13**, 133–143.
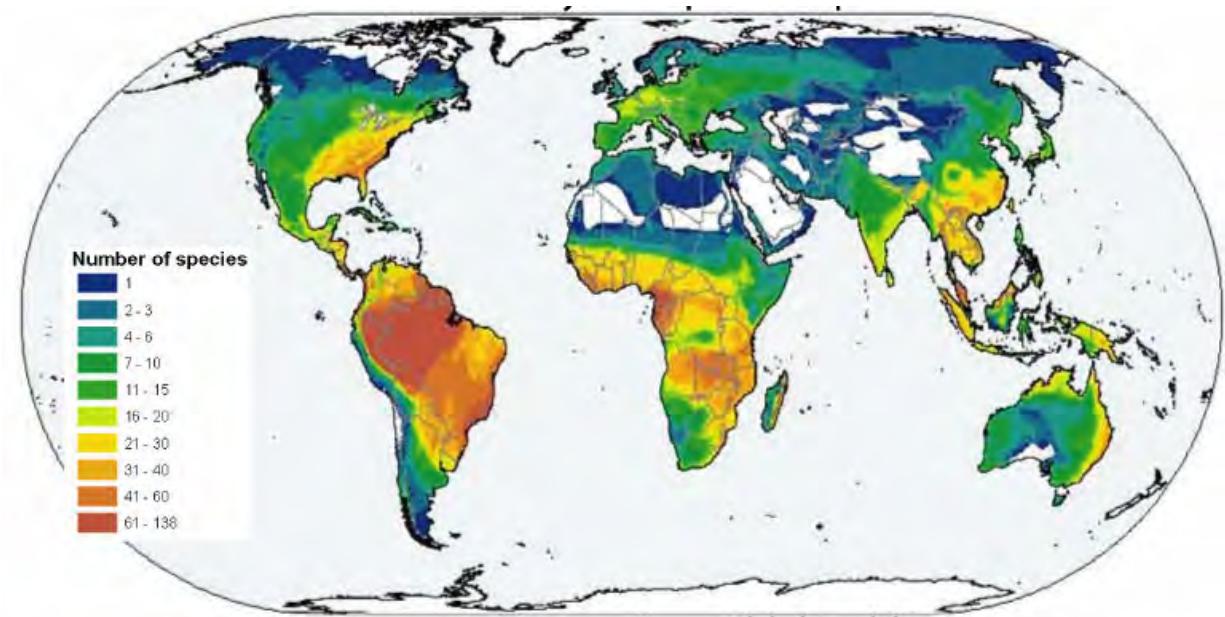
Fig. 1.1: Global diversity of Amphibian species. From Global Amphibian Assessment
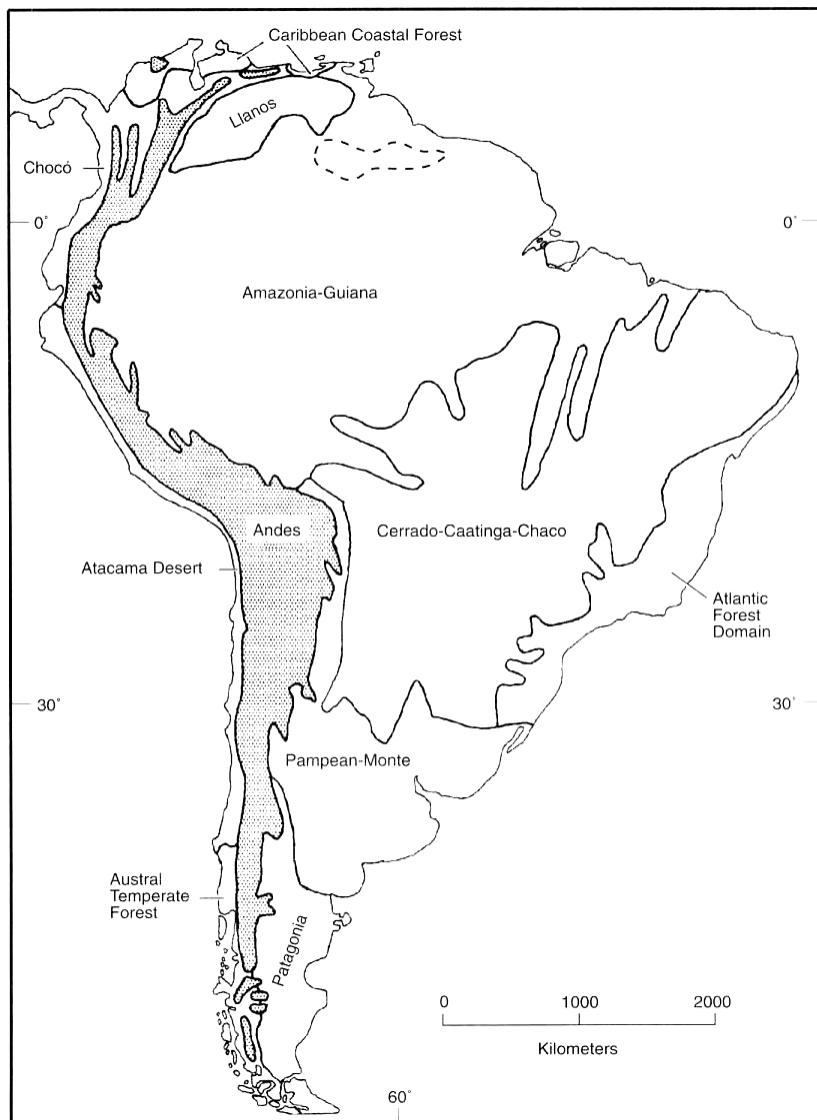
Fig. 1.2: Natural regions of South America based primarily on the morphoclimatic domains of Ab-Saber (1977). From Duellman (1999).
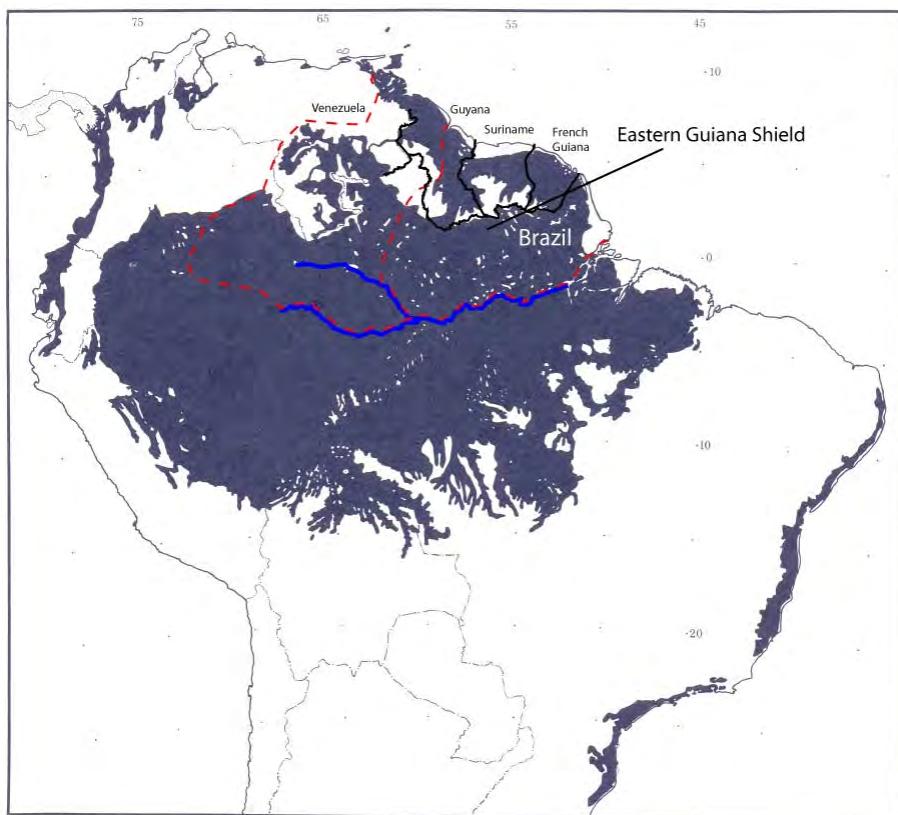
Fig. 1.3: Tropical lowland forest (black) and Savannas, Cerrados, and highlands (white) in South America. Rio Amazonas and Rio Negro are indicated in blue. The limits of the Guiana Shield are indicated in red dashed lines, with the boundary between the western and the eastern parts also shown. Adapted from Dixon (1982) and Hammond (2005).
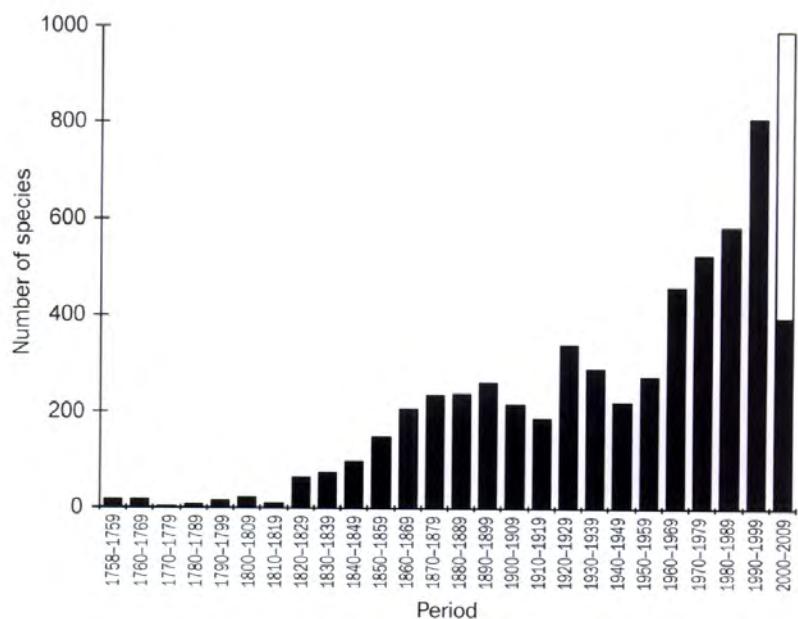
Fig. 1.4: Number of new amphibian species described per decade. The white box represents the projected number of newly described species. From Köhler et al. (2005).
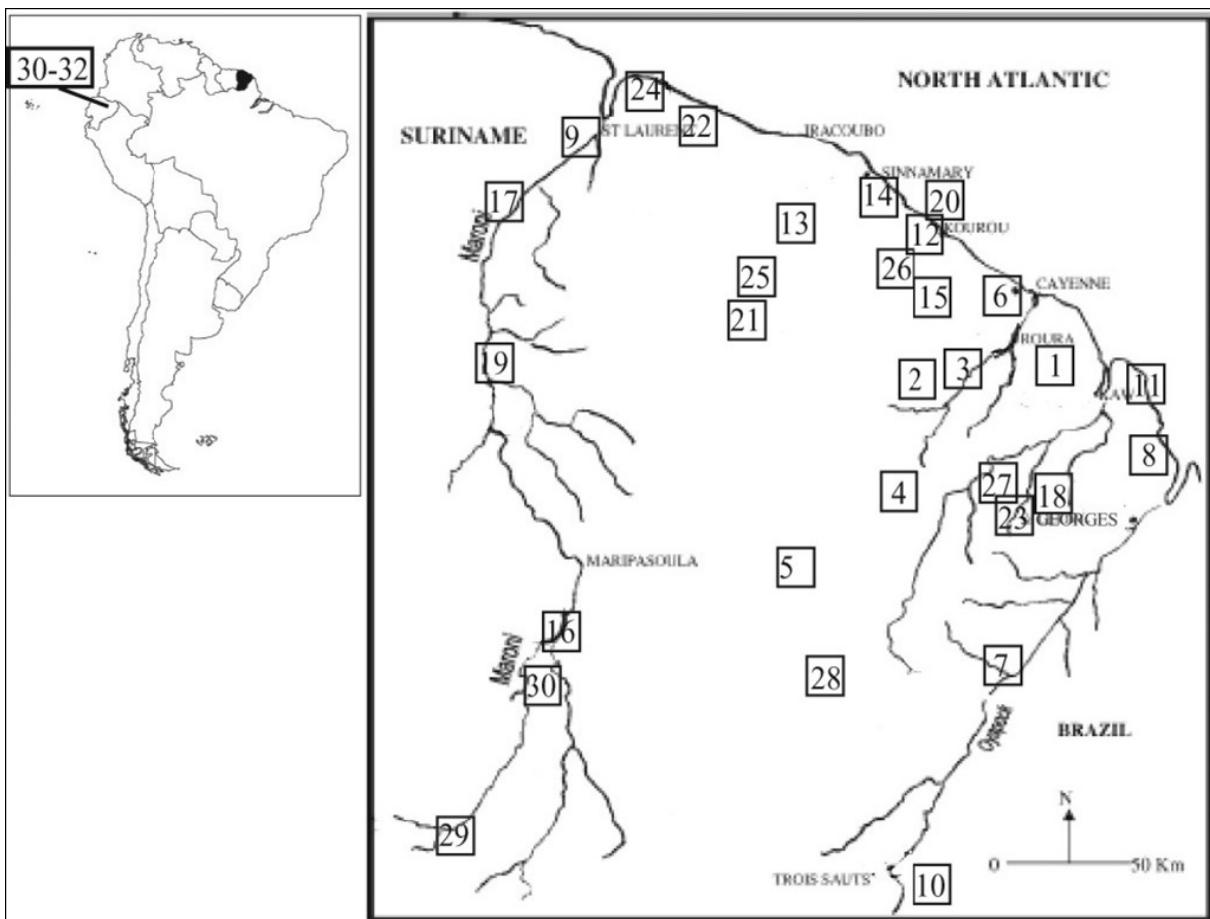
Fig. 2.1: Map of French Guiana showing the collection localities. © Service du Patrimoine Naturel M.N.H.N. Paris, 2000. Kaw =1; La Compté = 2; Cacao = 3; Nouragues = 4; Saül = 5; Cayenne = 6; Camopi = 7; Ouanary = 8; St Laurent = 9; Trois-saut = 10; Montagne d'Argent = 11; Kourou = 12; Petit-Saut = 13; route CSG Sinnamary = 14; Montsinnery = 15; Antecum Pata = 16; Apatou = 17; route Regina St.-George = 18; Grand Santi = 19; Ile royale = 20; Crique Grand Leblond = 21; km7 on road 8 = 22; Mataroni = 23; Mana = 24; Piste St Elie = 25; Montagne des Singes = 26; Cisame = 27; Mt Barka = 28; Trijonction = 29; Litany = 30; Jatun Sacha (Napo, Ecuador) = 31; AUCA14 road (Orellana, Ecuador) = 32; Comunidad Serena (Napo, Ecuador) = 33. All localities are in French Guiana except for 31–33.

b

96/78 S. ruber A
S. x-signatus
99/84 S. ruber B
S. ruber C
*/88 S. nasicus
S. cruentommus
0.1

97/94 C1
C2
Guyana
*/99
S. ruber C

70/ A1
A4
A5
A2
85/ A1
A6
76/ X1
X2
*/87 Peru
*/63
S. x-signatus X

97/ B3
*/63 B4
B5
*/86 B6
B1
79/56 B2
Ecuador
*/97
1/57
1/61
S. ruber A

S. ruber B

S. ruber D

S. nasicus

60/60 E2
E3
/ E1
S. fuscovarius
S. ruber E

F1
F6
F3
89/51 F7
67/50 F2
F5
*/ F4
G2
97/89 G1
S. boesemani F

S. boesemani G

89/ H2
H7
H9
H4
/ H5
H3
H6
H1
H8
S. cruentommus H

52/

67/

a

*/91 S. ruber species group

71/63 I1
I2
I3
/ I4
I5
S. sp. 1 I

89/66 S. elaeochrous
80/ S. staufferi
S. squalirostris
70/-

S. uruguayus

/ S. proboscideus 2
*/91 S. proboscideus 1
S. garbei
99/81 */98 S. jolyi 1
96/56 S. jolyi 2
96/73 S. rostratus
/ S. sp. 2
S. boulengeri
90/84 S. nebulosus 2
/ S. nebulosus 1
S. nebulosus 3

S. rostratus species group

*/99

94/63

67/*

S. catharinae
S. berthae
S. acuminatus
*/99 Dendropsophus leucophyllatus
67/64 Dendropsophus nanus
*/89 Sphaenorhynchus lacteus

0.1

c

/ S. ruber A
*/83 S. ruber B
S. ruber C
97/67 S. x-signatus
S. cruentommus
54/63
*/76 S. ruber E
96/
*/83 S.boesemani A
S.boesemani B
81/53 S. sp.1
S. elaeochrous

S. ruber species group
97/

96/55 S. rostratus
*/83 S. sp.2
S. proboscideus
64/ S. jolyi
*/ S. nebulosus

S. rostratus species group

*/91 D. leucophyllatus
D. nanus
*/99 Sphaeno. lacteus

0.01

Scinax ruber A

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Fig. 2.2: (a) Phylogram of lineages and species of *Scinax*, based on a Bayesian analysis of mitochondrial DNA sequences (781 bp of 16S rDNA and 12S rDNA), rooted with *Sphaenorhynchus lacteus*, *Dendropsophus leucophyllatus*, and *D. nanus*. Support values are Bayesian posterior probabilities and ML, nonparametric bootstrap values (1000 replicates) in percent. Asterisks indicate values of 100%. No values are given if below 50% or "–" if the respective analysis was not supporting the topology shown. (b) Phylogram based on a Bayesian analysis on a more extended mitochondrial DNA sequence dataset (1332 bp of cytochrome *b*, 16S rDNA and 12S rDNA), rooted on *S. cruentommus*. Support values on phylogram represent posterior probabilities and ML, bootstrap values in percent (1000 replicates), respectively. (c) Phylogram from a Bayesian analysis of nuclear DNA sequences (1677 bp of 18S rDNA and tyrosinase), rooted on *Sphaenorhynchus lacteus*, *Dendropsophus leucophyllatus*, and *D. nanus*. Only one individual by previously identified major lineage were available for the 18S fragment and therefore only these ones were used. Support values are as in (a).
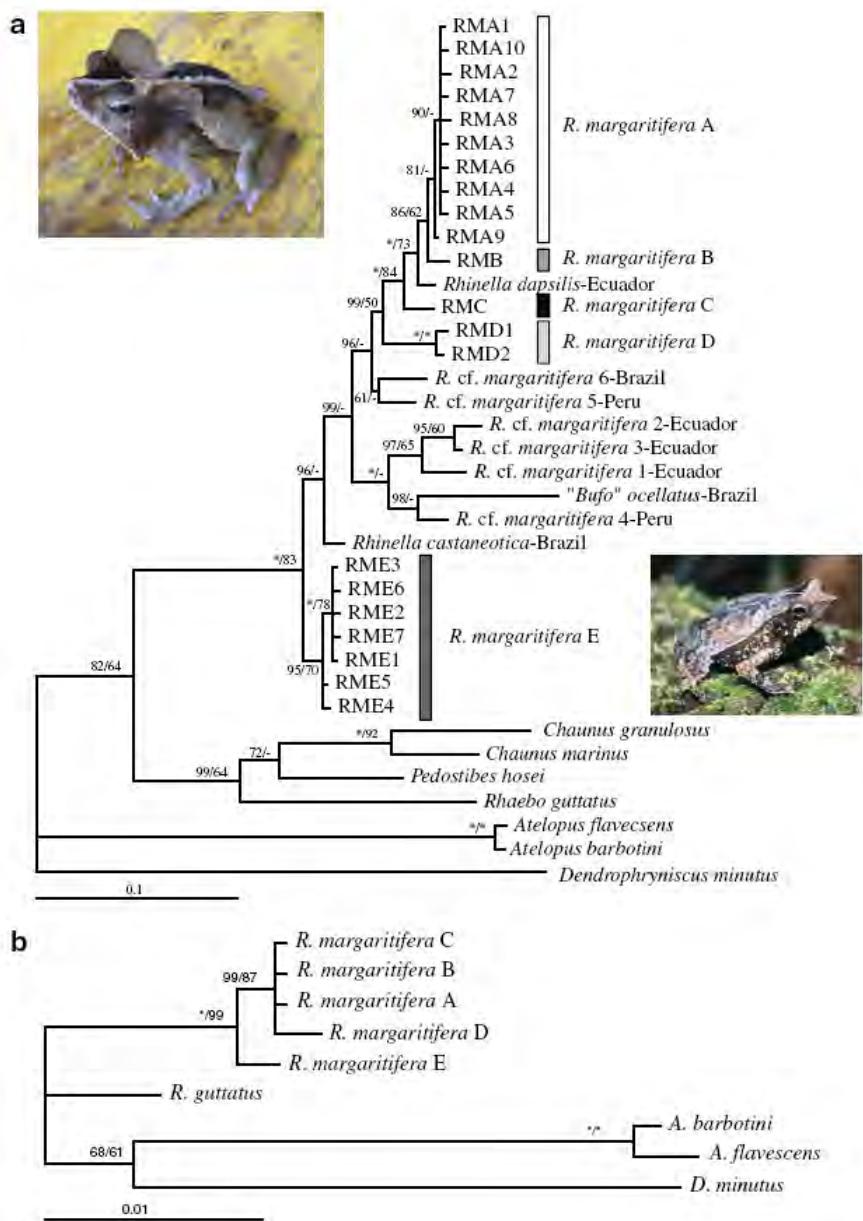
Fig. 2.3: (a) Phylogram of lineages in the *Rhinella margaritifera* group and other species of *Bufonidae*, from a Bayesian analysis of mitochondrial DNA sequences (798 bp of 16S rDNA and 12S rDNA), rooted on *Dendrophryniscus minutus*, *Atelopus flavescens*, and *A. barbotini*. Support values are Bayesian posterior probabilities and ML nonparametric bootstrap values in percent. Asterisks indicate values of 100%. No values are given if below 50% or "–" if the respective analysis was not supporting the topology shown. (b) Phylogram from a Bayesian analysis of nuclear DNA sequences (1864 bp of 18S rDNA and tyrosinase), rooted on *Atelopus flavescens* and *A. barbotini*. Only one individual per previously identified major lineage were available for the 18S fragment and therefore only these ones were used. Support values are as in (a).
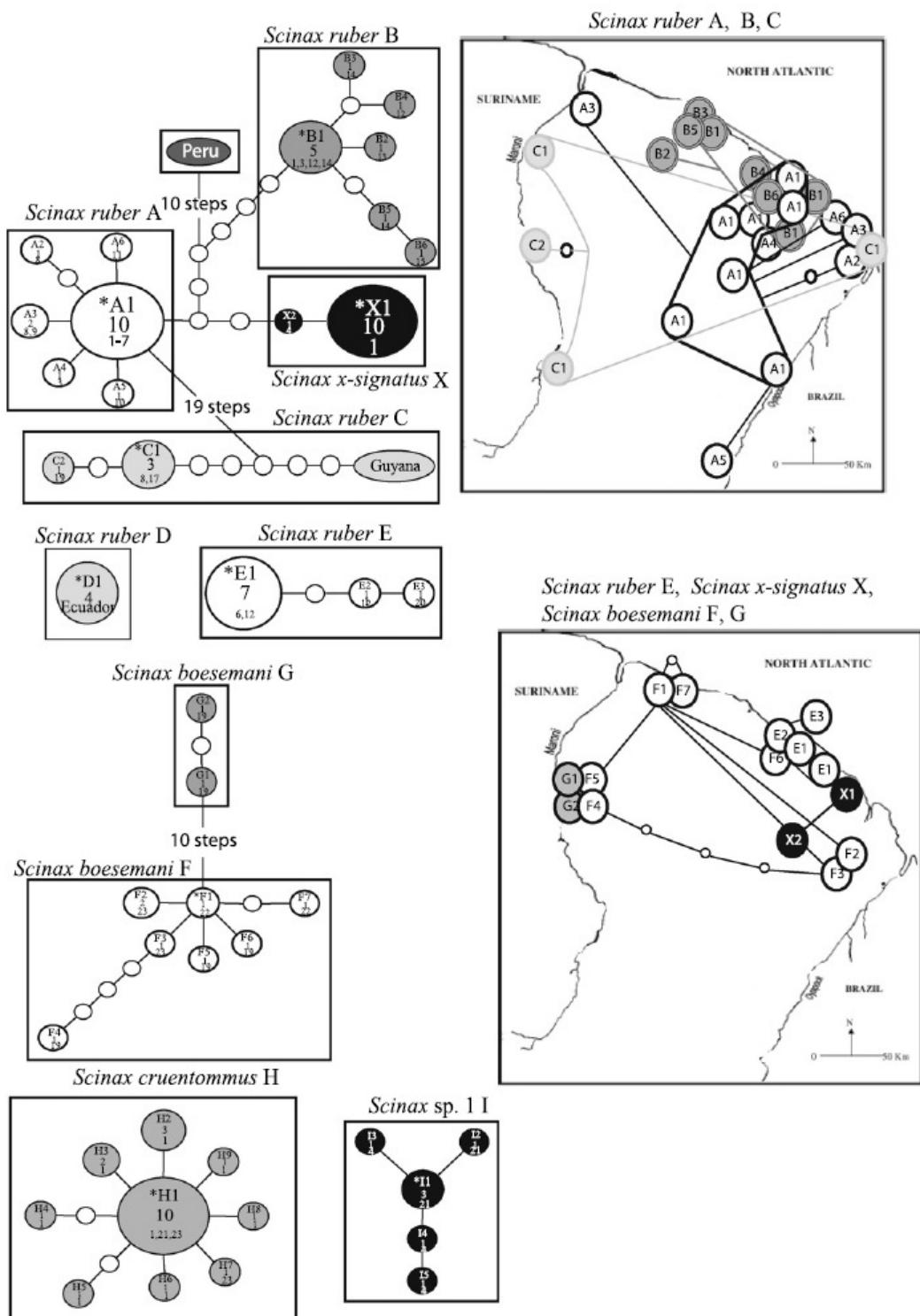
Fig. 2.4: Haplotype networks for the major *Scinax* lineages sampled, based on mitochondrial DNA sequences (763 bp of 12S rDNA and 16S rDNA). Asterisks indicate the central haplotype, and from top to bottom the numbers represent the name of each haplotype, the number of individuals and of the localities where it has been sampled. *S. ruber* is divided into six haplogroups.

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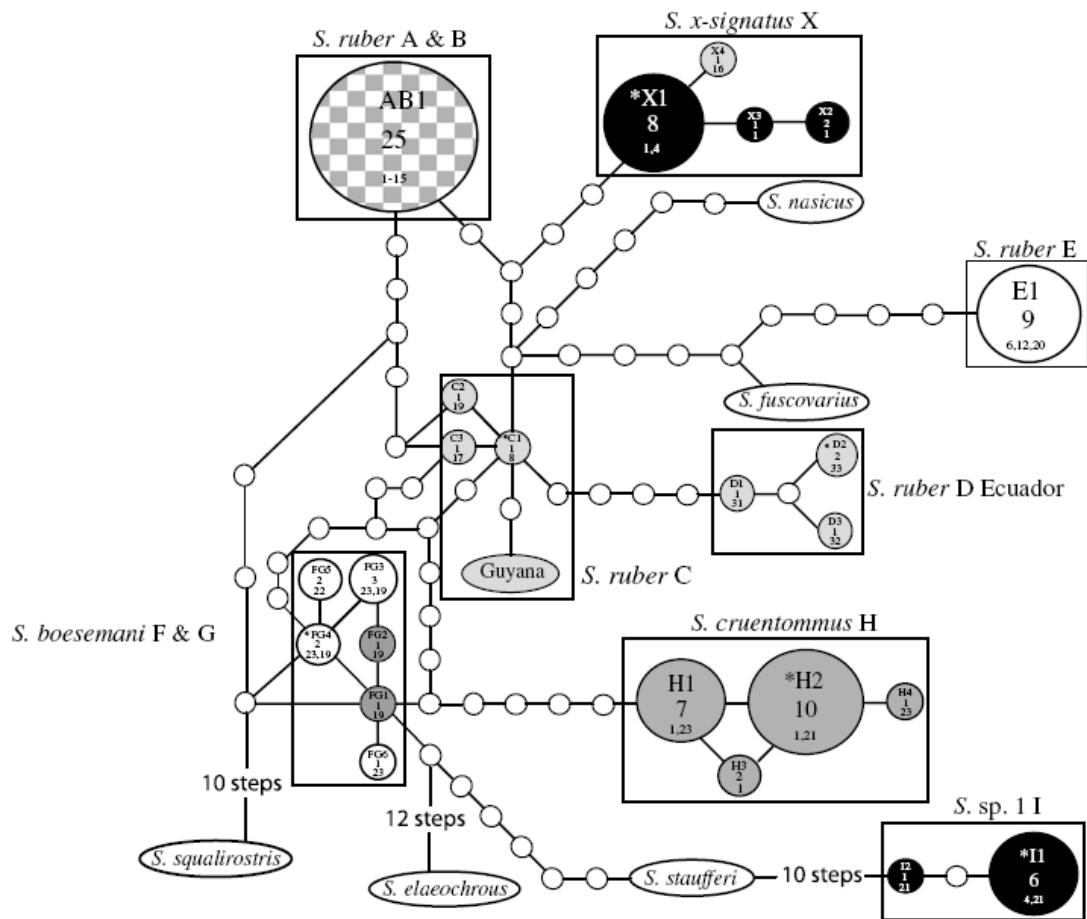
Fig. 2.5: Haplotype networks for the major *Scinax* lineages sampled, based on nuclear DNA sequences (360 bp of tyrosinase). From top to bottom the numbers represent the name of each haplotype, the number of individuals and of the localities where it has been sampled. Asterisks denote the central haplotype of each cluster.
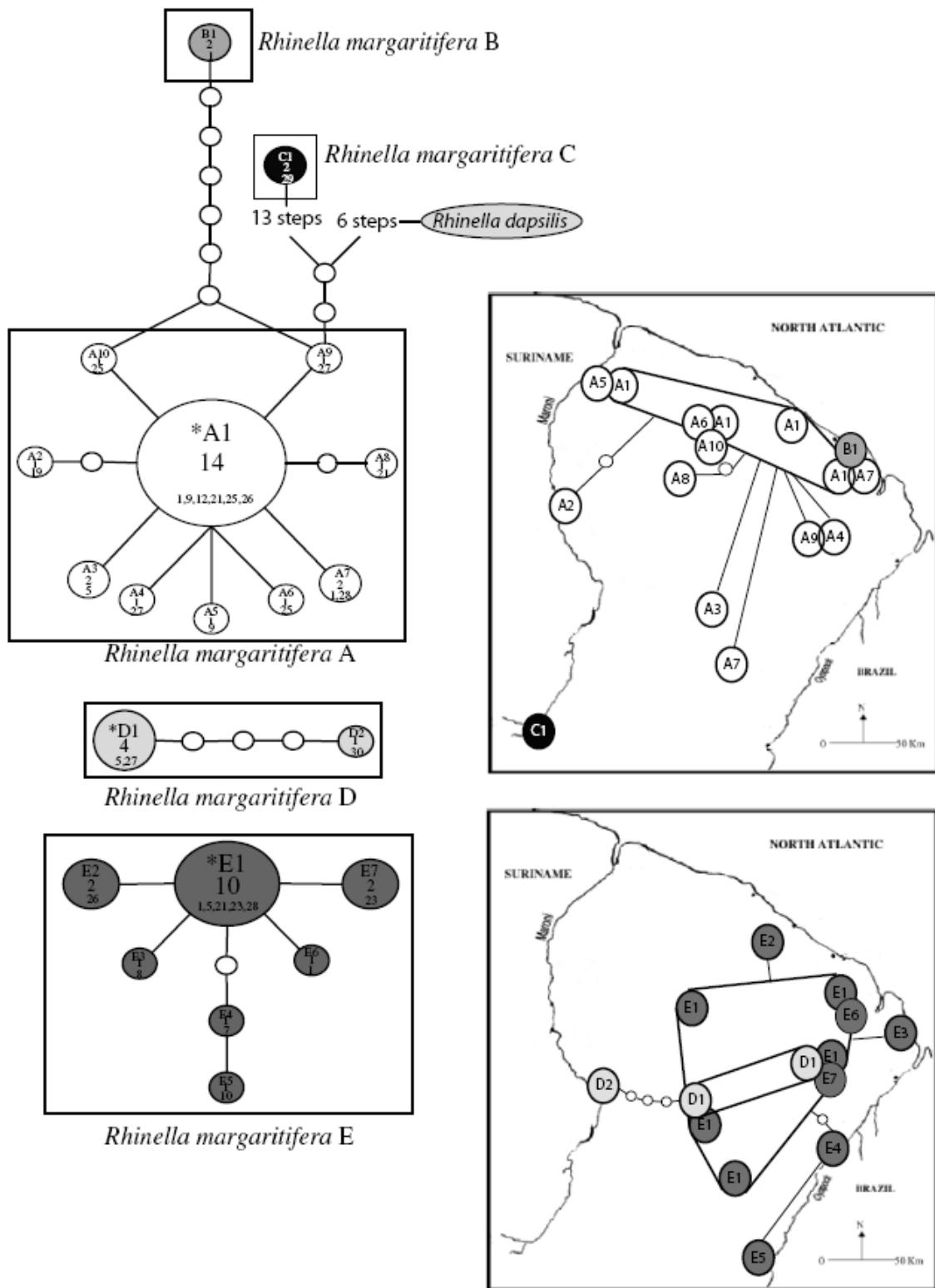
Fig. 2.6: Haplotype networks for the different lineages of the *Rhinella margaritifera* group based on mitochondrial DNA sequences (777 bp of 12S rDNA and 16S rDNA). Asterisks indicate the central haplotype, and from top to bottom the numbers represent the name of each haplotype, the number of individuals and of the localities where it has been sampled.
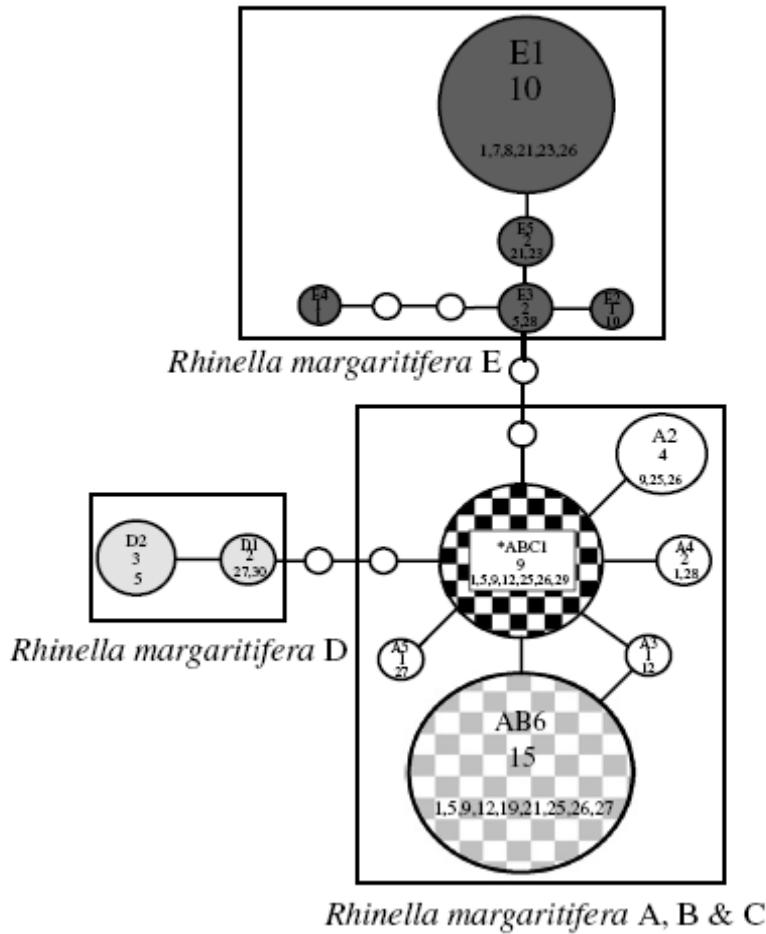
Fig. 2.7: Haplotype network for the different lineages of the *Rhinella margaritifera* group based on nuclear DNA sequences (539 bp of tyrosinase). From top to bottom the numbers represent the name of each haplotype, the number of individuals and of the localities where it has been sampled.
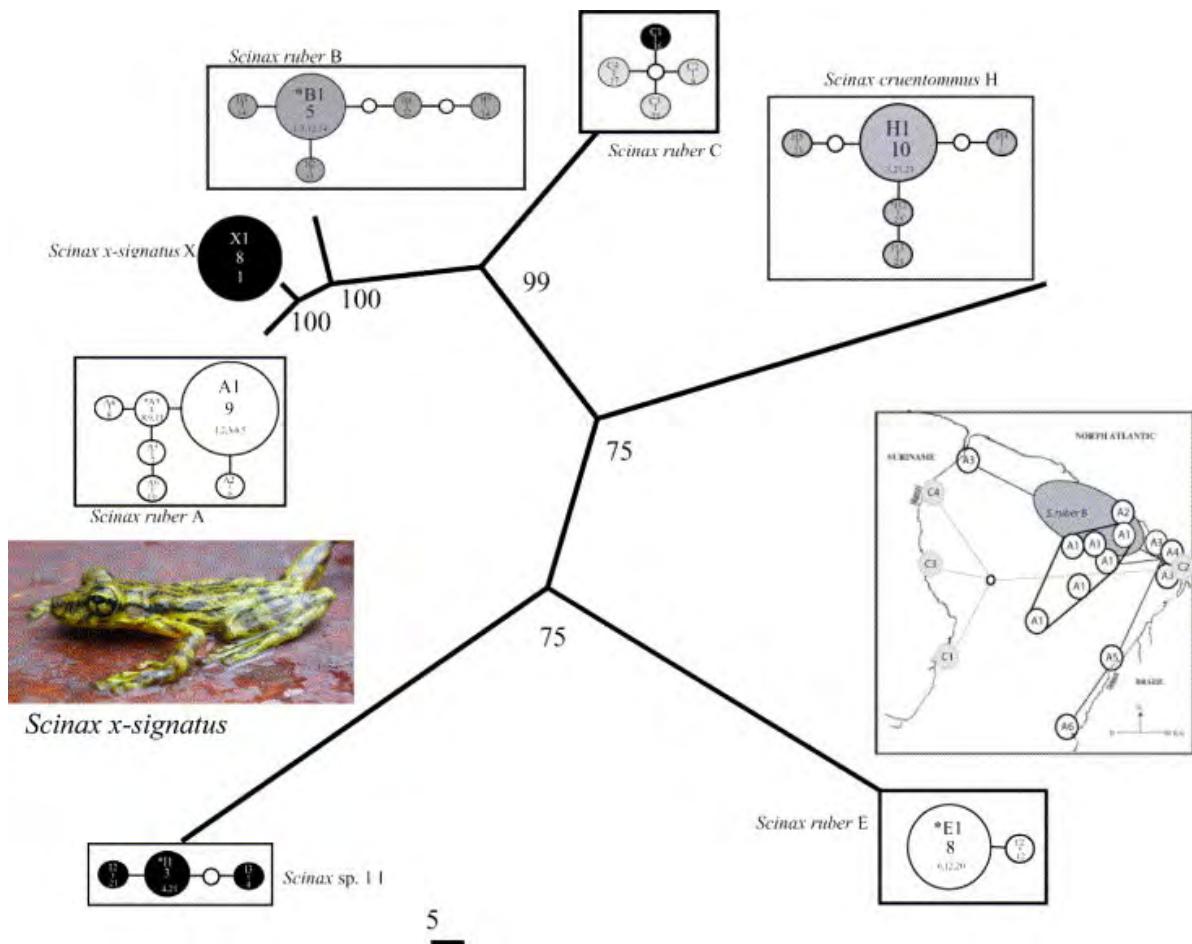
Fig. S2.1: Unrooted NJ tree and haplotype networks using Cytb sequences for the *Scinax ruber* species group.
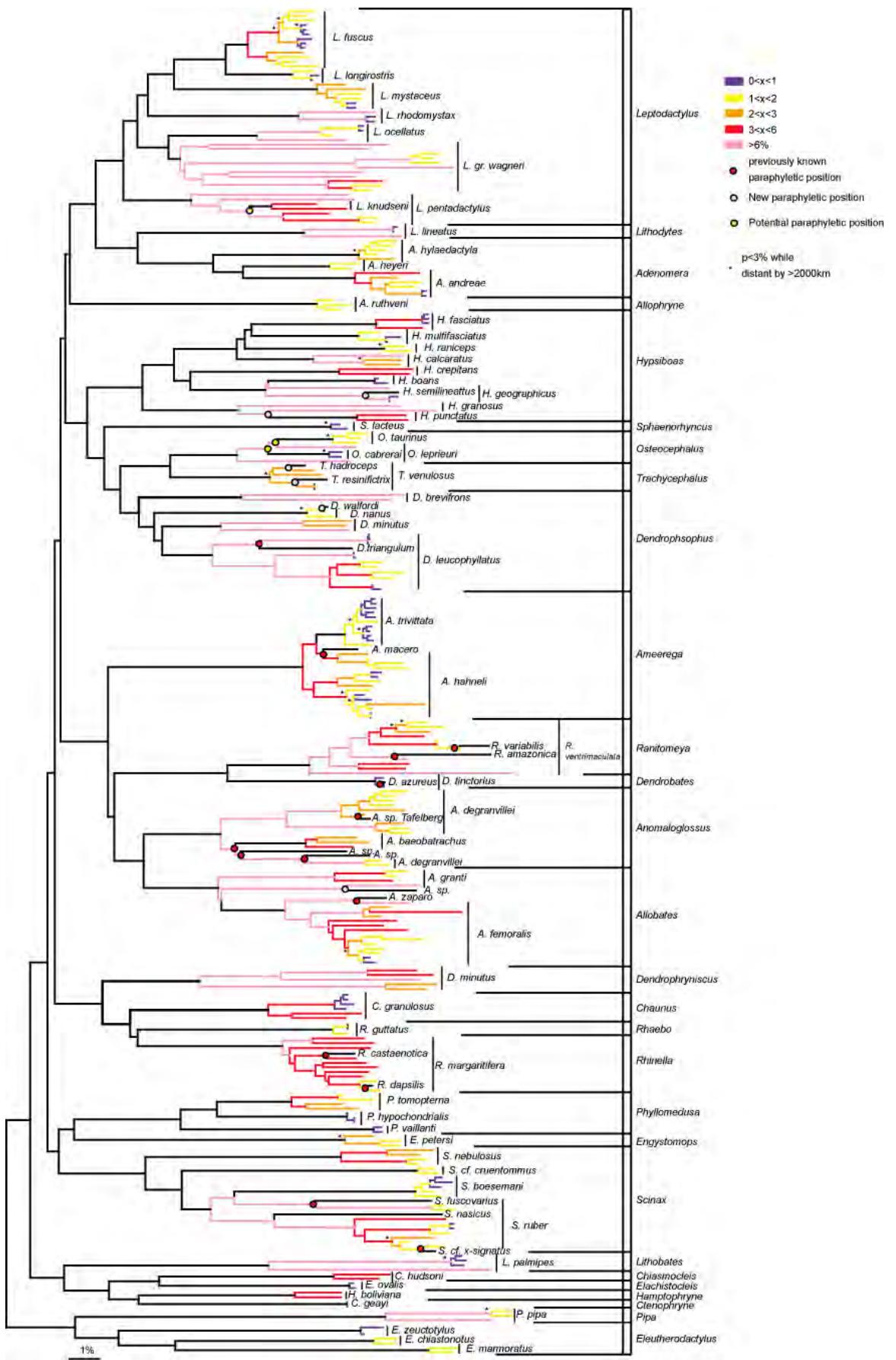
Fig. 3.1: A Neighbour-Joining phylogram using p distances among 285 sequences representing 60+18 species. Branches are coloured in blue for intraspecific distances between 0 and 1%, in yellow for distances between 1 and 2%, in orange for distances between 2 and 3%, in red for distances between 3 and 6% and in pink for distances higher than 6%. Circles represent paraphyletic position either revealed by previous study (red) or in the present study (blue) supported by high (>75) bootstrap values (ML and MP) and posterior probabilities, Yellow circles when the relationship between the species is not resolved and potentially paraphyletic. Asterisks represent close lineages (<3%) which occur at localities more distant than 2000km.
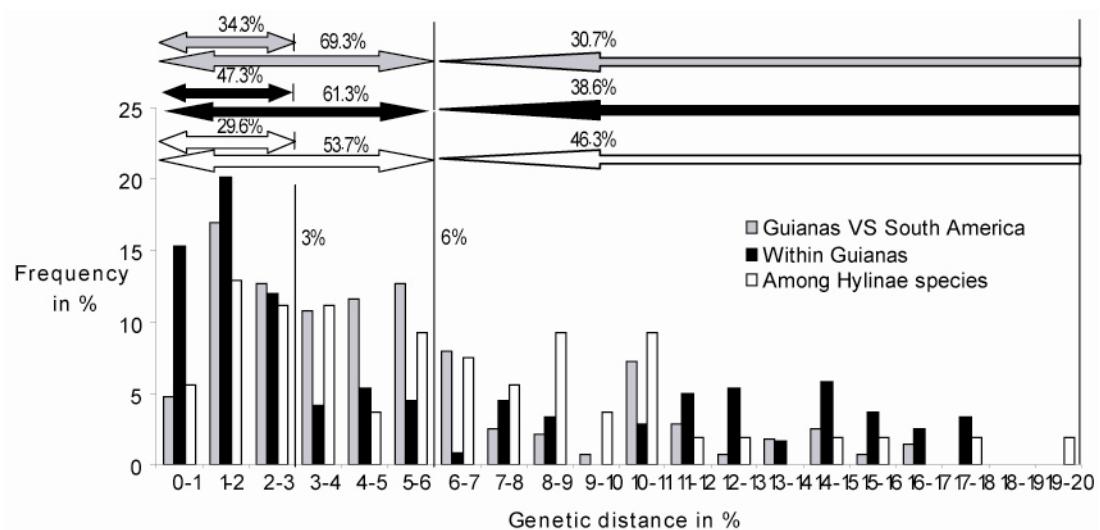
Fig. 3.2: A histogram showing the distribution of the pairwise genetic distances among (1) conspecific populations from the Guianas versus other populations in South America (grey), (2) conspecific populations within Guianas (black), (3) closest Hylinae species from the dataset of Faivovich et al. (2005) (white). The arrows above the histogram provide summary data showing the proportion of distances in each of the three categories situated between 0 and 3%, 0 and 6% and above 6%.
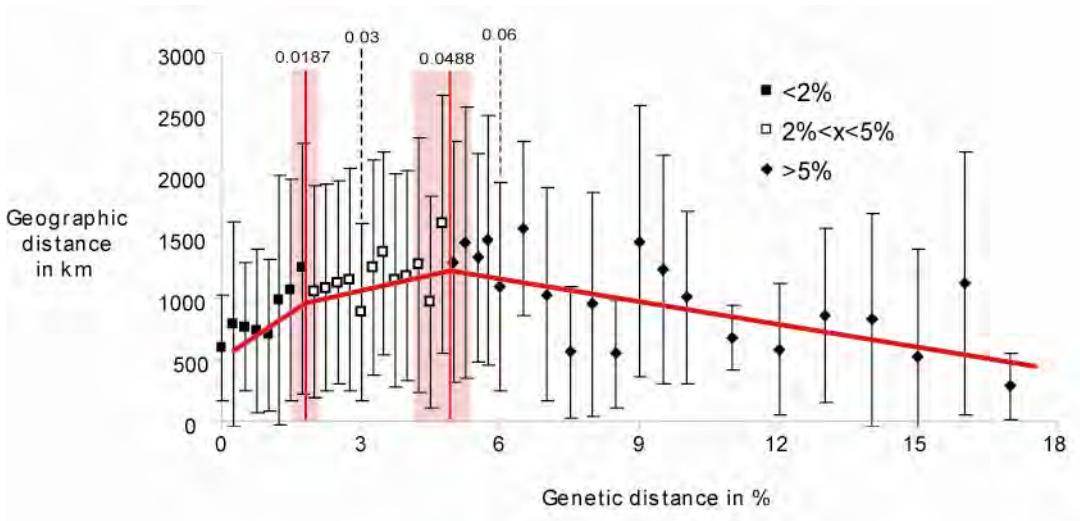
Fig. 3.3: The distribution of the pairwise genetic distances among conspecific populations against geographical distances (N=822). Genetic data are segregated by 0.025% classes from 0 to 6%, by 0.5% classes from 6 to 10% and then by 1% for higher values. Linear models computed from the distribution of the raw data.
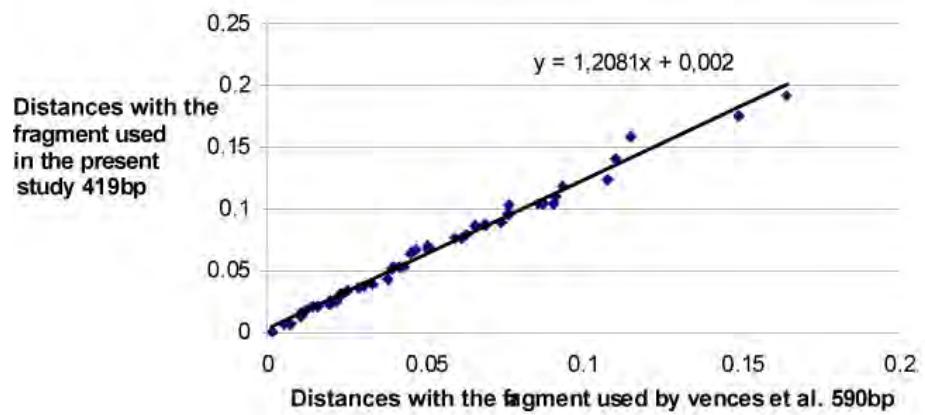
Fig. S3.1: Distribution of the pairwise distances between the Hylinae sister species from Faivovich et al. (2005) with two sizes of the same 16S rDNA fragment: One with 590bp corresponding to the fragment used by Vences (2005) and one with 419bp for the present study.
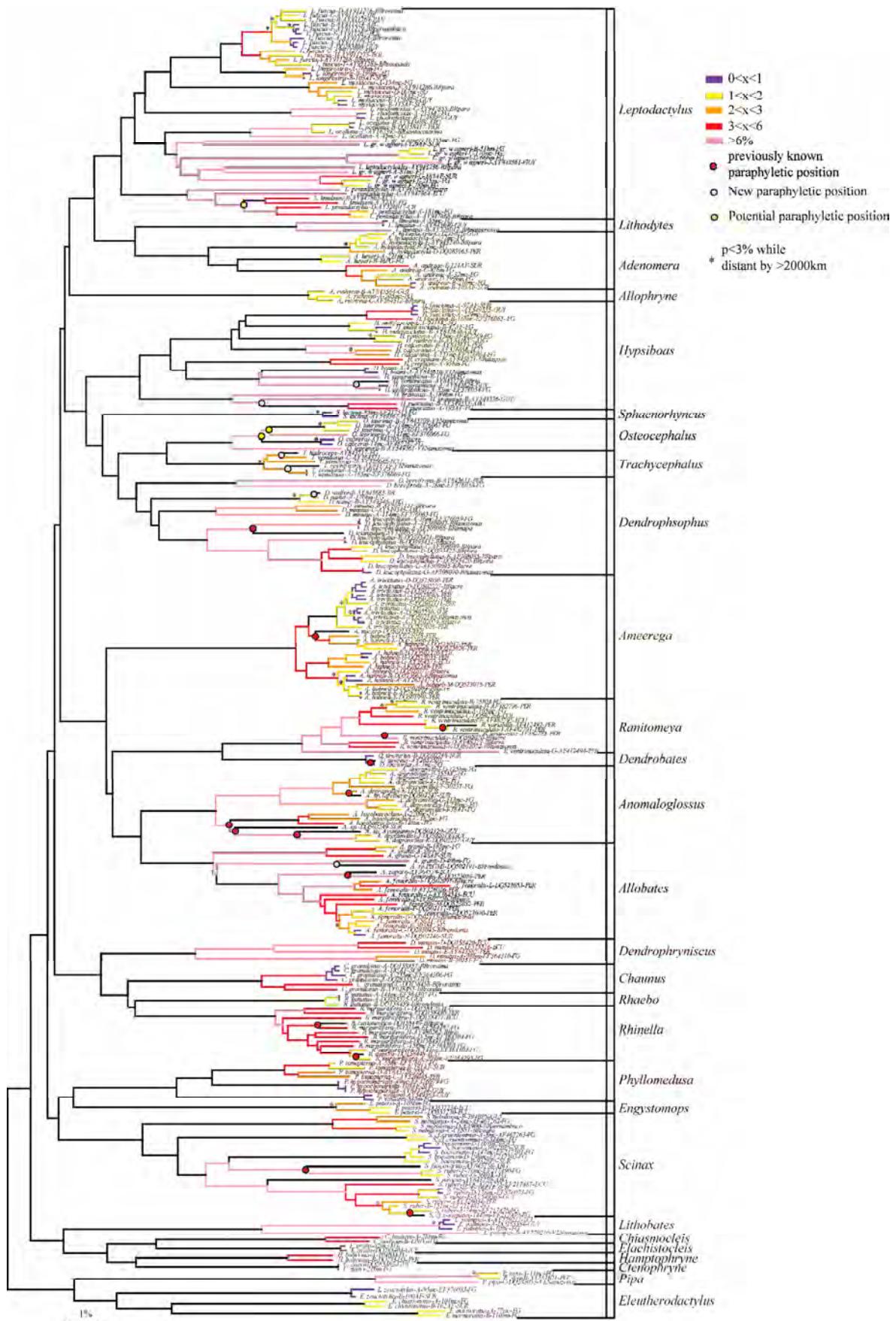
Fig. S3.2: Tree from Fig. 3.1 with sample labels and geographical indications: FG=French Guiana; SUR=Suriname; GUY=Guyana; VEN=Venezuela; BR=Brazil; COL=Colombia; PAN=Panama; CR=Costa Rica; ECU=Ecuador; PER=Peru; BOL=Bolivia; PAR=Paraguay; ARG=Argentina

Fig. S3.3: Consensus tree derived from Bayesian analysis of the data.

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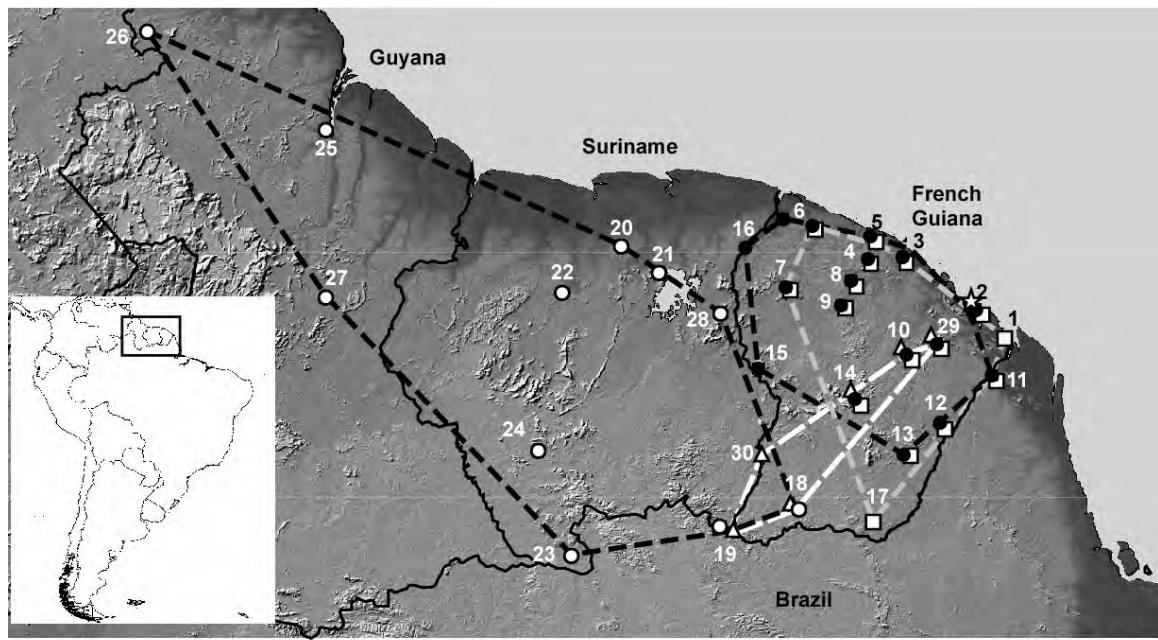
Fig. 4.1: Map of sampled areas adapted from Fouquet et al. (2007) and additional unpublished data. Black circles: *Rhinella margaritifera* (clade A), white star: *R. margaritifera* (clade B), white circles: *R. martyi* (clade C), white triangles: *R. lescurei* (clade D), white squares: *Rhinella* sp. (clade E).

1 = Ouanary; 2 = Kaw; 3=Guatemala; 4 = Petit-Saut; 5 = Montagne tortue; 6 = St Laurent du Maroni; 7 = Lucifer; 8 = St Elie; 9 = Trinité; 10 = Nouragues; 11 = St Goerges; 12 = Camopi; 13 = Mont Bakra; 14 = Saül; 15 = Montagne Kotika; 16 = Grand Santi; 17 = Trois Sauts; 18 = Haute Wanapi; 19 = Mitaraka; 20 = Goliathberg; 21 = Brownsberg; 22 = Ralleighvallen; 23 = Sipaliwini; 24 = Ellerts de Haan (Kayser); 25 = Bartica; 26 = Baramita; 27 = Kurupukari; 28 = Lely Mountain; 29 = Cisame; 30 = Litany.
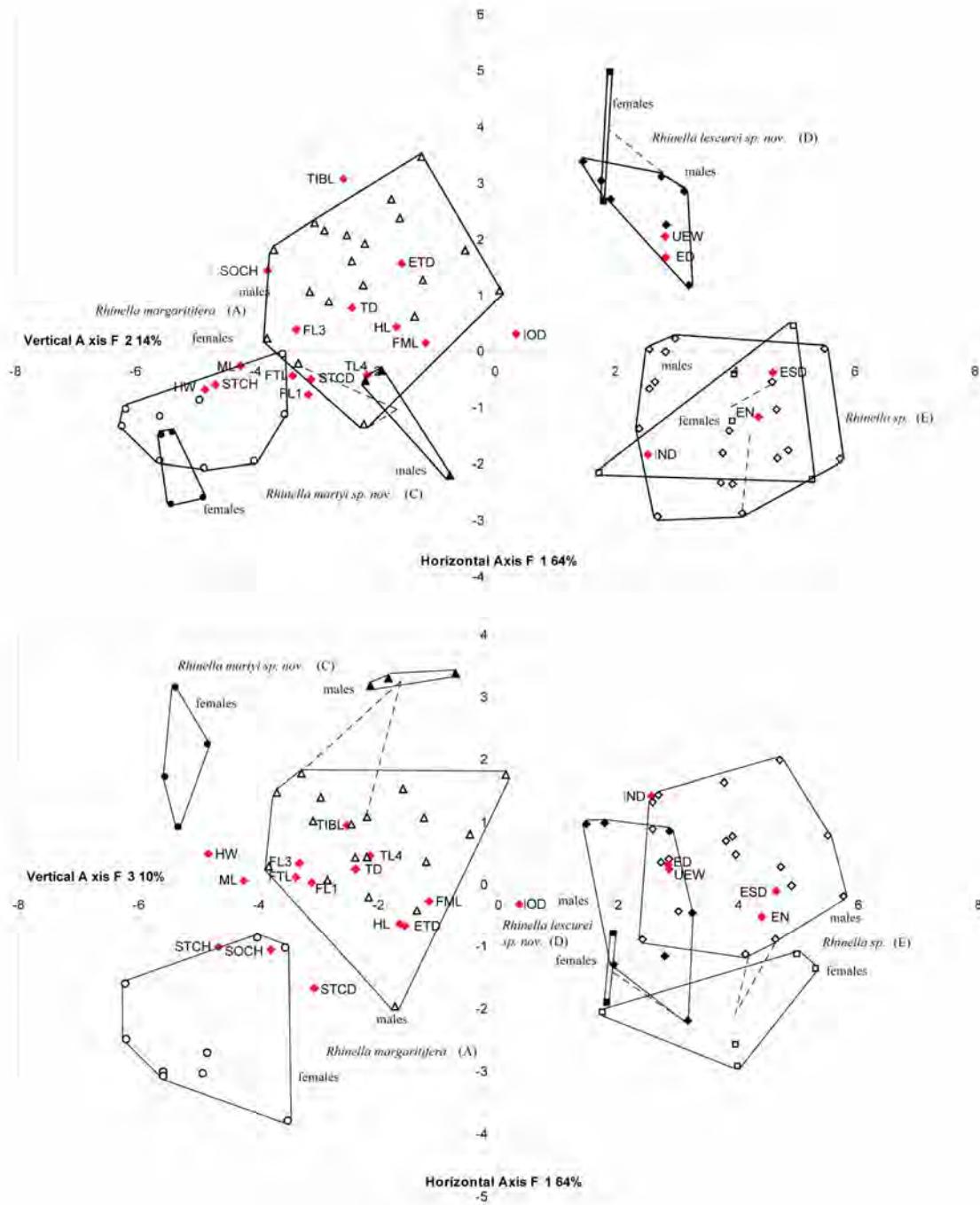
Fig. 4.2: Graphical representations along three axes of discriminant analysis on morphological measurements taken from the Guianan *Rhinella margaritifera* species group. Variables in red diamonds and dashed lines indicate individuals that switched groups.

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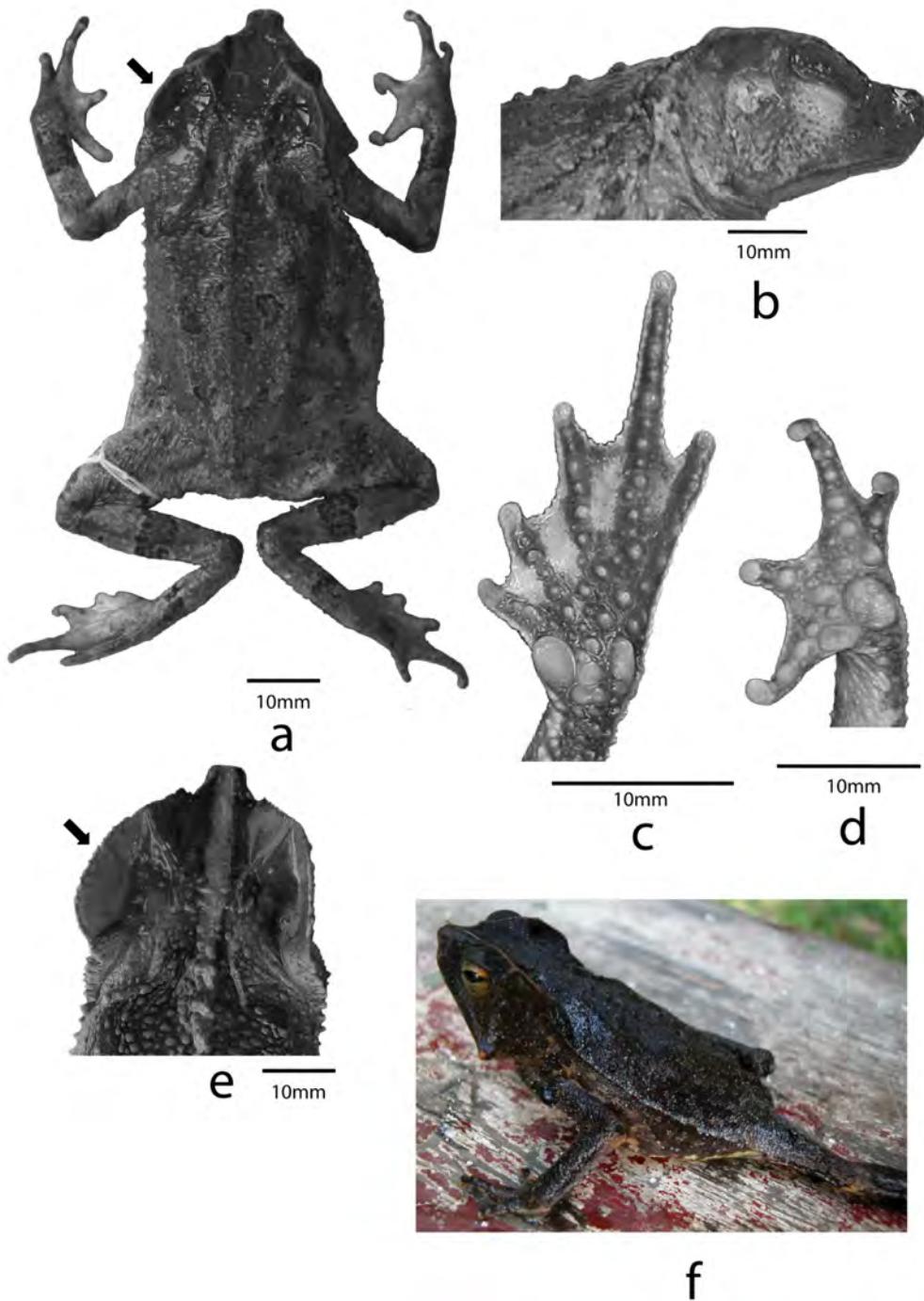
Fig. 4.3: Holotype of *R. martyi* (2006.2601 MNHN): a. dorsal view, b. profile of head, c. ventral view of left foot, d. ventral view of left hand; e: *Rhinella margaritifera* (clade A) (138bm), female, in dorsal view, f. living specimen 2006.2602 MNHN. Arrows indicate one of the main character to differenciate the two species.
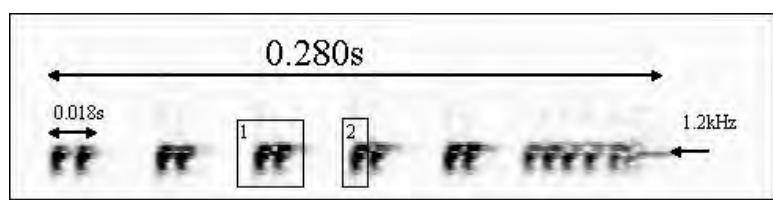
Fig. 4.4: *Rhinella martyi* (C) vocalization (one call): (1) pulse-group; (2) pulse.
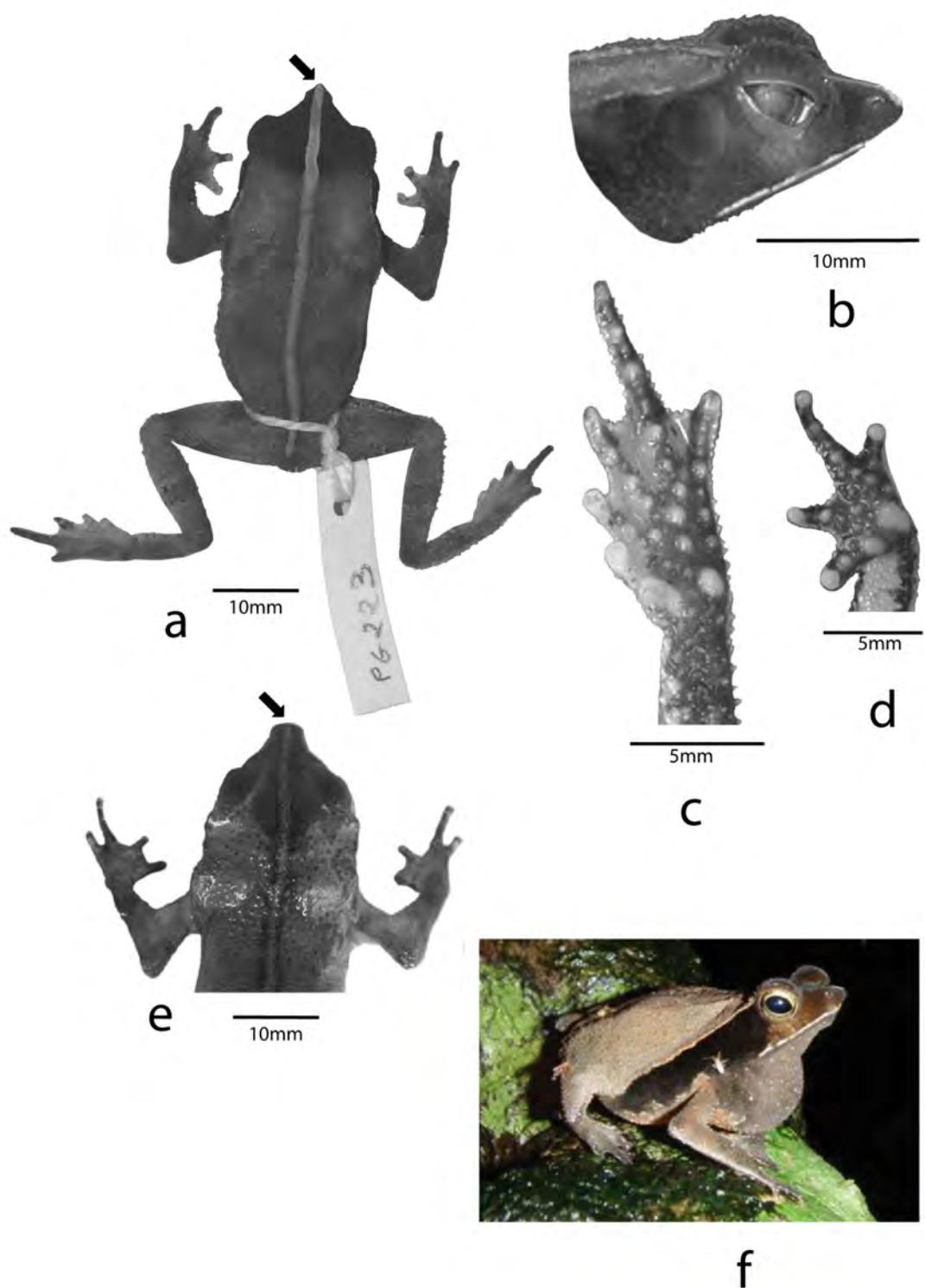
Fig. 4.5: Holotype of *R. lescurei* (2006.2608MNHN): a. dorsal view, b. profile of head, c. ventral view of left foot, d. ventral view of left hand; e: *Rhinella* sp. E (198bm), male, in dorsal view, f. living specimen, a male calling while perched on a vine. Arrows indicate one of the main character to differenciate the two species.
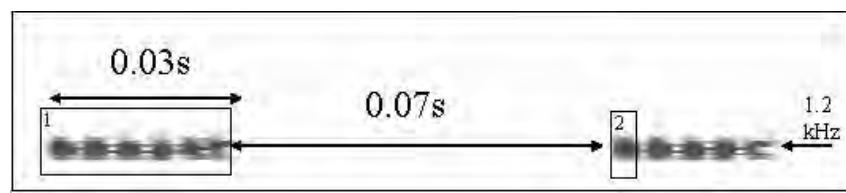
Fig. 4.6: *Rhinella lescurei* (D) fragment of vocalization (two pulse-groups). (1) pulse-goup; (2) pulse.
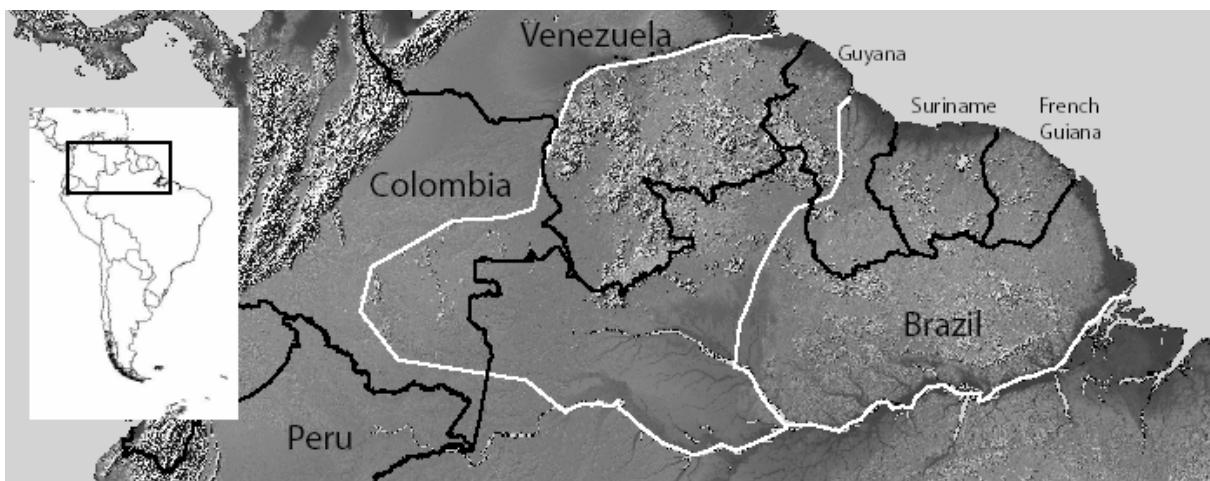
Fig. 5.1: Map of the Guiana Shield (after Hammond, 2005), the white border shows the eastern and the western sub-regions.
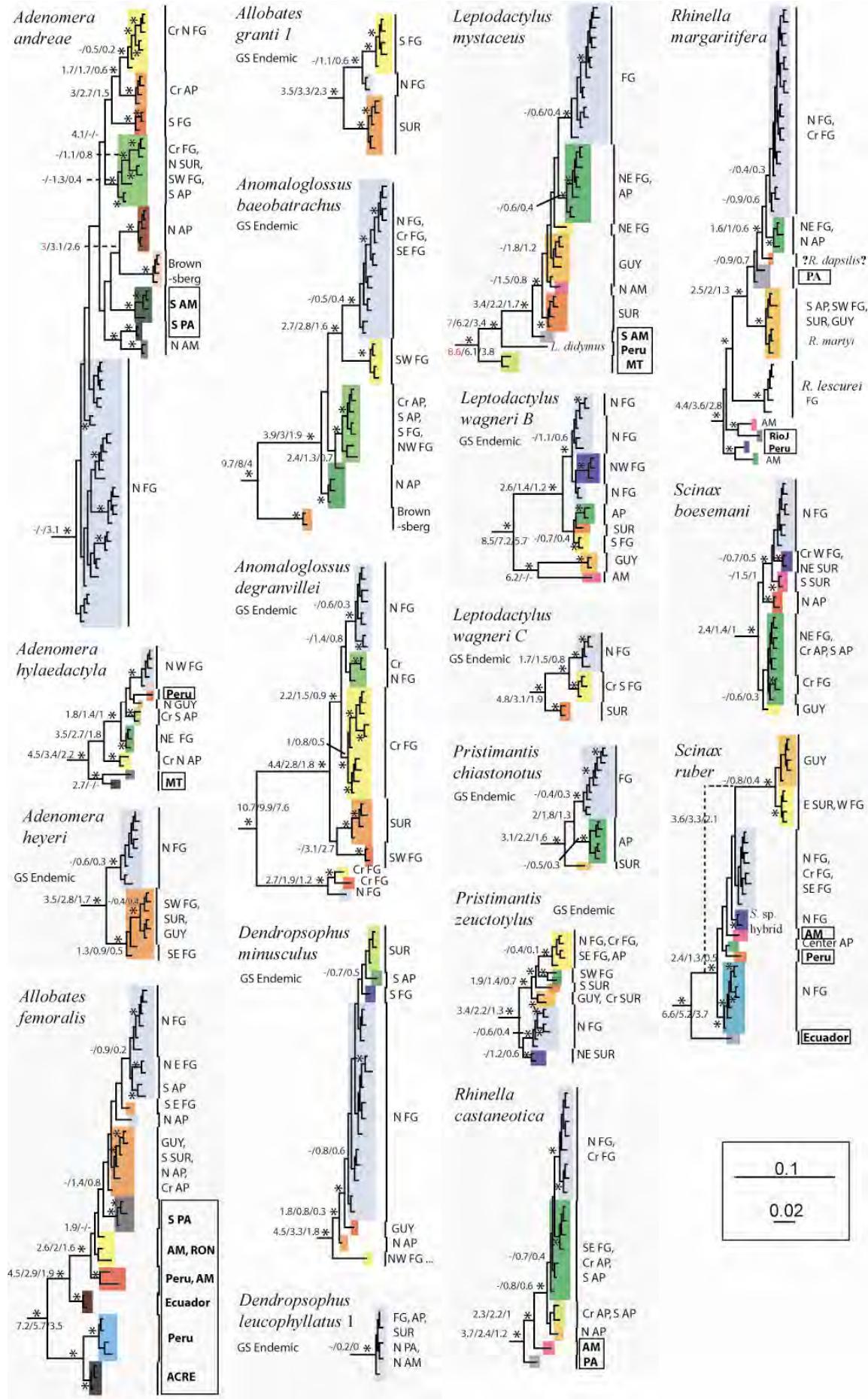
Fig. 5.2: 18 sub-trees derived from 8 full trees (Fig. S5.1-8) hypothesized from Bayesian analysis run on each frog genera. All the tree lengths have been equally scaled. Asterisks indicate significant support for either Bayesian analysis or Maximum parsimony. Higher NCA clades have been coloured differently when corresponding to geographically segregated lineages and their location indicated as follow FG=French Guiana, AP=Amapà, SUR=Suriname, GUY=Guyana, PA=Parà, AM=Amazonas, MT=Mato Grosso, N=North, W=West, E=East, S=South, Cr=Center. The same colour code has been used in full trees (Fig. S5.1-8), statistical parsimony networks (Fig. S5.9-16; 25-32) and maps (Fig. S5.17-24). The boxed and bold names of areas indicate localities outside the GS. Time estimations of the nodes have been indicated in million years (m.y.) as follows: Relaxed Bayesian molecular clock / Pairwise distances / Coalescent time for populations. The dashed line in *Scinax ruber* indicates the alternative topology from Fouquet et al. (2007a,b; Chapters 2,3) which is also indicated in Fig. 5.3.
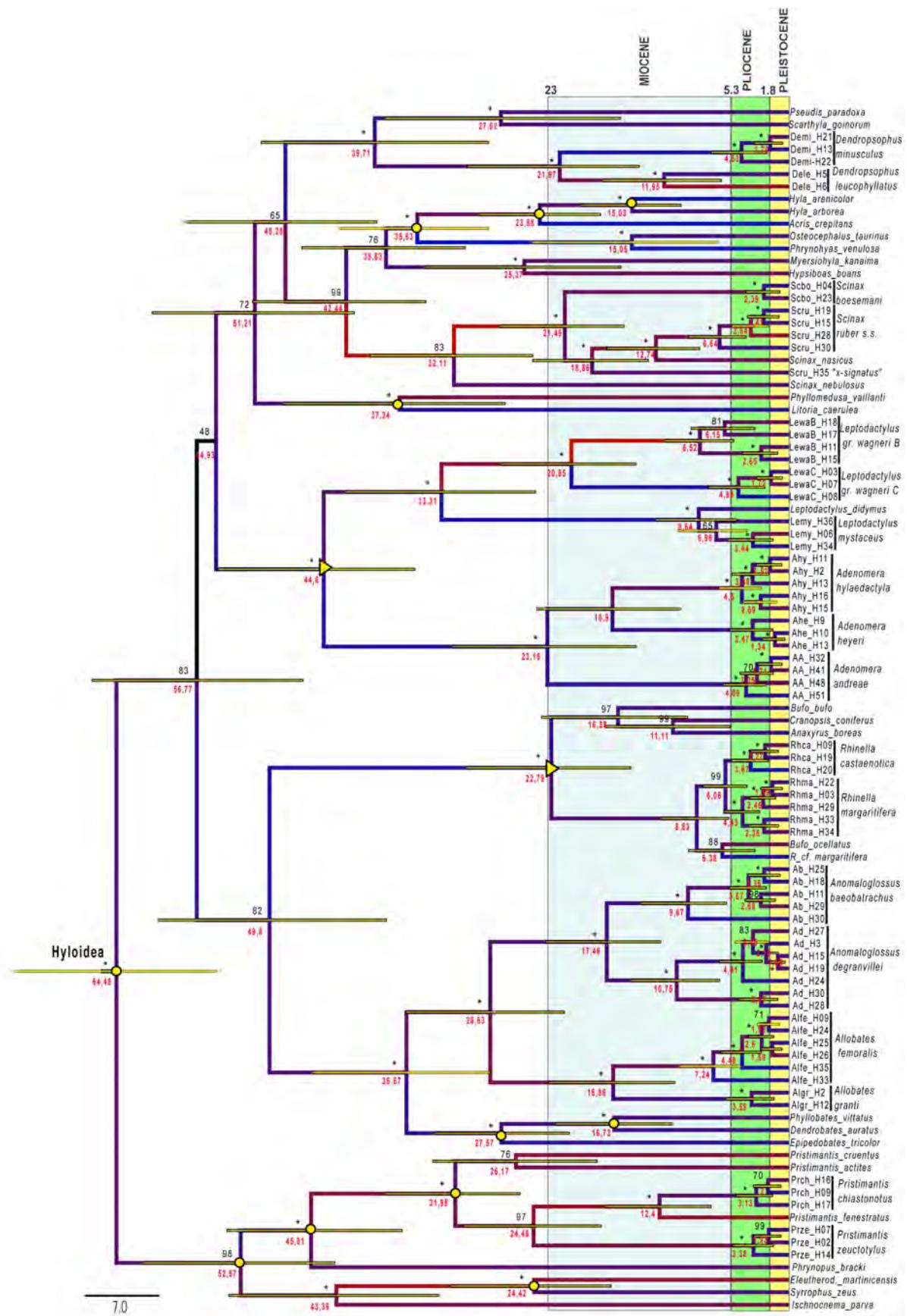
Fig. 5.3: Relaxed Bayesian molecular clock tree based on a 843 bp mtDNA dataset (12S+16SrDNA). Calibration points are indicated by yellow dots (n=11) for normal distributions and by yellow triangles for upper limits (n=2). Divergence time estimates are indicated in red under branches and 95% Credibility intervals are represented as yellow bars centred on the nodes. Posterior probabilities (pp) are indicated above the branches and asterisks refer to a pp equal to 1. Branches are coloured according to the estimated rates of molecular evolution with the hotter the colour the higher the rate (branches in black indicate unresolved topologies with no rates associated). Miocene, Pliocene and Pleistocene epochs are highlighted in blue green and yellow background respectively.
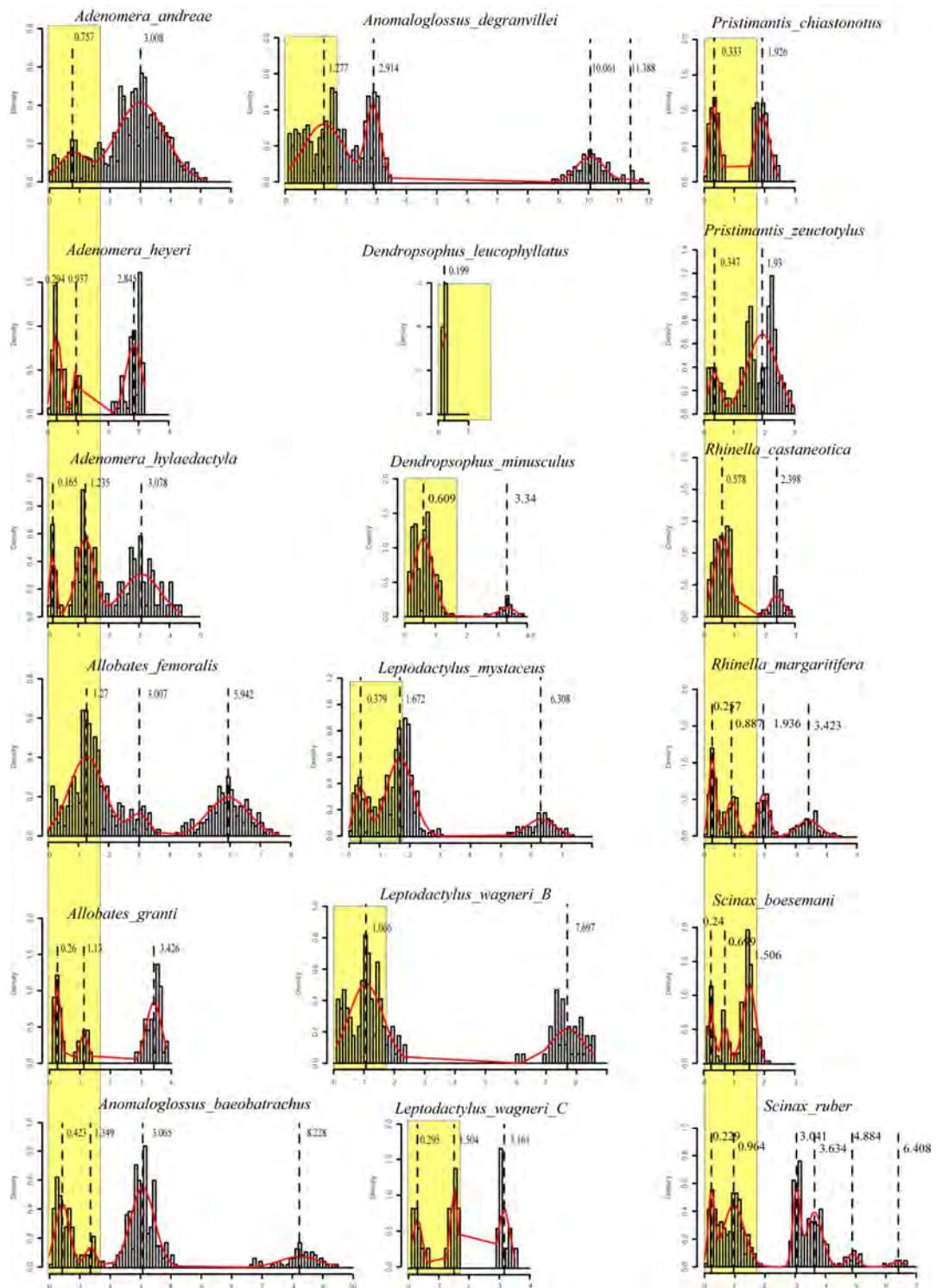
Fig. 5.4: Mismatch distributions from pairwise distances for each of the 18 focal frog species. All the plots have been equally scaled in million years (distances have been multiplied by the rates of evolution estimated for each species). Estimated normal distributions matching the data according to the BIC criterion are indicated in red. Each peak of these normal distributions is indicated with dashed line and the peak values indicated on the top. The Pleistocene epoch is represented by a yellow background.
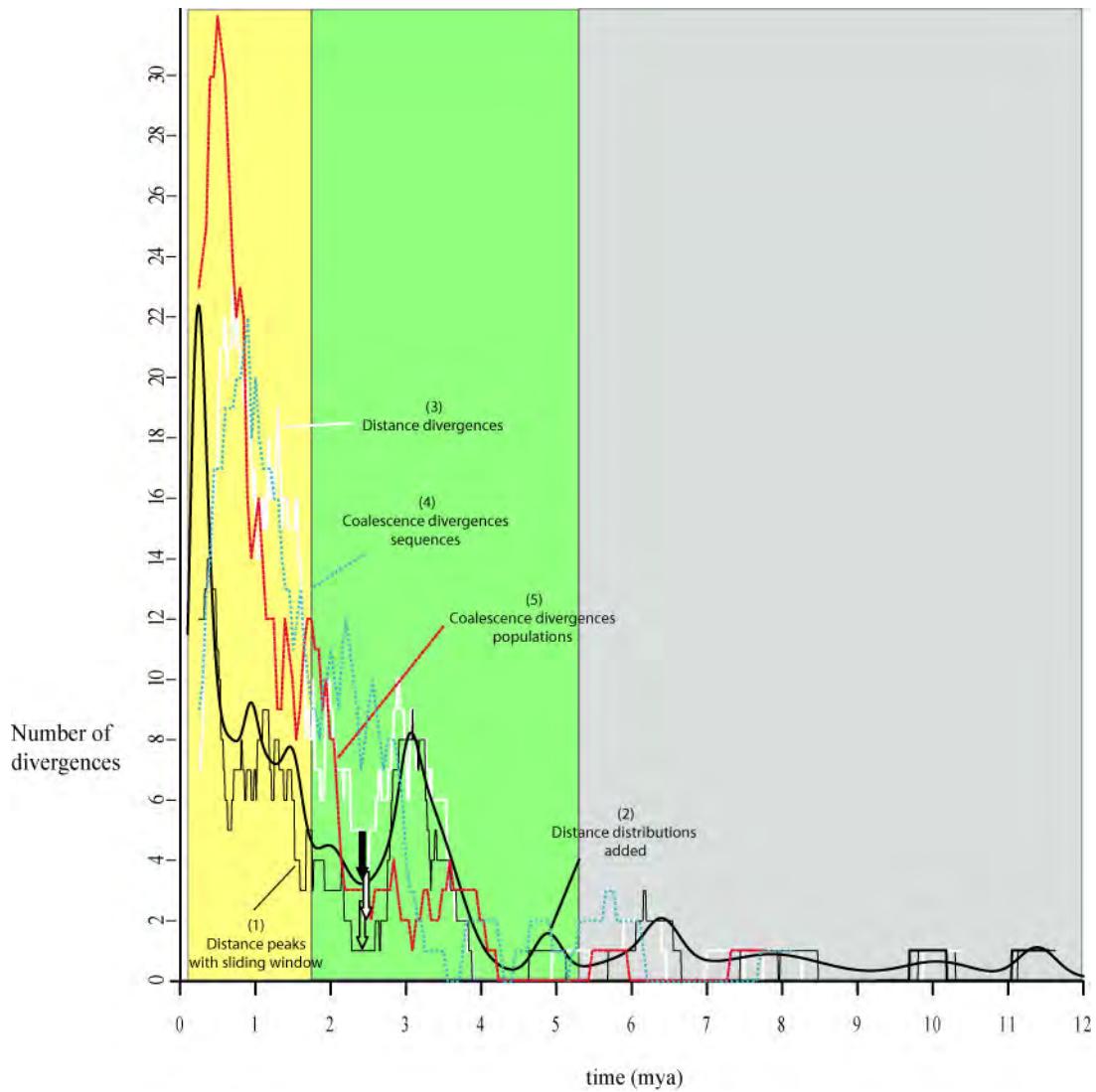
Fig. 5.5: Cumulated estimations of divergence time. (1) In fine black stroke, the distribution estimated with sliding window method of the peaks of each normal distribution from mismatch distributions. (2) In thick black stroke, cumulated and equally weighted normal distributions from mismatch distributions. The ordinte axis is arbitrarily scaled for this distribution. (3) In white, the distribution estimated with sliding window method of mean corrected pairwise distances point estimates (based on phylogenetic results, corresponding divergences for the two following distributions 4 and 5) of divergence time (4) In blue dashed line, the distribution estimated with sliding window method of the coalescence time point estimates (based on phylogenetic results) for the gene. (5) In red dashed line, the distribution estimated with sliding window method of the coalescence time point estimates (based on phylogenetic results) for the populations. Miocene, Pliocene and Pleistocene epochs are highlighted in blue green and yellow background, respectively.

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a: Total

![red]	65-75%
	55-65%
	45-55%
	35-45%
	25-35%
	15-25%
	5-15%
![hatch]	0-5%

b: Pre-pleistocene

![red]	65-75%
	55-65%
	45-55%
	35-45%
	25-35%
	15-25%
	5-15%
![hatch]	0-5%

c: Pleistocene

![red]	29-32%
	26-29%
	23-26%
	20-23%
	17-20%
	14-17%
	11-14%
	8-11%
	5-8%
![hatch]	0-5%

d: Ranges overlap

	16-18 sp. 88.9%
	15-16 sp. 83.3%
	14-15 sp. 77.8%
	13-14 sp. 72.2%
	12-13 sp. 66.7%
	11-12 sp. 61.1%
	10-11 sp. 55.6%
	9-10 sp. 50%
	8-9 sp. 44.4%
	7-8 sp. 38.9%
	6-7 sp. 33.3%
	5-6 sp. 27.8%
	4-5 sp. 22.2%
	3-4 sp. 16.7%
	2-3 sp. 11.1%
	1-2 sp. 5.6%
![hatch]	0%
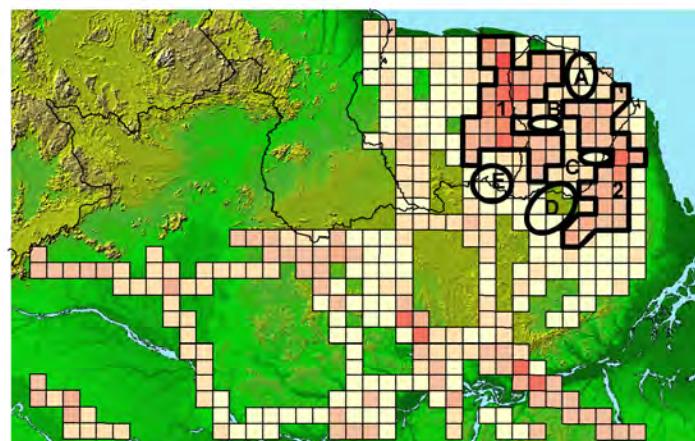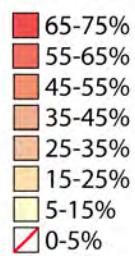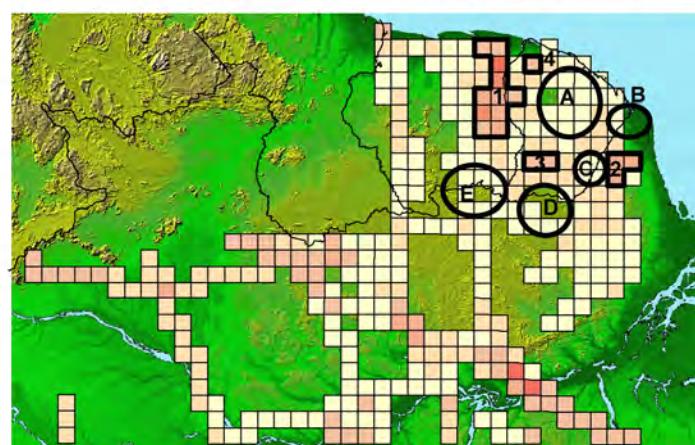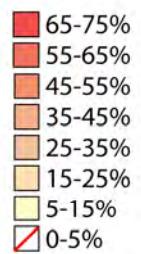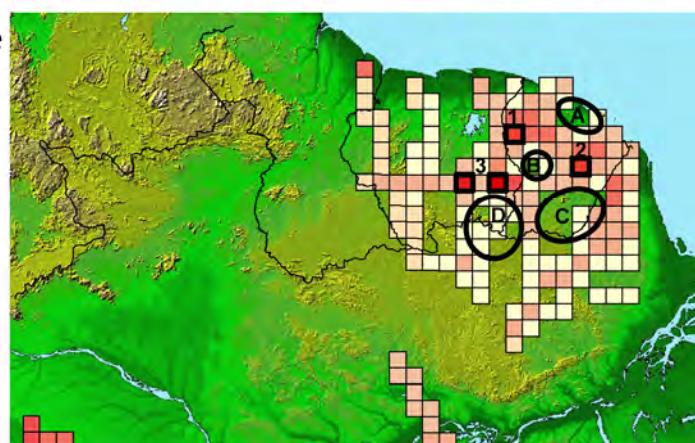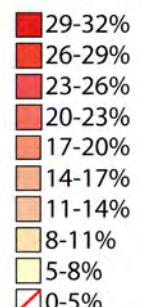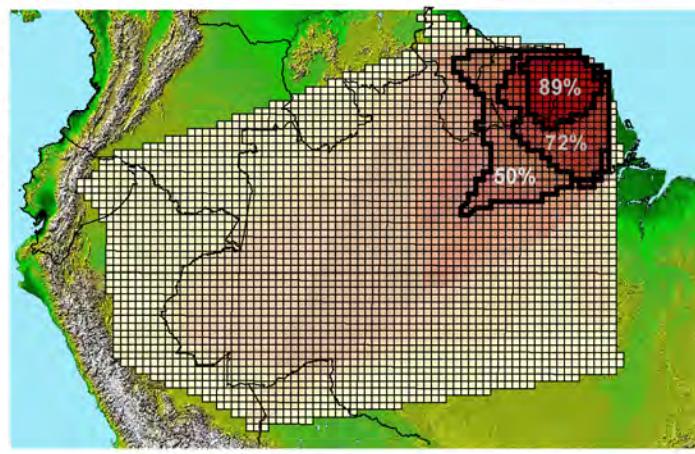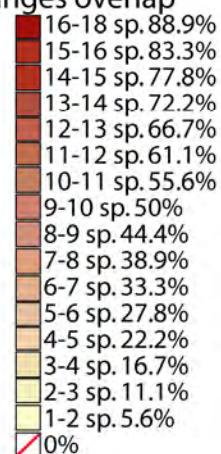
Fig. 5.6: Phylogeographic breaks mapped for a: the total number of breaks. b: breaks between lineages diverging before Pleistocene. c: breaks between lineages diverging during Pleistocene. d: cumulated ranges of all 18 focal frog species. The hotter the colour of the squares the more breaks intersect them. The areas concentrating the breaks (25% of the species having a phylogeographic break in the square) are delimited with thick black lines and annotated with numbers. Conversely, the uniform zones, with a low number of breaks (0 to 15% of the species) are delimited with black circles and annotated with letters. The proportion of species range sampled that overlap is indicated in figure 5d for 50% (from 9 species); 72% (from 13 species) and 89% (from 16 species).
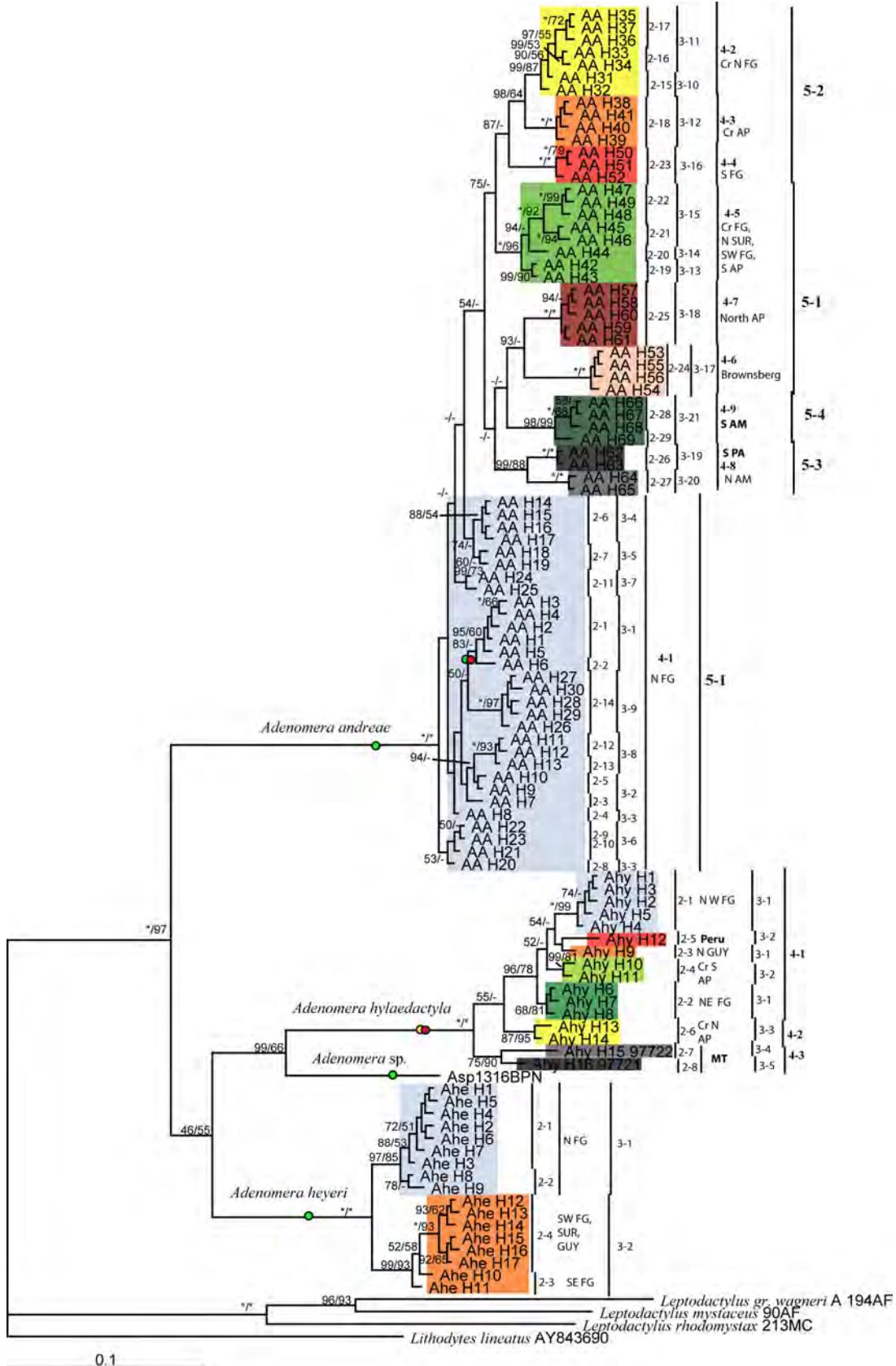
Fig. S5.1: Phylogram hypothesized from Bayesian analysis for the *Adenomera* genus (see legend page 175).

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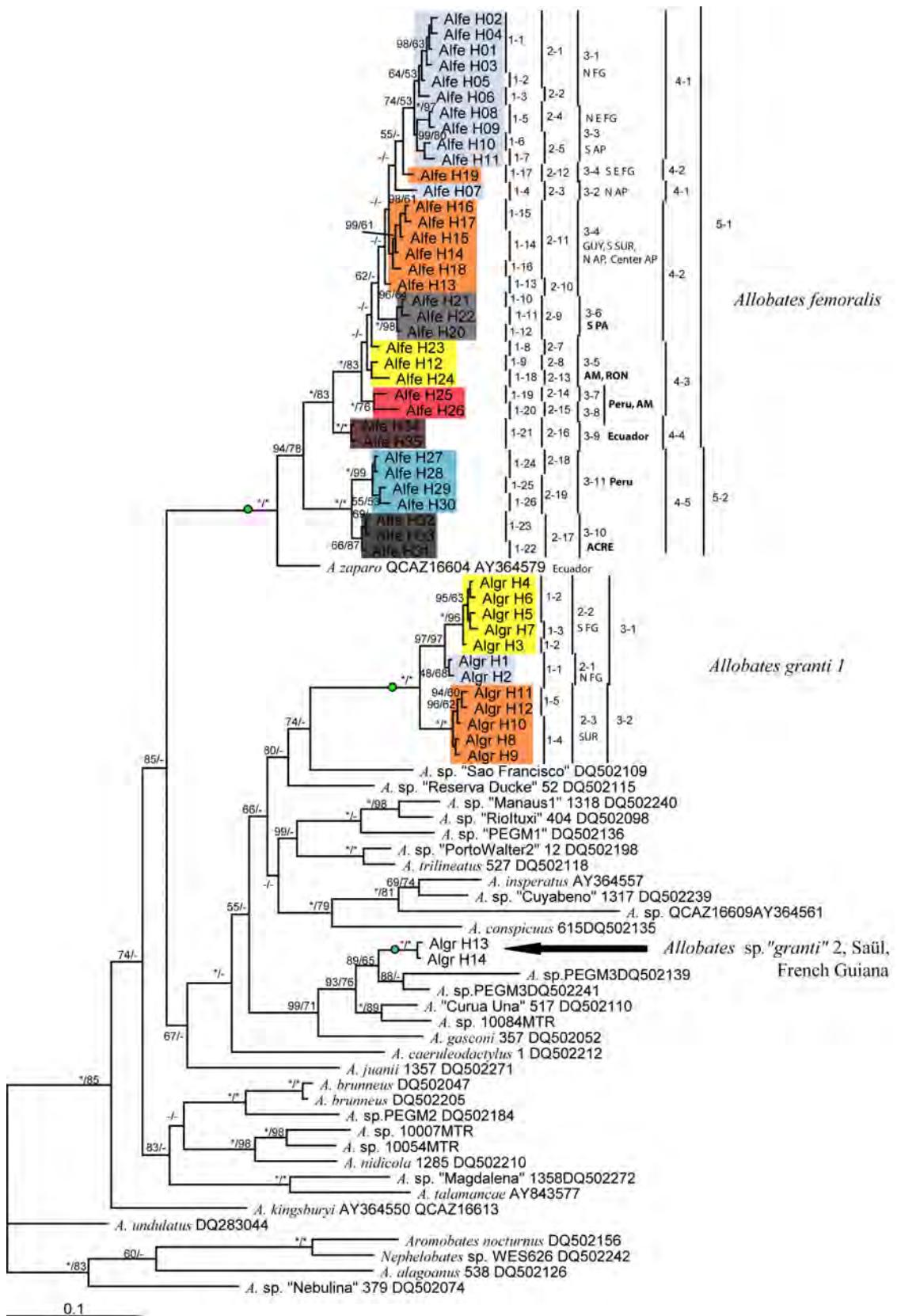
Fig. S5.2: Phylogram hypothesized from Bayesian analysis for the *Allobates* genus (see legend page 175).
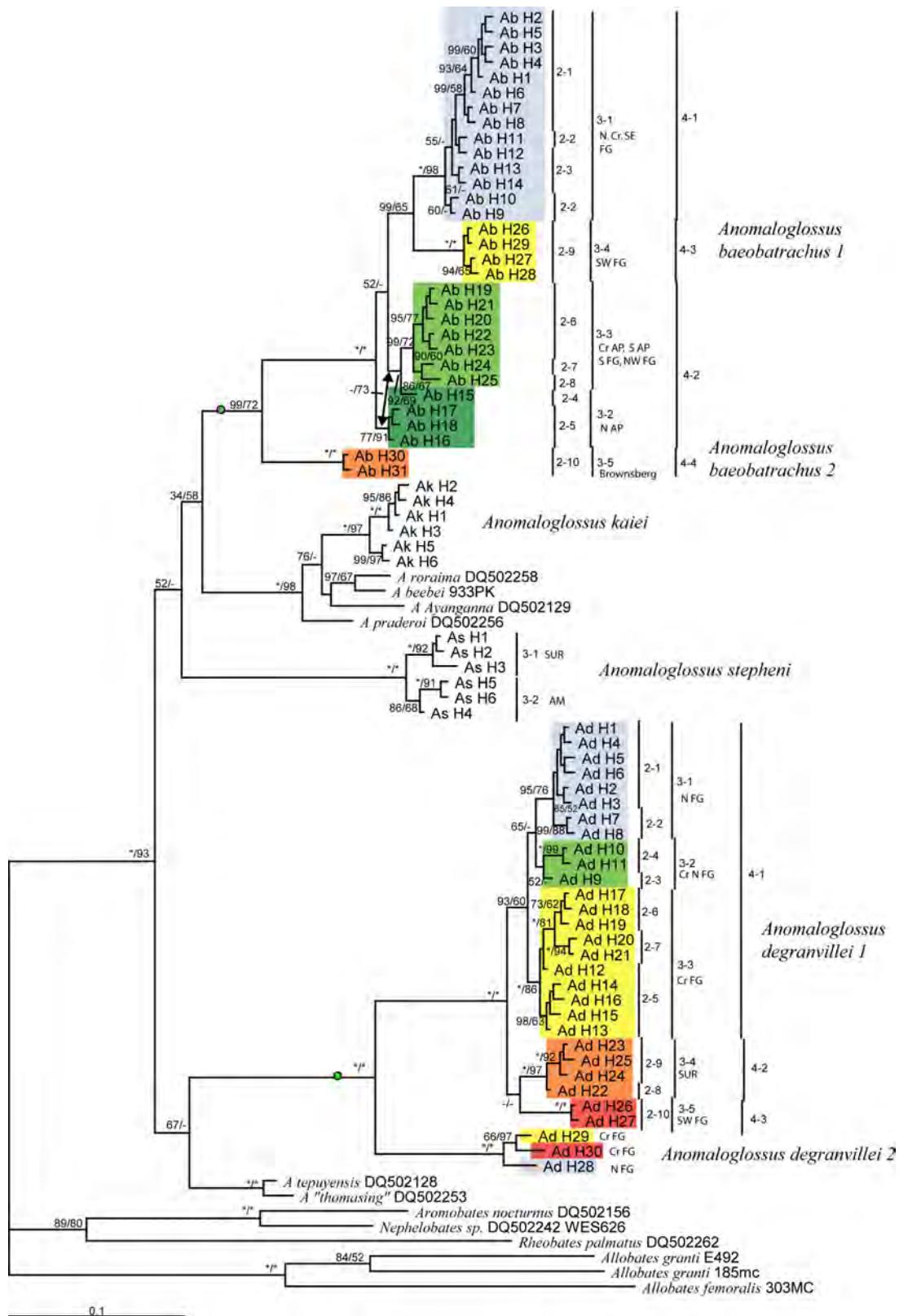
Fig. S5.3: Phylogram hypothesized from Bayesian analysis for the *Anomaloglossus* genus (see legend page 175).

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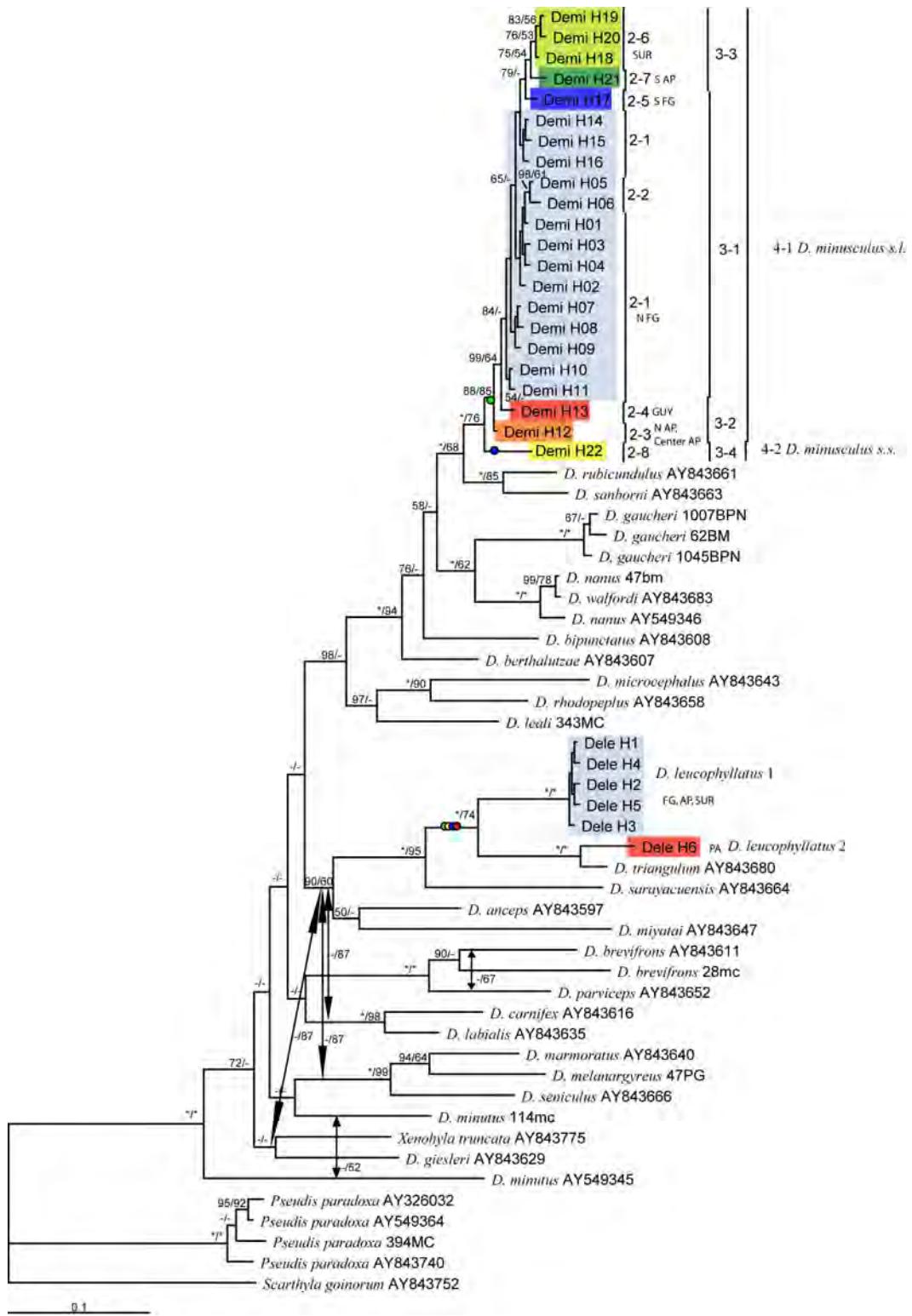
Fig. S5.4: Phylogram hypothesized from Bayesian analysis for the *Dendropsophus* genus (see legend page 175).
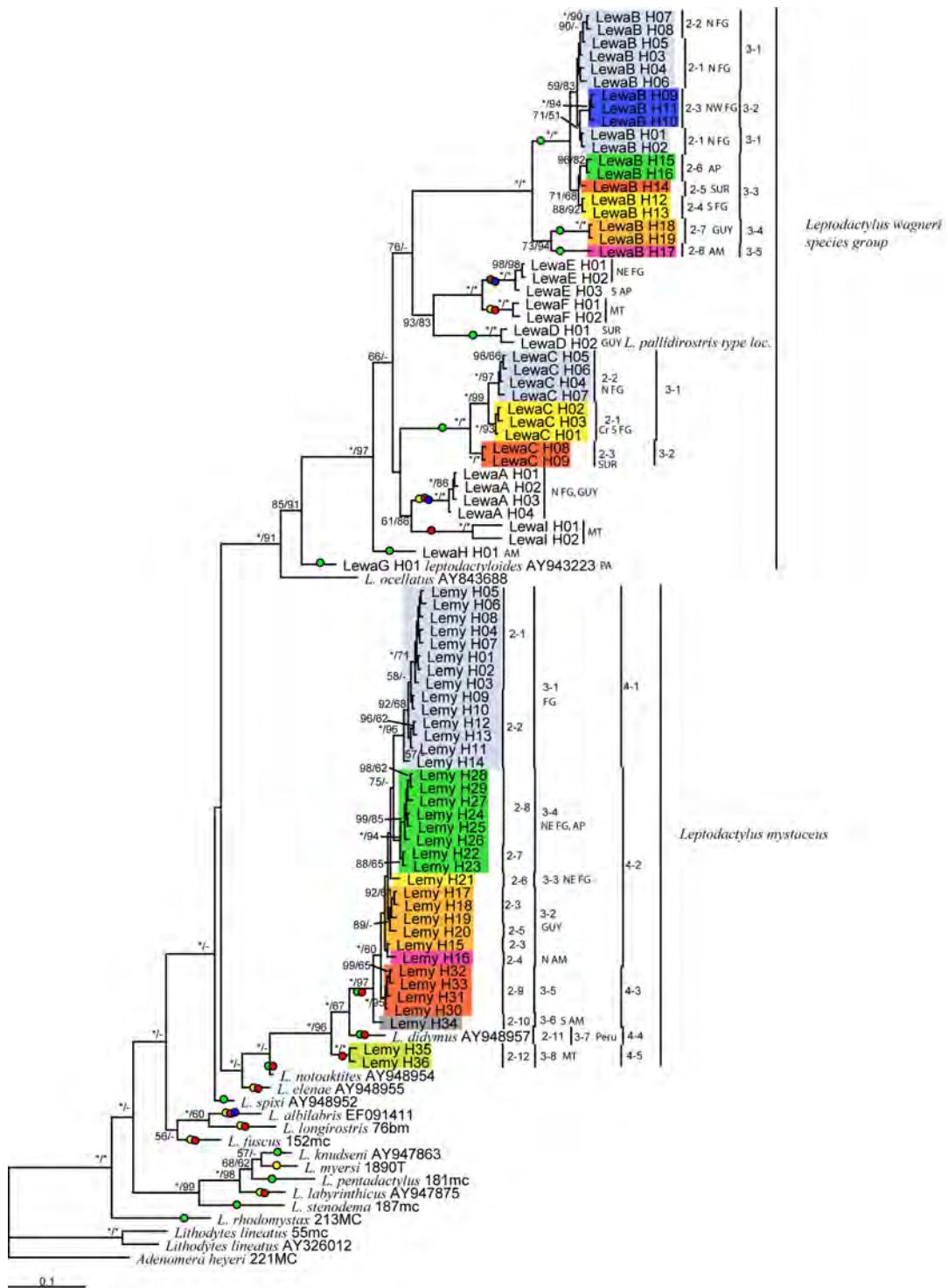
Fig. S5.5: Phylogram hypothesized from Bayesian analysis for the *Leptodactylus* genus (see legend page 175).
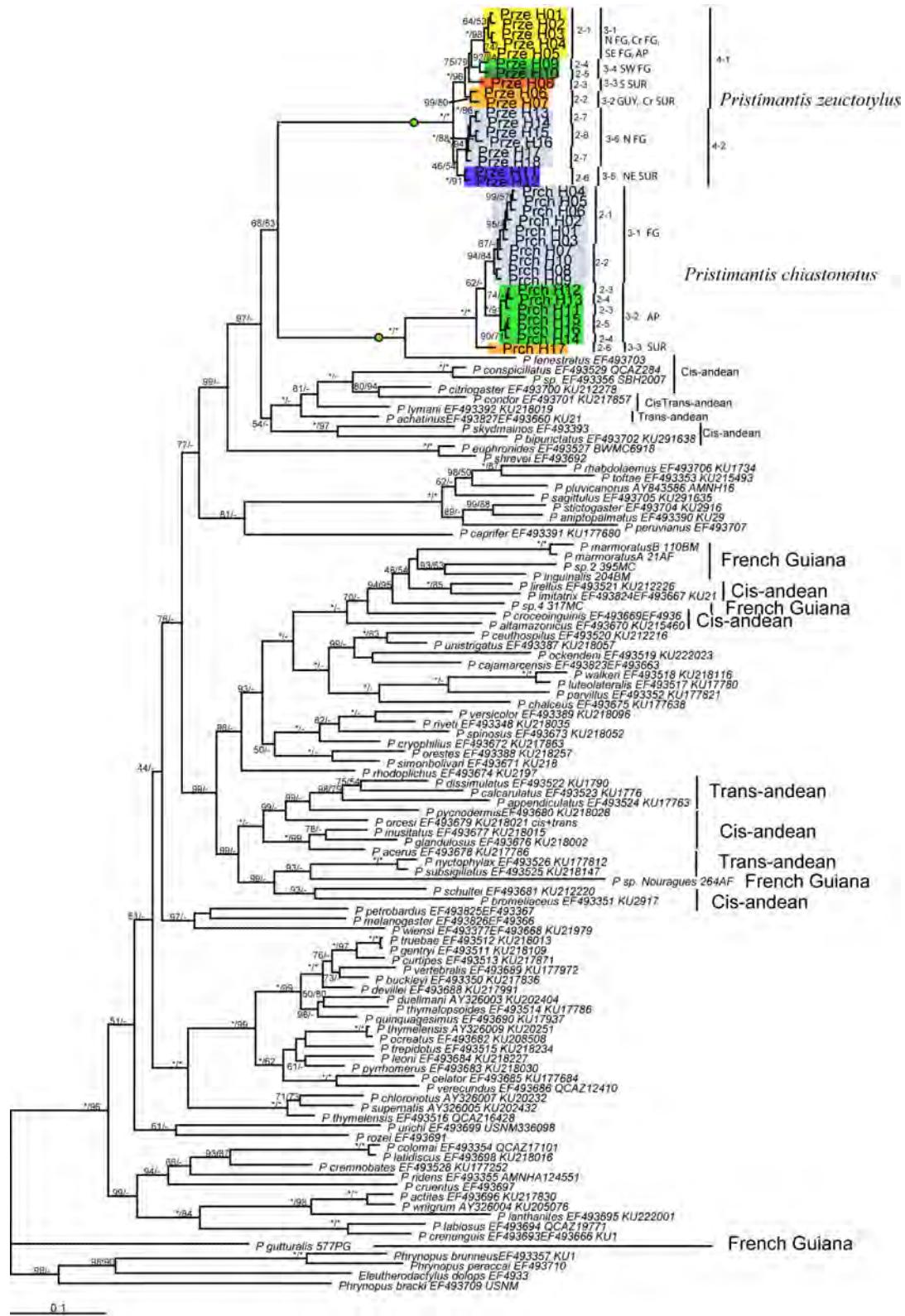
Fig. S5.6: Phylogram hypothesized from Bayesian analysis for the *Pristimantis* genus (see legend page 175).
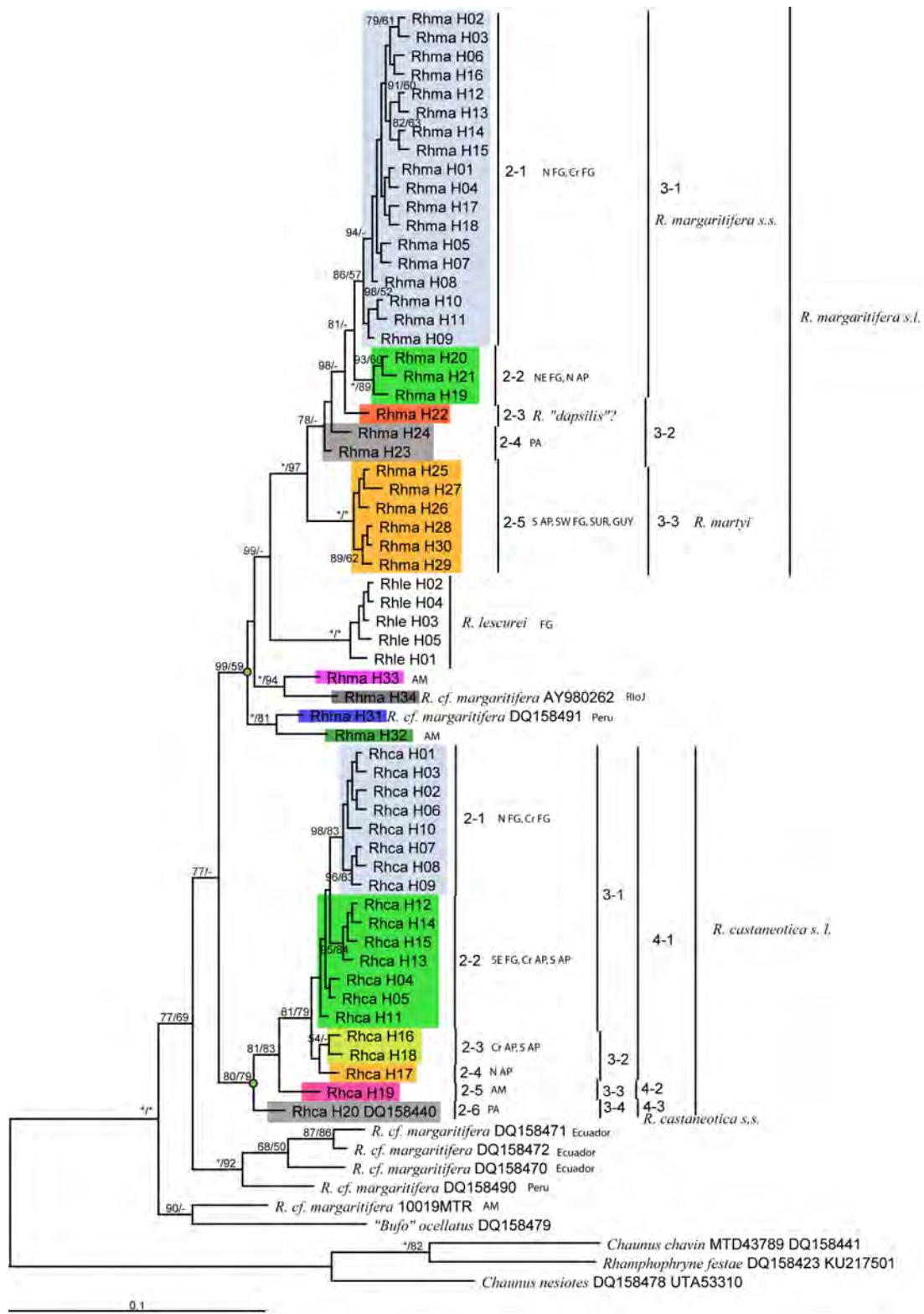
Fig. S5.7: Phylogram hypothesized from Bayesian analysis for the *Rhinella* genus (see legend page 175).
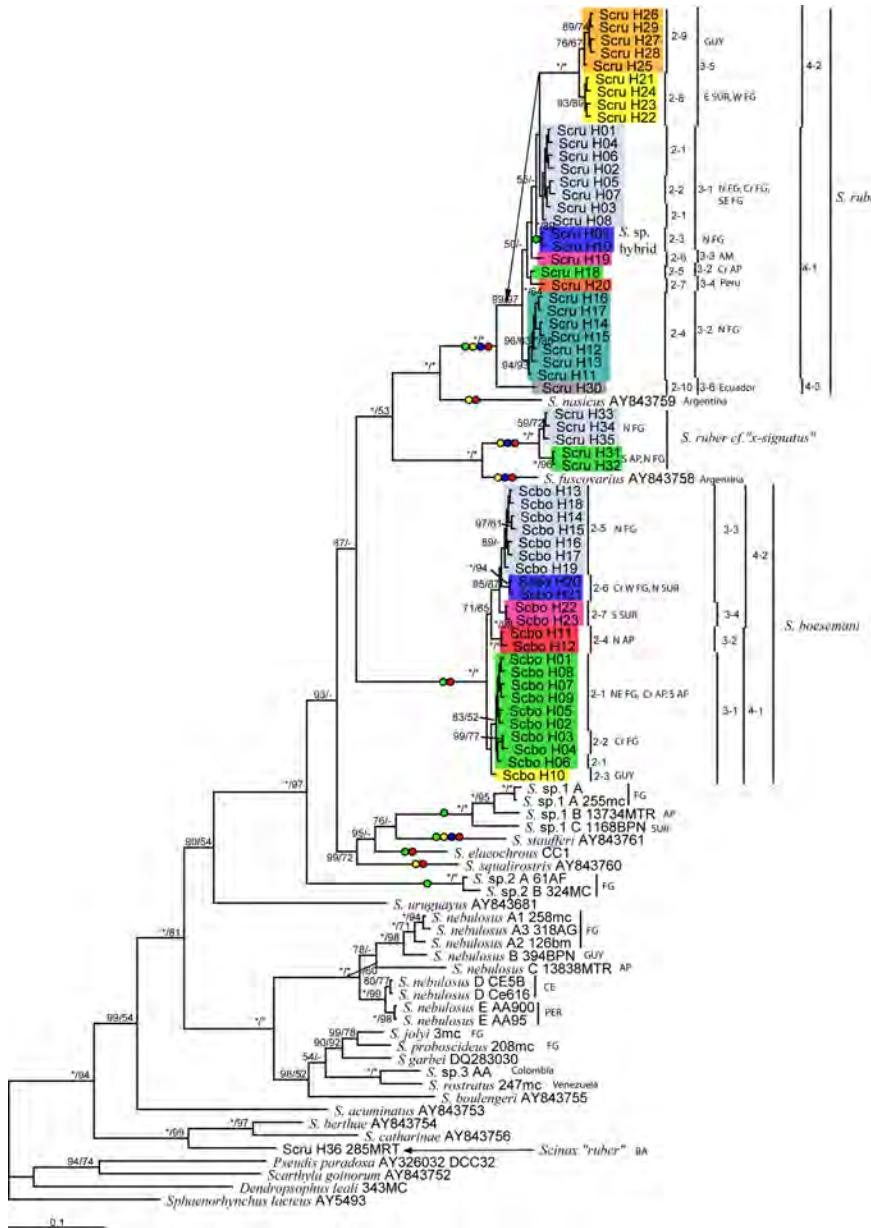
Fig. S5.8: Phylogram hypothesized from Bayesian analysis for the *Scinax* genus (see legend below).

Figs S5.1-8: Full trees hypothesized from Bayesian analysis for each genus. Supports for nodes are indicated with posterior probability (pp left) and Maximum Parsimony bootstrap support (MP right). pp=1 and MP boostrap=100 are indicated with asterisks. Higher clades corresponding to geographically segregated lineages have been coloured (same colour code has been used statistical parsimony networks (Fig. S5.9-16; 25-32) and maps (Fig. S5.17-24)) and their location indicated as follow FG=French Guiana, AP=Amapà, SUR=Suriname, GUY=Guyana, PA=Parà, AM=Amazonas, MT=Mato Grosso, N=North, W=West, E=East, S=South. Corresponding NCPA clades are indicated from level 2. Arrows indicate alternative topologies hypothesised from MP analyses. Corresponding bootstrap supports are indicated beside the arrow. Habitats were the individuals have been sampled and/or known to occur are indicated with coloured dots in the branches as follows: green = forest; red = modified, yellow = open habitats, blue = wetlands.
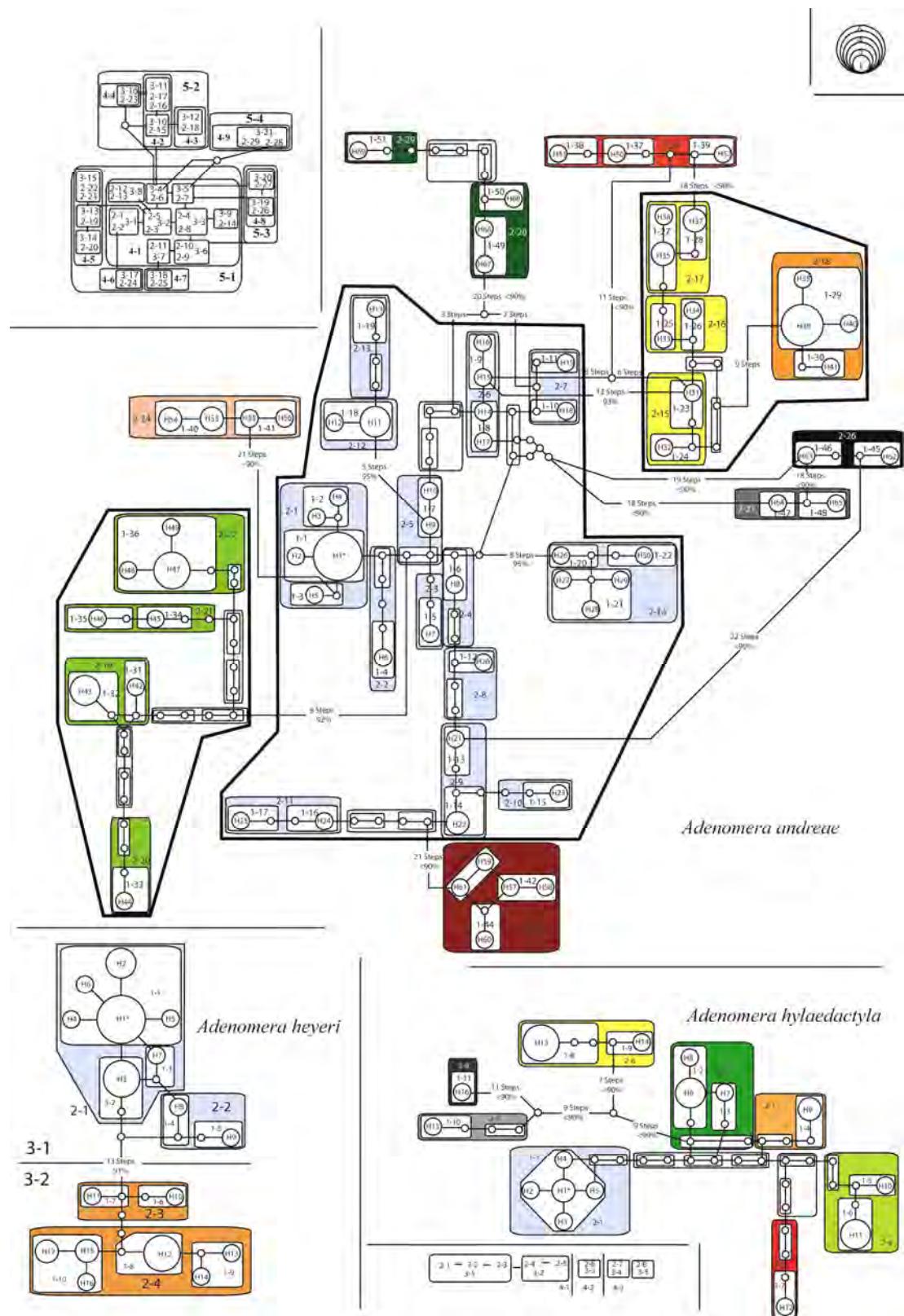
Fig. S5.9: mtDNA networks for the *Adenomera* species (see legend page 183).

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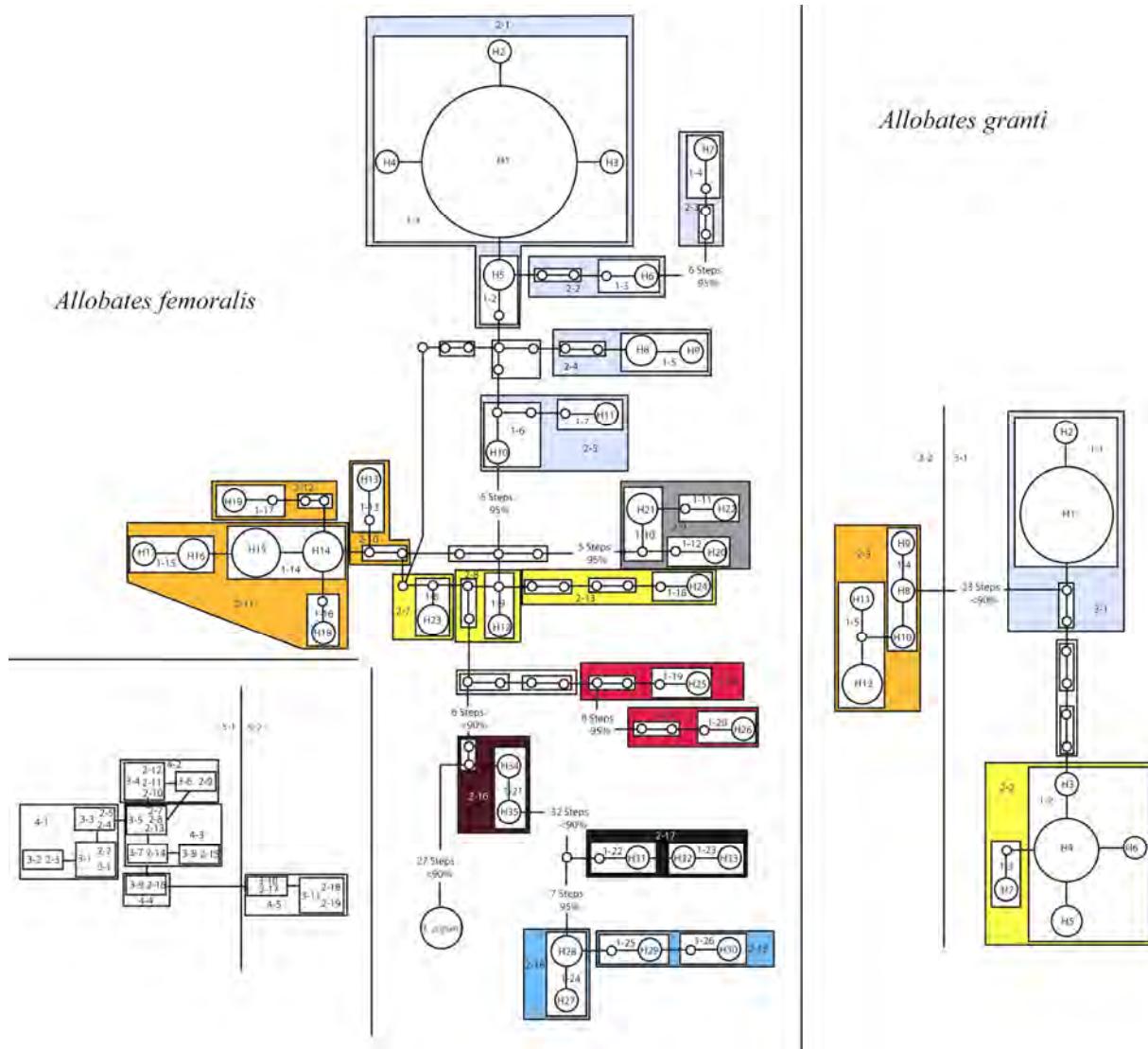
Fig. S5.10: mtDNA networks for the *Allobates* species (see legend page 183).
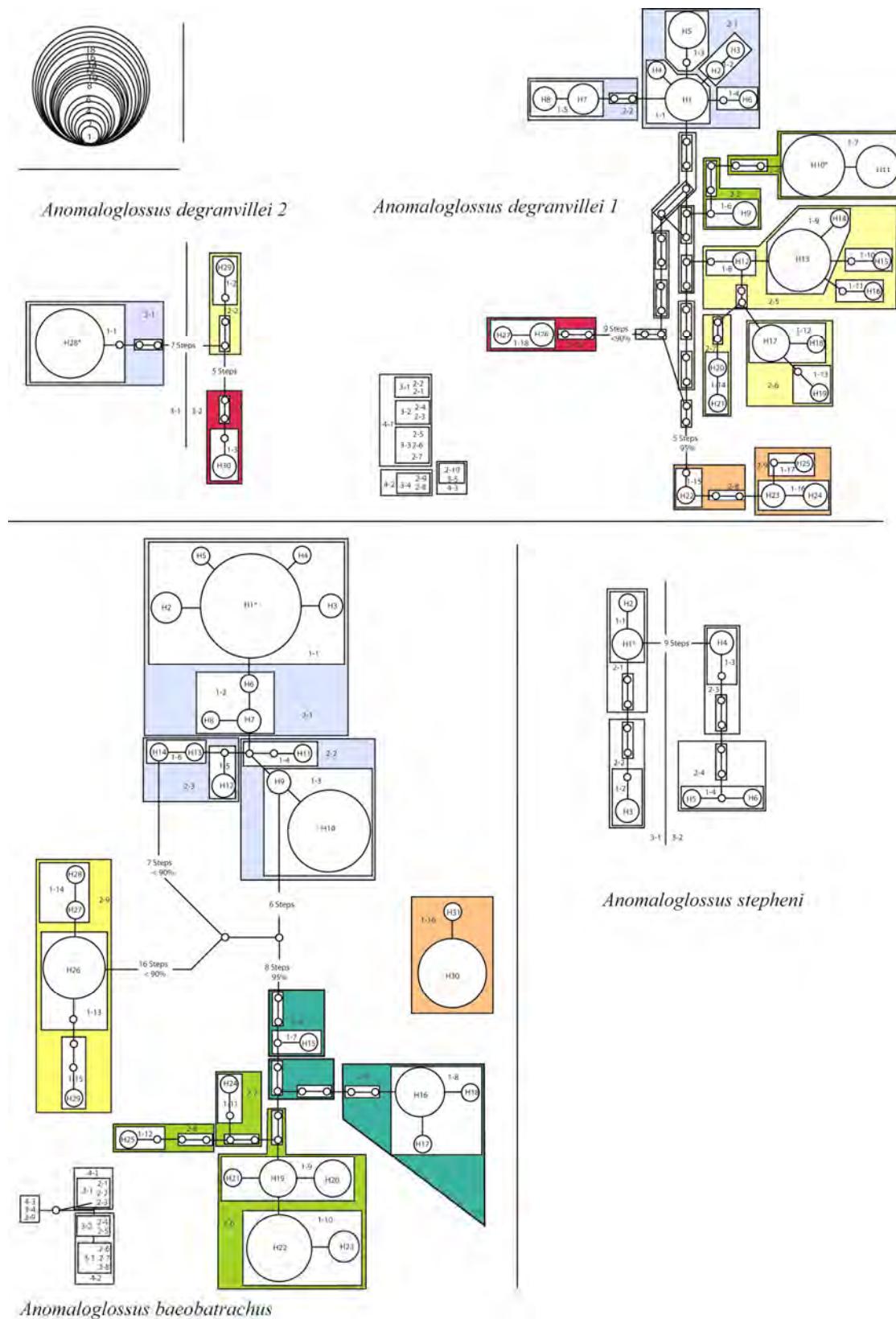
Fig. S5.11: mtDNA networks for the *Anomaloglossus* species (see legend page 183).

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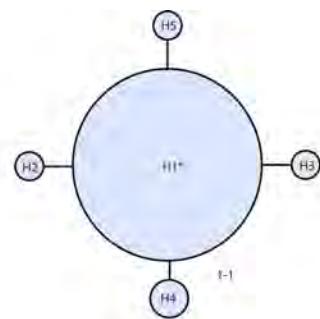
Dendropsophus leucophyllatus 1
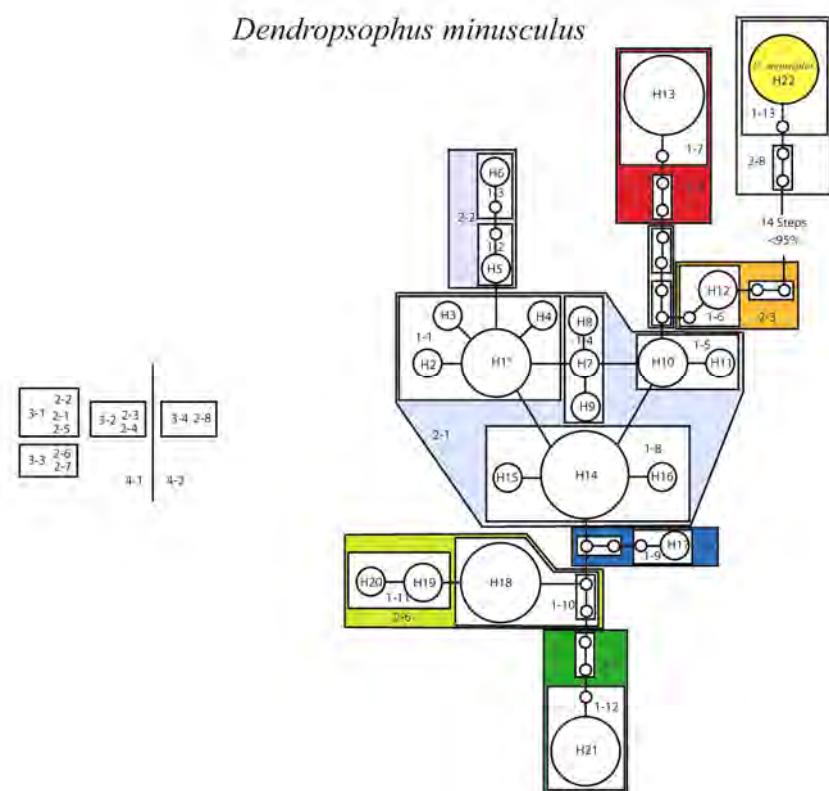
Fig. S5.12: mtDNA networks for the *Dendropsophus* species (see legend page 183).
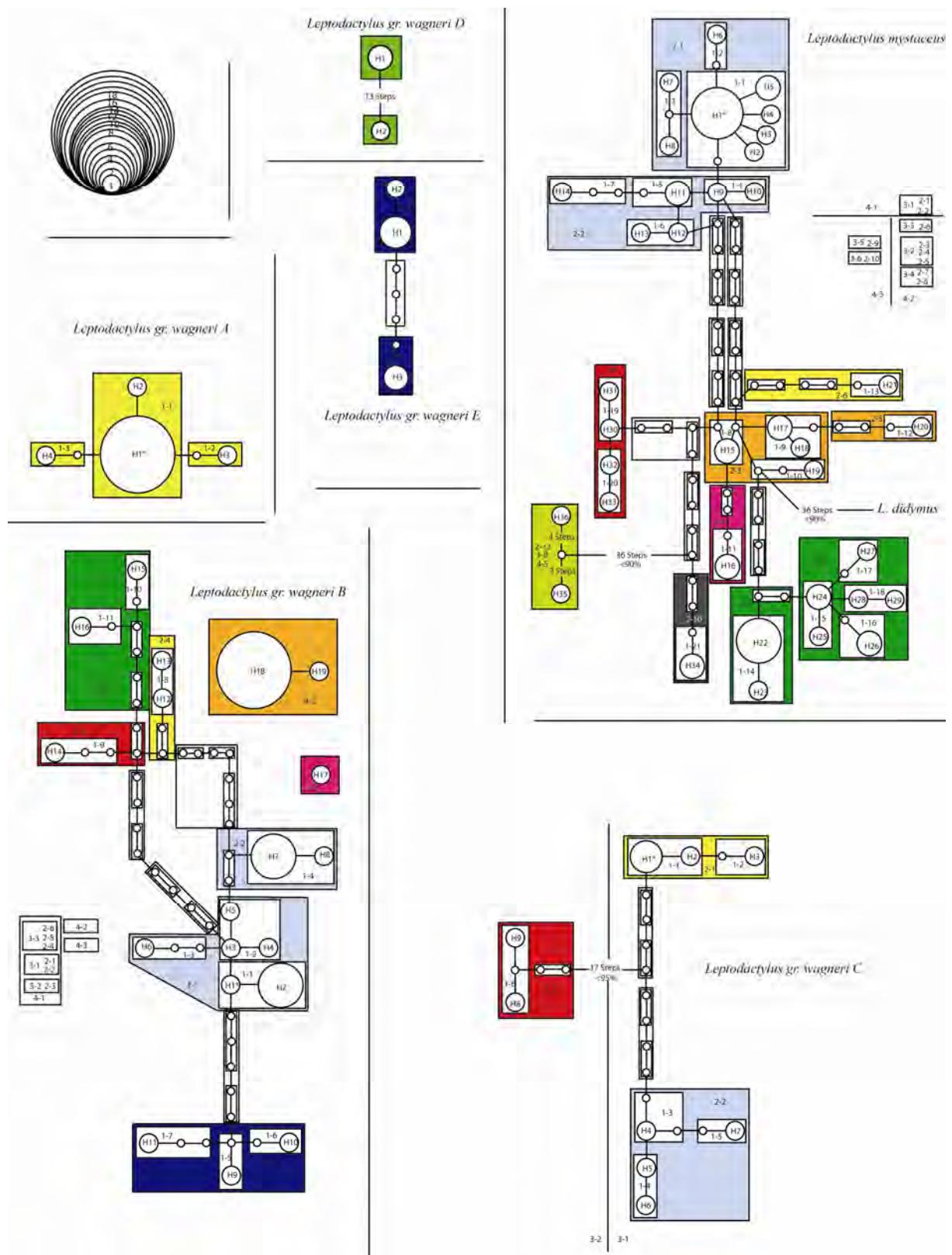
Fig. S5.13: mtDNA networks for the *Leptodactylus* species (see legend page 183).
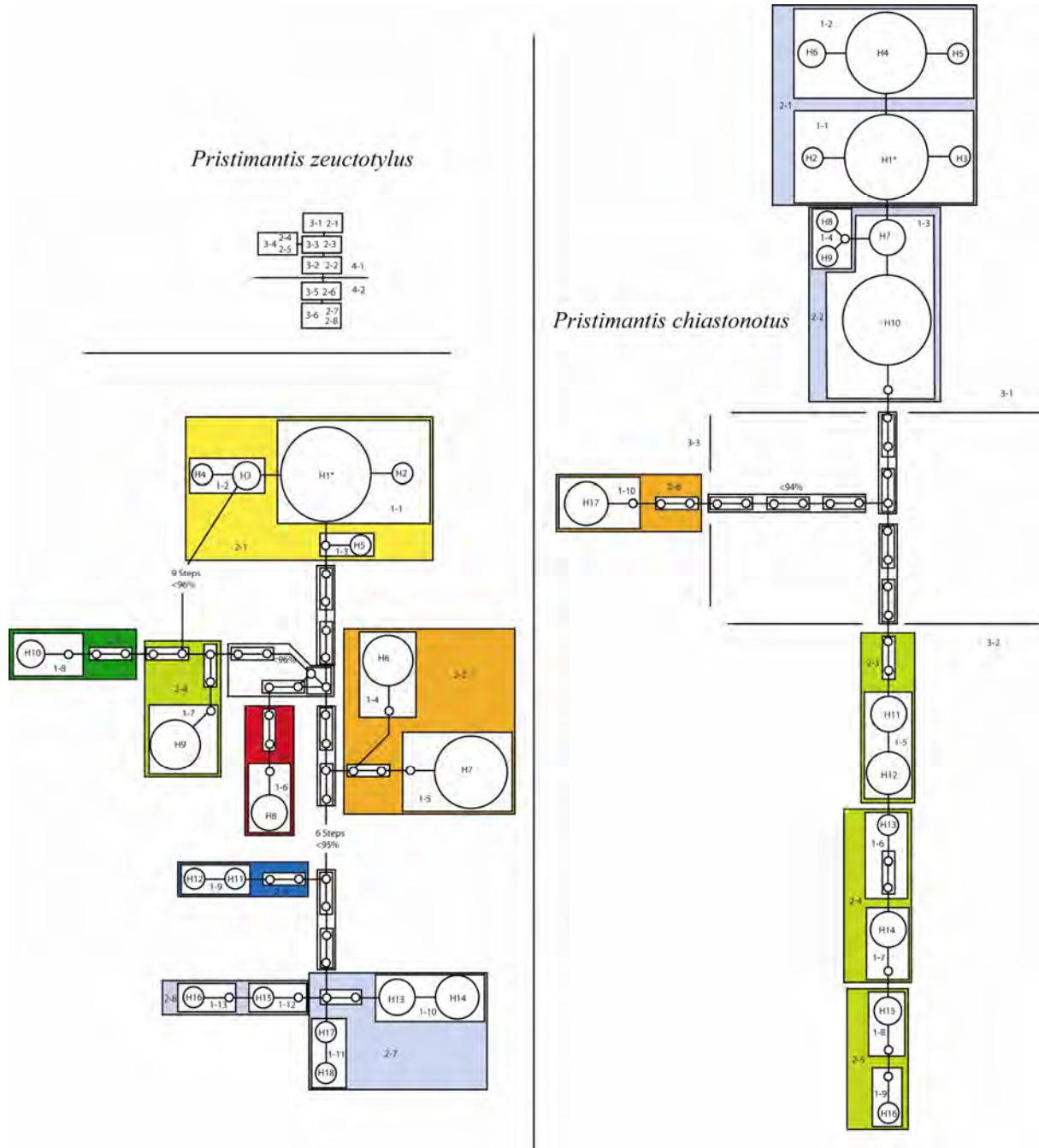
Fig. S5.14: mtDNA networks for the *Pristimantis* species (see legend page 183).
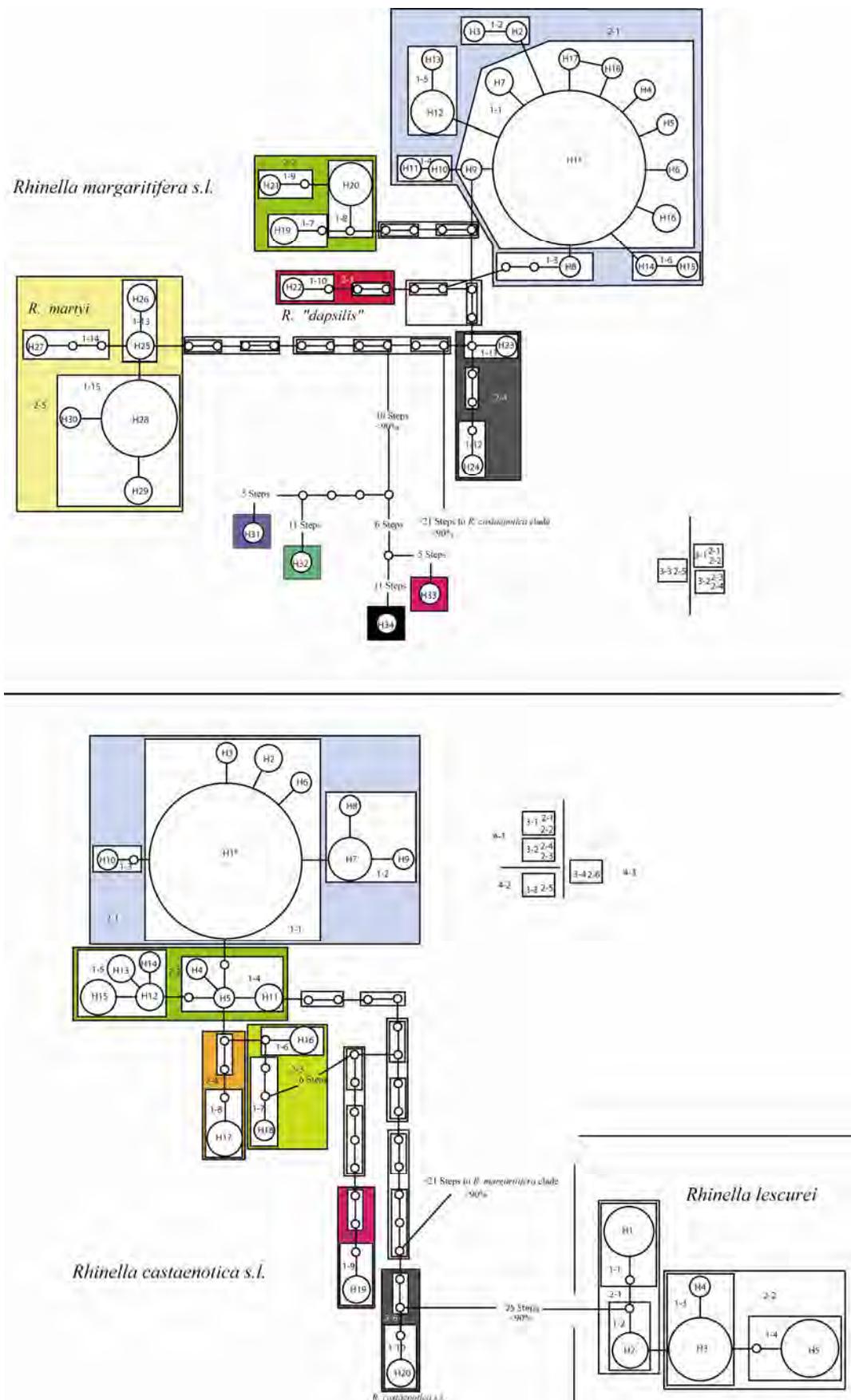
Fig. S5.15: mtDNA networks for the *Rhinella* species (see legend page 183).
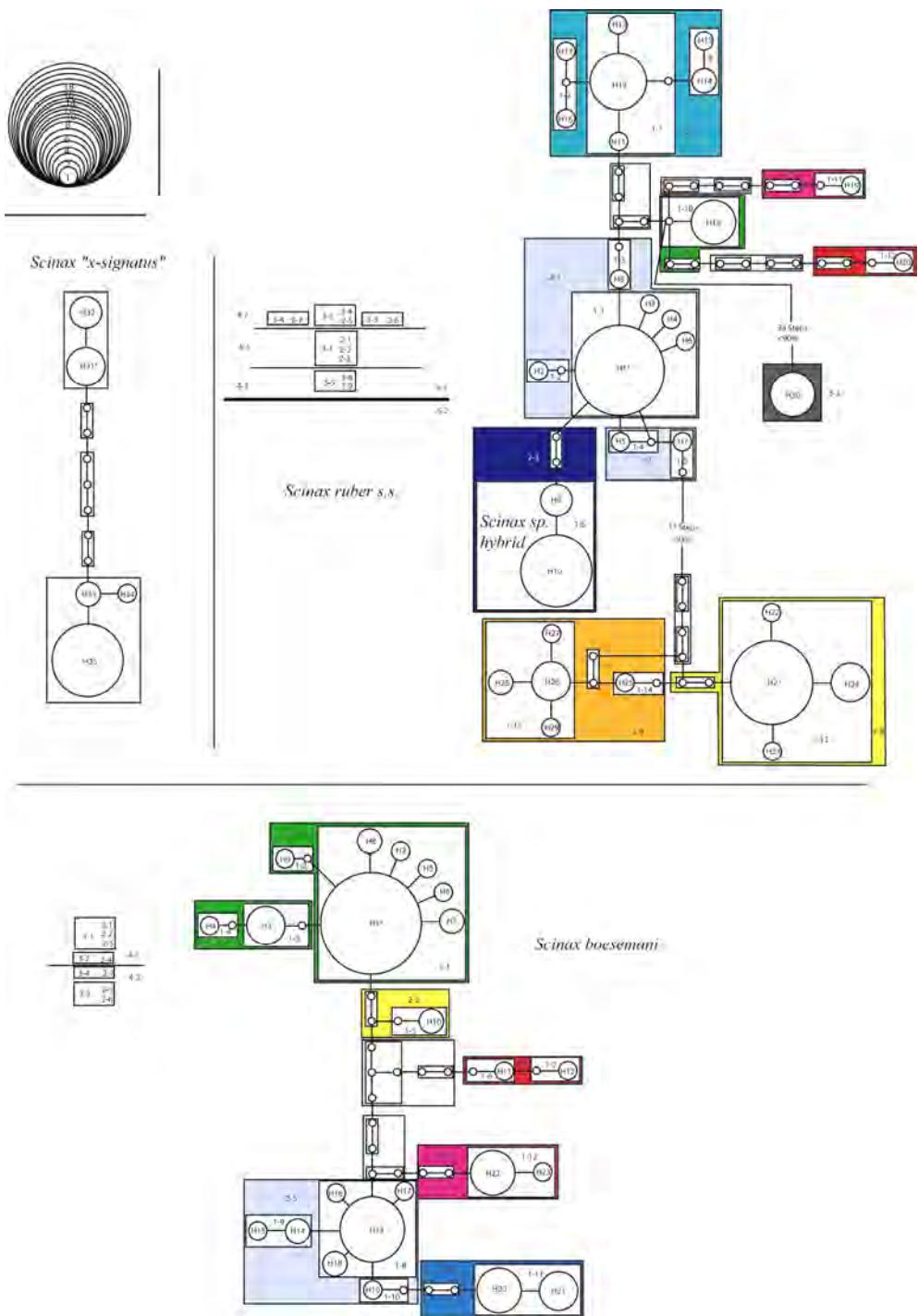
Fig. S5.16: mtDNA networks for the *Scinax* species (see legend below).

Fig. S5.9-16: mtDNA networks and NCPA. The size of the circle representing haplotypes is proportional to the number of individuals with the haplotype number indicated in the circle. When connection probability limit is below 95% it has been indicated. The same colour code for higher clades has been used in full trees (Fig. S5.1-8), statistical parsimony networks (Fig. 25-32) and maps (Fig. S5.17-24) From level 3 NCPA is represented on the side of the network by only higher clades.

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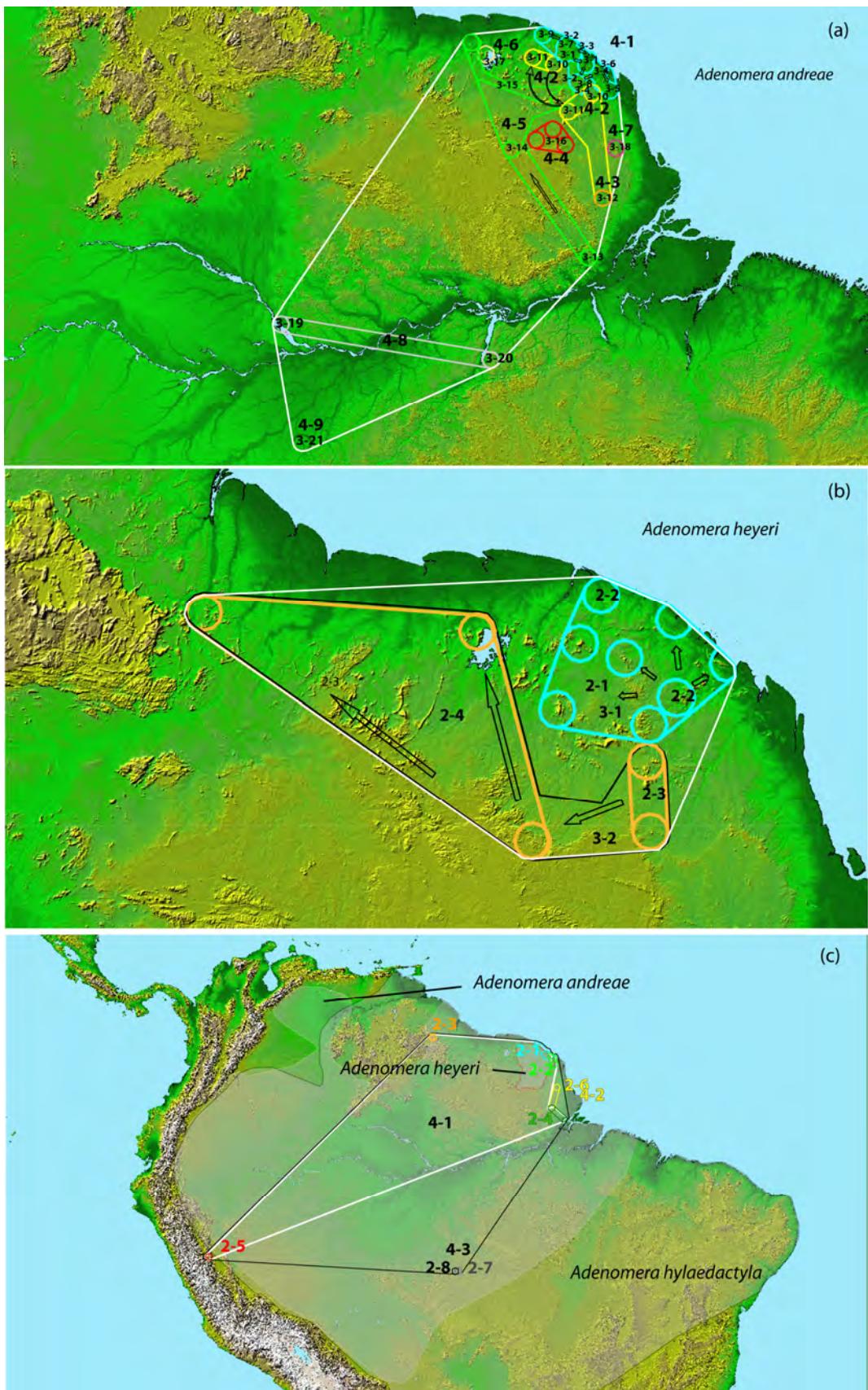
Fig. S5.17: Distribution maps of the *Adenomera* species and clades (see legend page 192).

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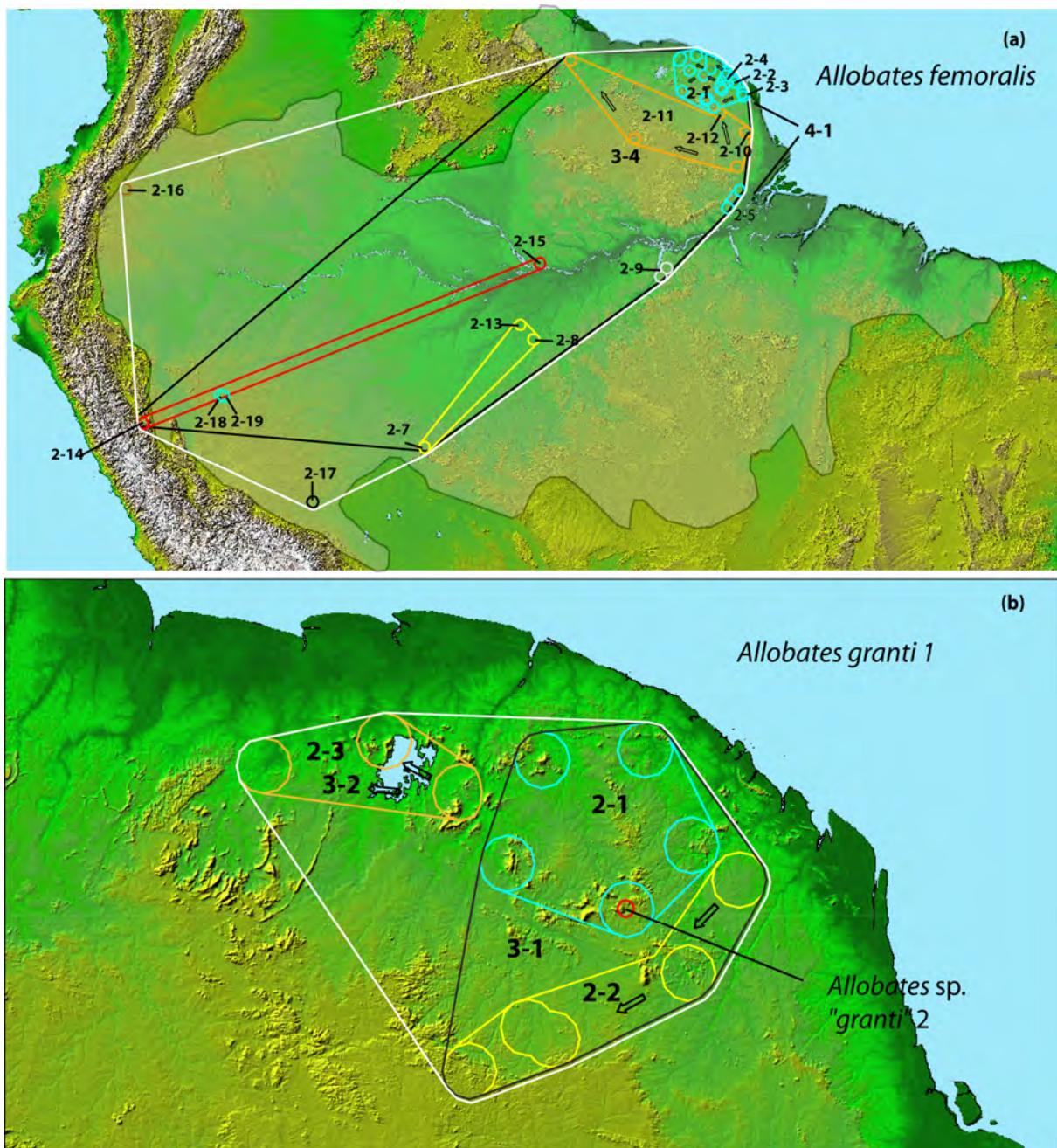
Fig. S5.18: Distribution maps of the *Allobates* species and clades (see legend page 192).
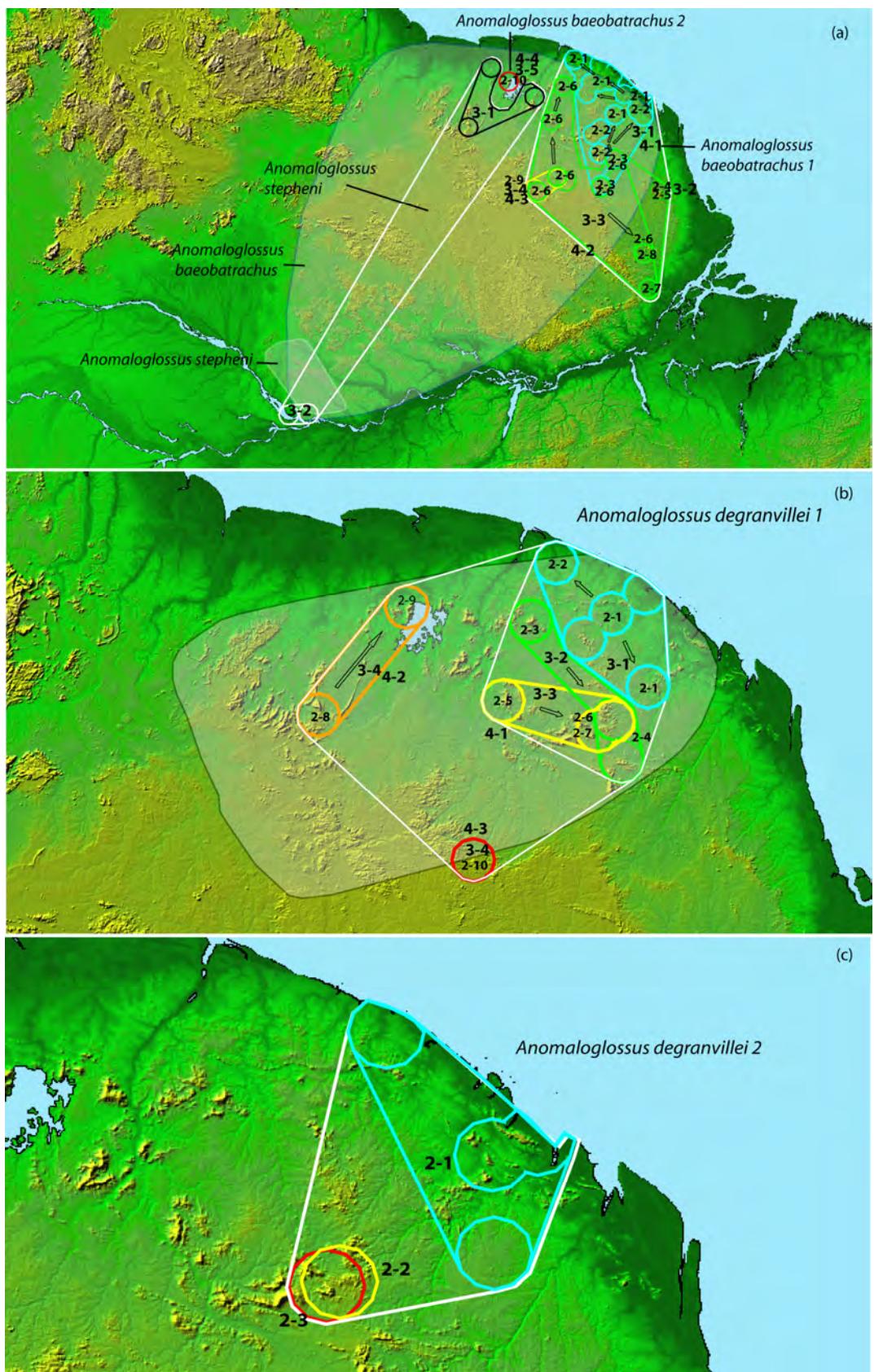
Fig. S5.19: Distribution maps of the *Anomaloglossus* species and clades (see legend page 192).
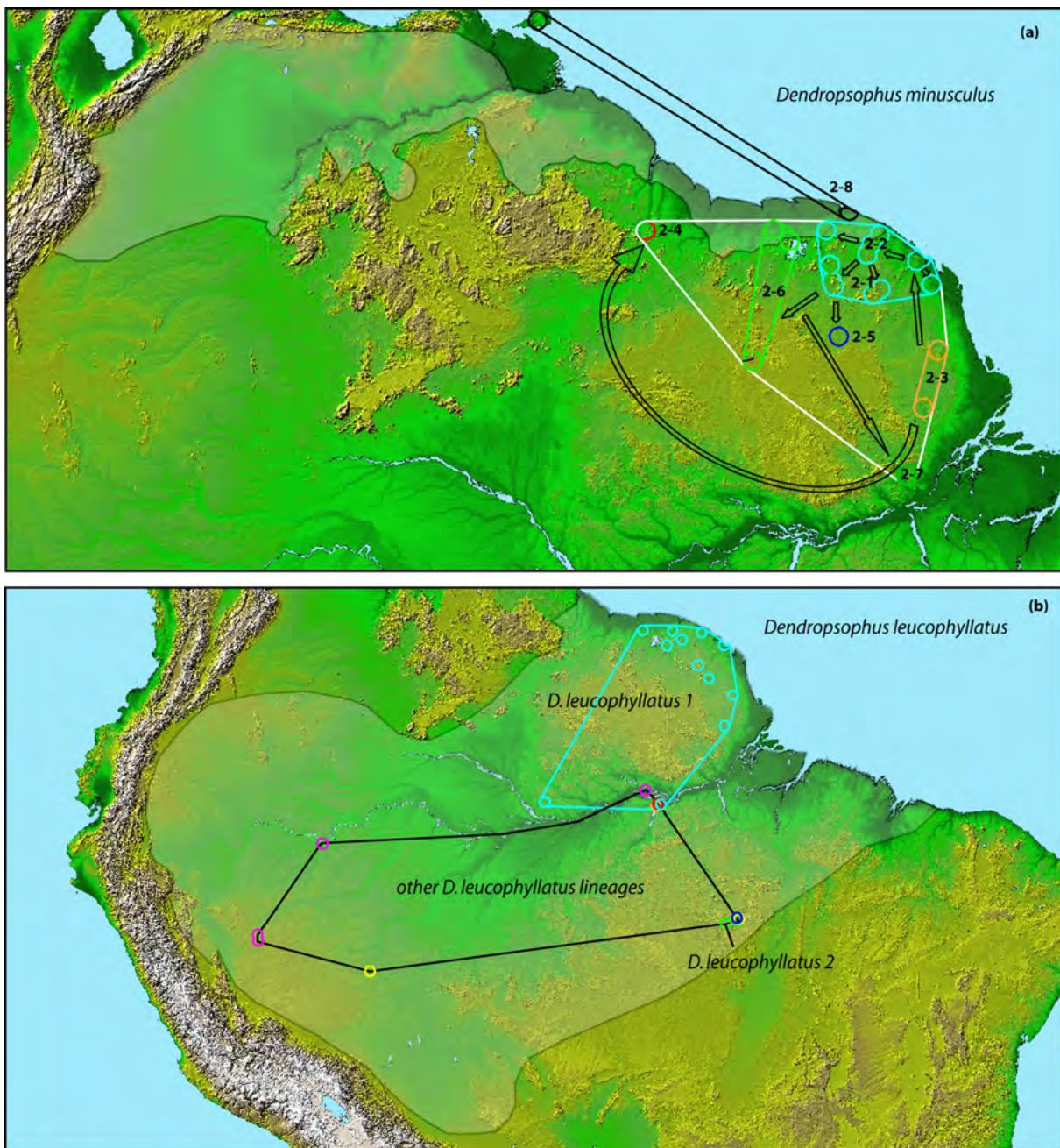
Fig. S5.20: Distribution maps of the *Dendropsophus* species and clades (see legend page 192).
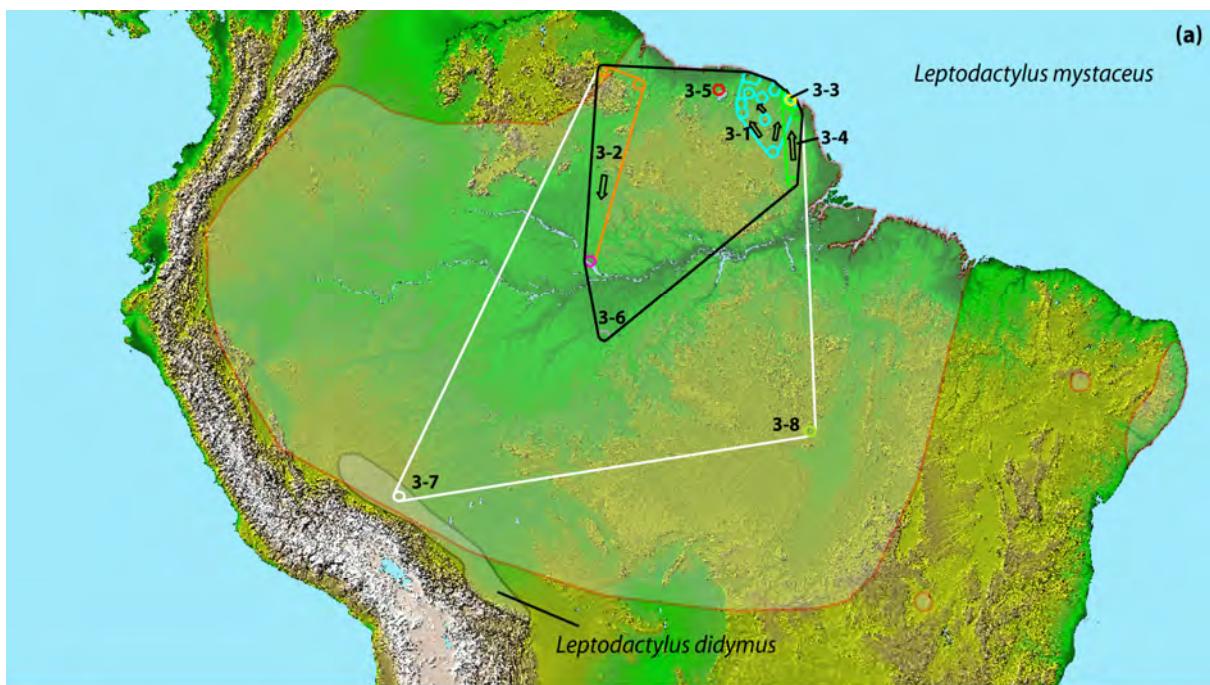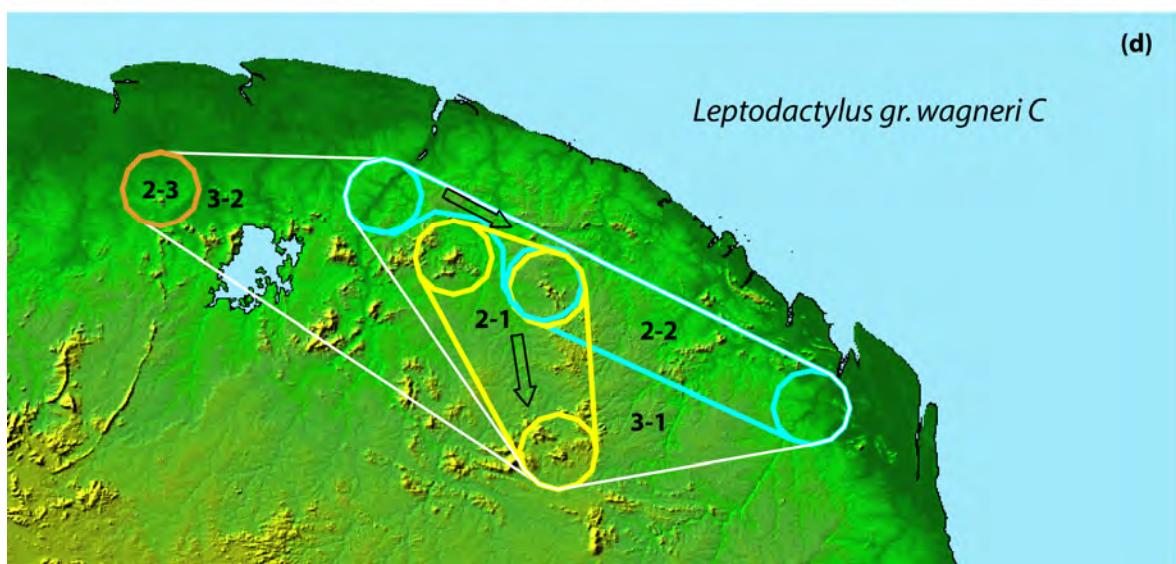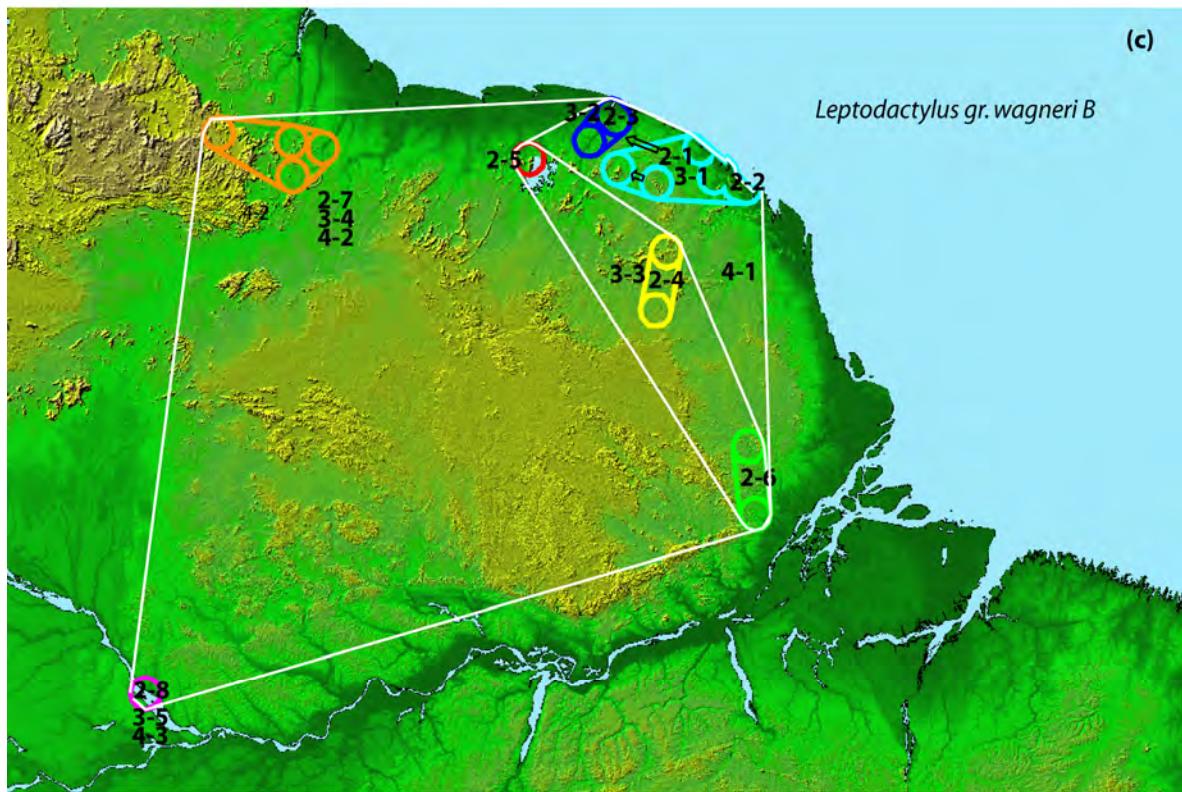
Fig. S5.21: Distribution maps of the *Leptodactylus* species and clades (see legend page 192).
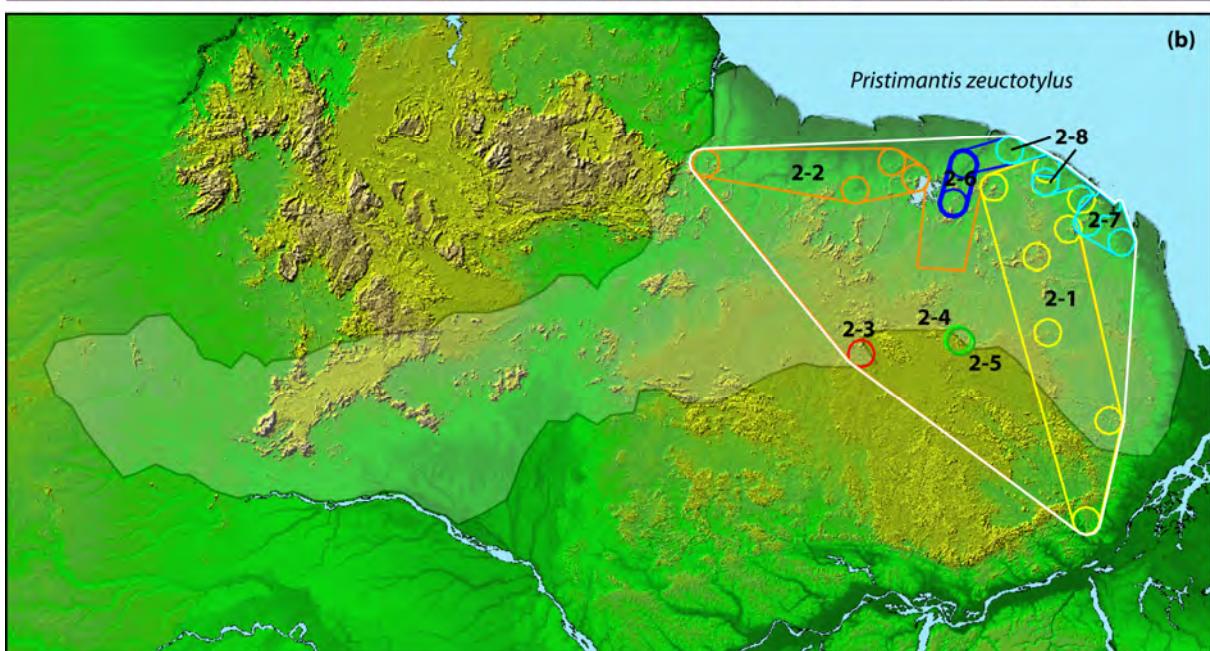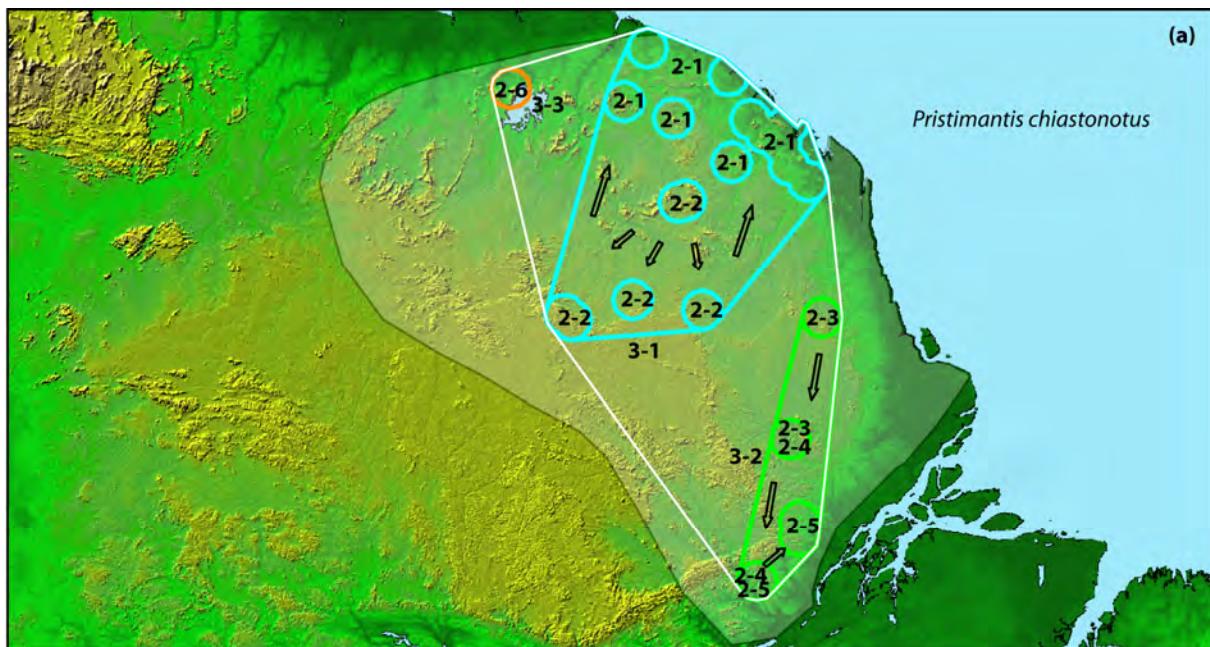
Fig. S5.22: Distribution maps of the *Pristimantis* species and clades (see legend page 192).

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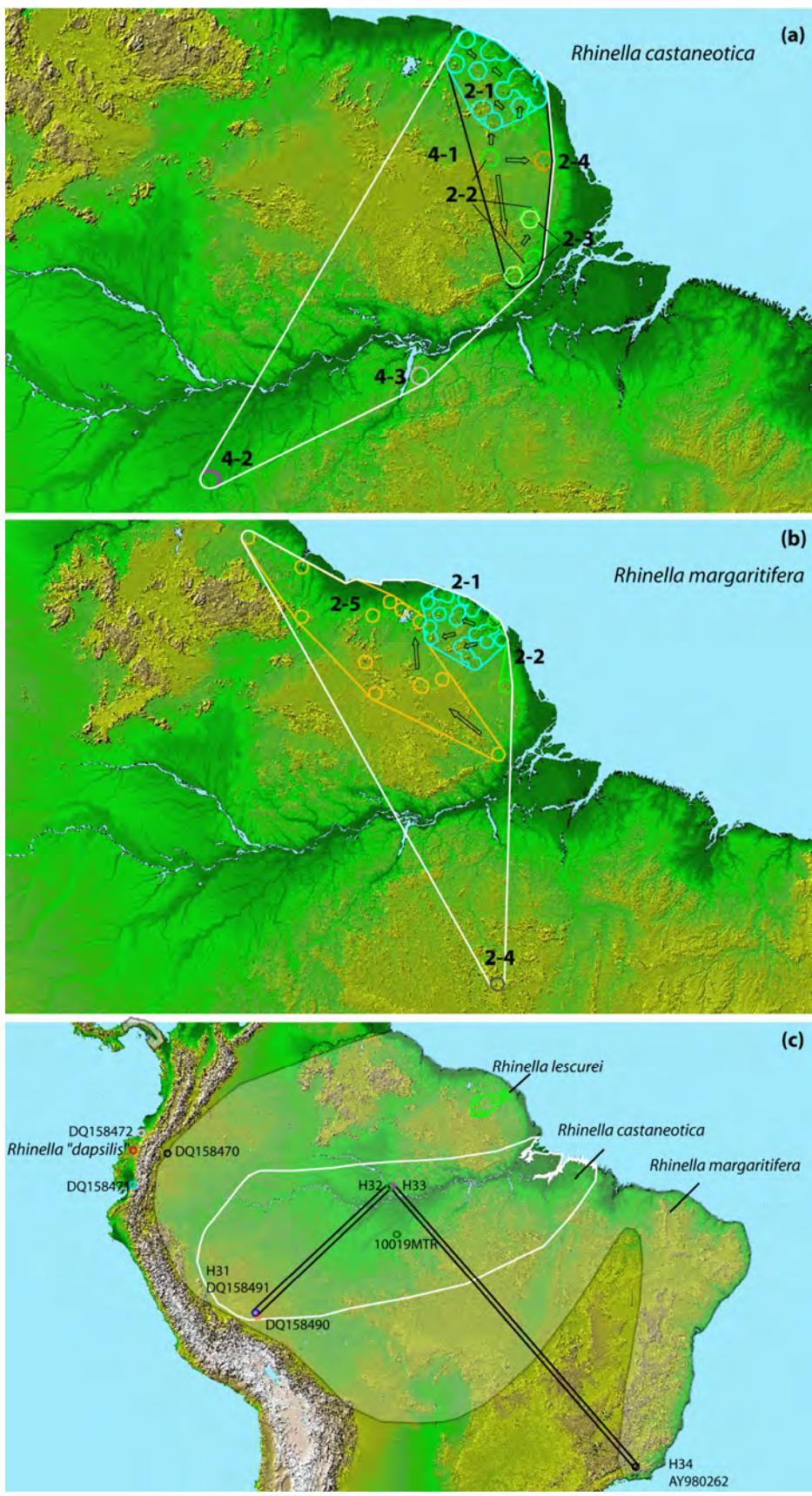
Fig. S5.23: Distribution maps of the *Rhinella* species and clades (see legend page 192).
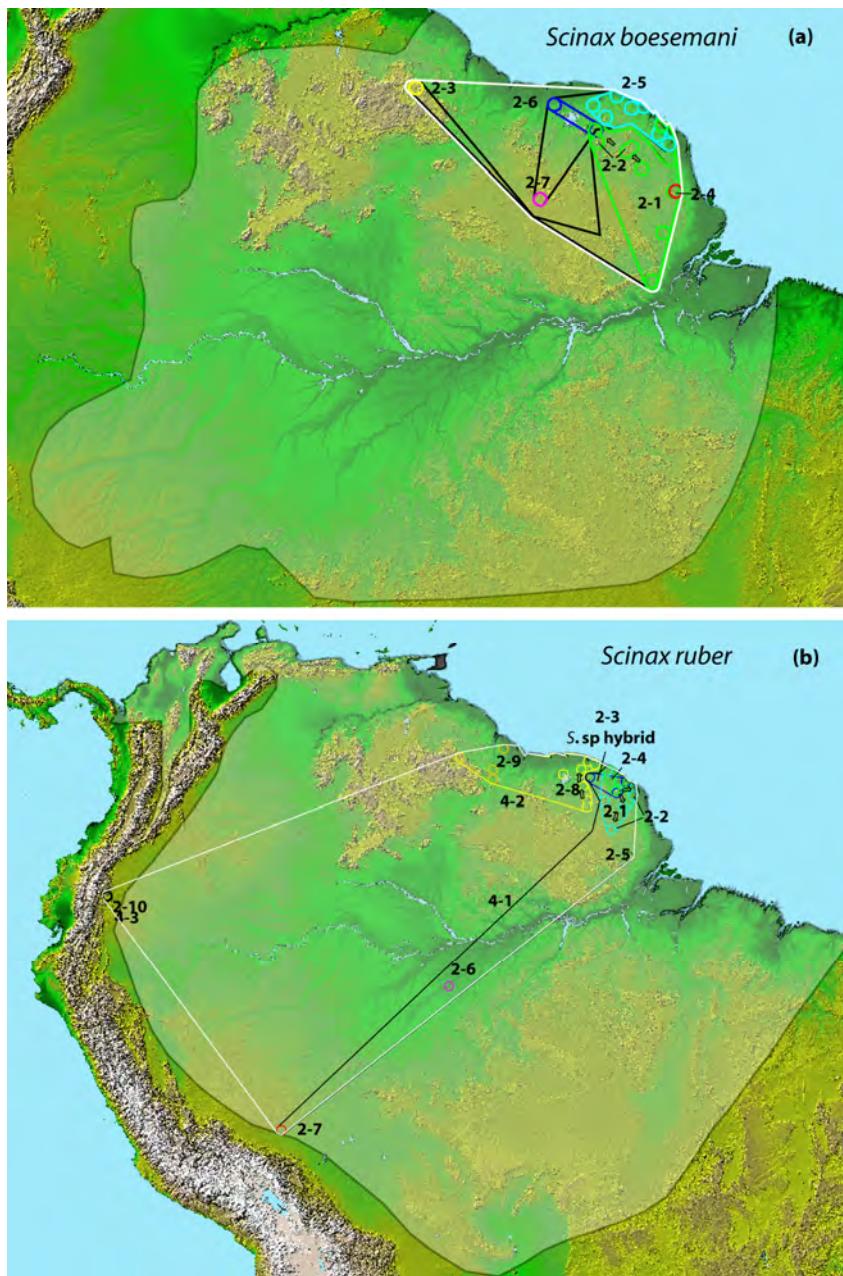
Fig. S5.24: Distribution maps of the *Scinax* species and clades (see legend page below).

Fig. S5.17-24: Maps for each species lineages distribution. Convex polygons for the total sampled range of the species considered are indicated in white. Higher clades are also indicated with corresponding colours (same colour code has been used in full trees (Fig. S5.1-8) and statistical parsimony networks (Fig. S5.9-16; 25-32)). Currently, recognized range of each species is represented by shade areas according to the GAA distribution maps. Additional species ranges have been indicated due to taxonomic uncertainties. This is the case for *Anomalloglossus stepheni*, *Leptodactylus didymus*, *Leptodactylus wagneri* species group (*L. leptodactyloïdes*, *L. petersii*, *L. pallidirostris*, *L. diedrus*, *L. wagneri*, *L. podicipinus*), *L. lescurei* and *L. martyi*. Arrows indicate probable recent range expansion inferred from networks and NCPA.

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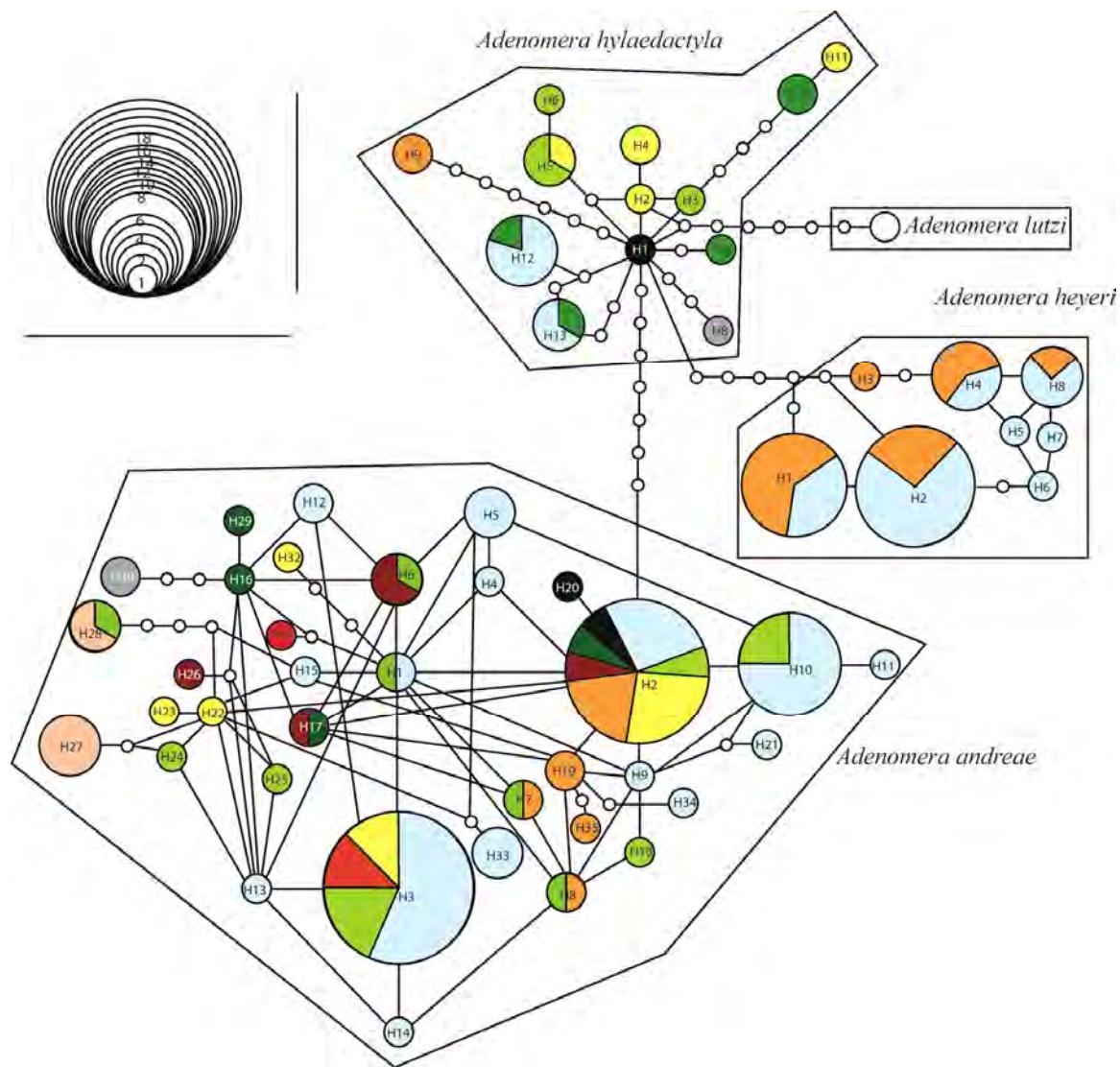
Fig. S5.25: nuDNA networks for the *Adenomera* species (see legend page 200).
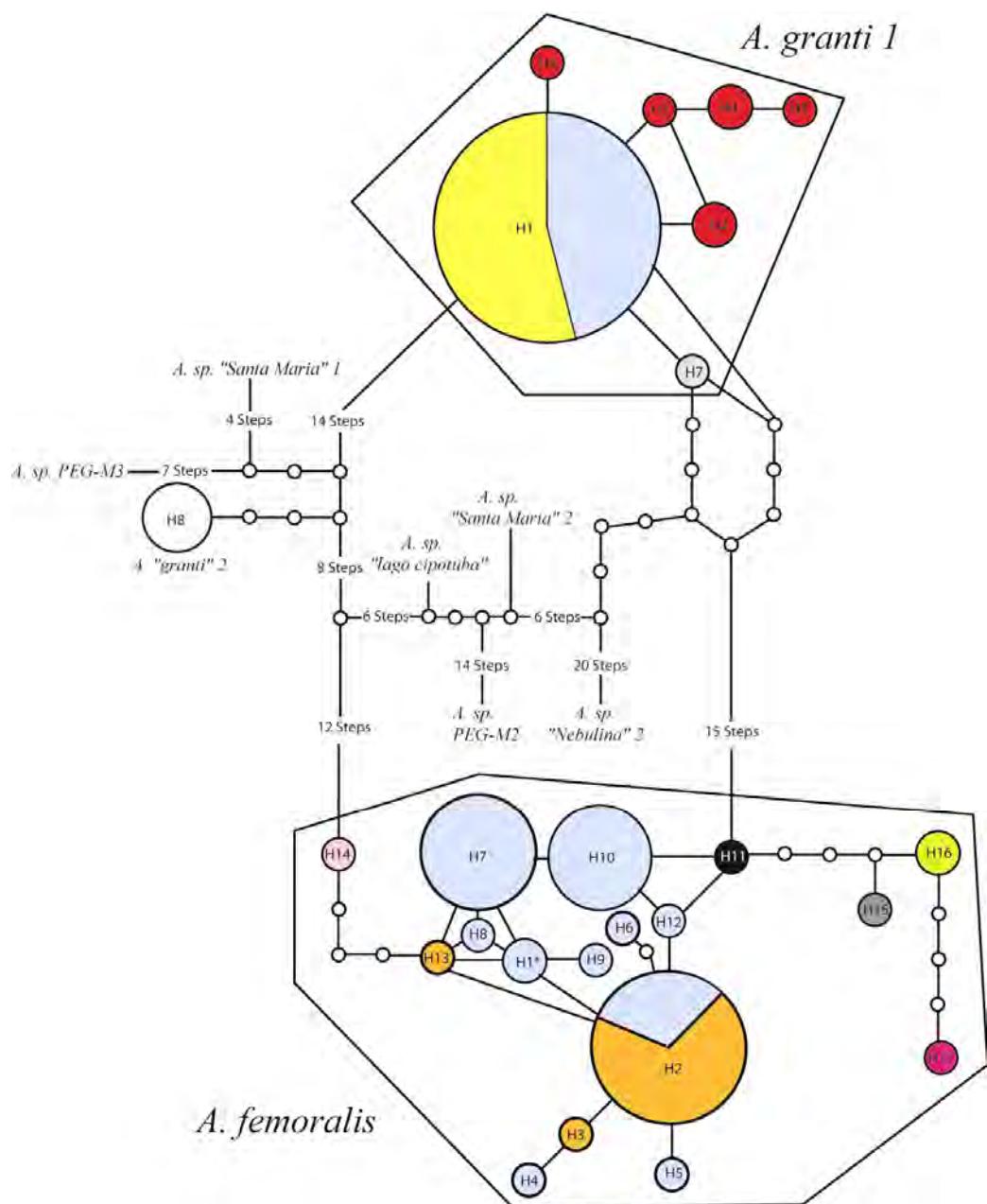
Fig. S5.26: nuDNA networks for the *Allobates* species (see legend page 200).
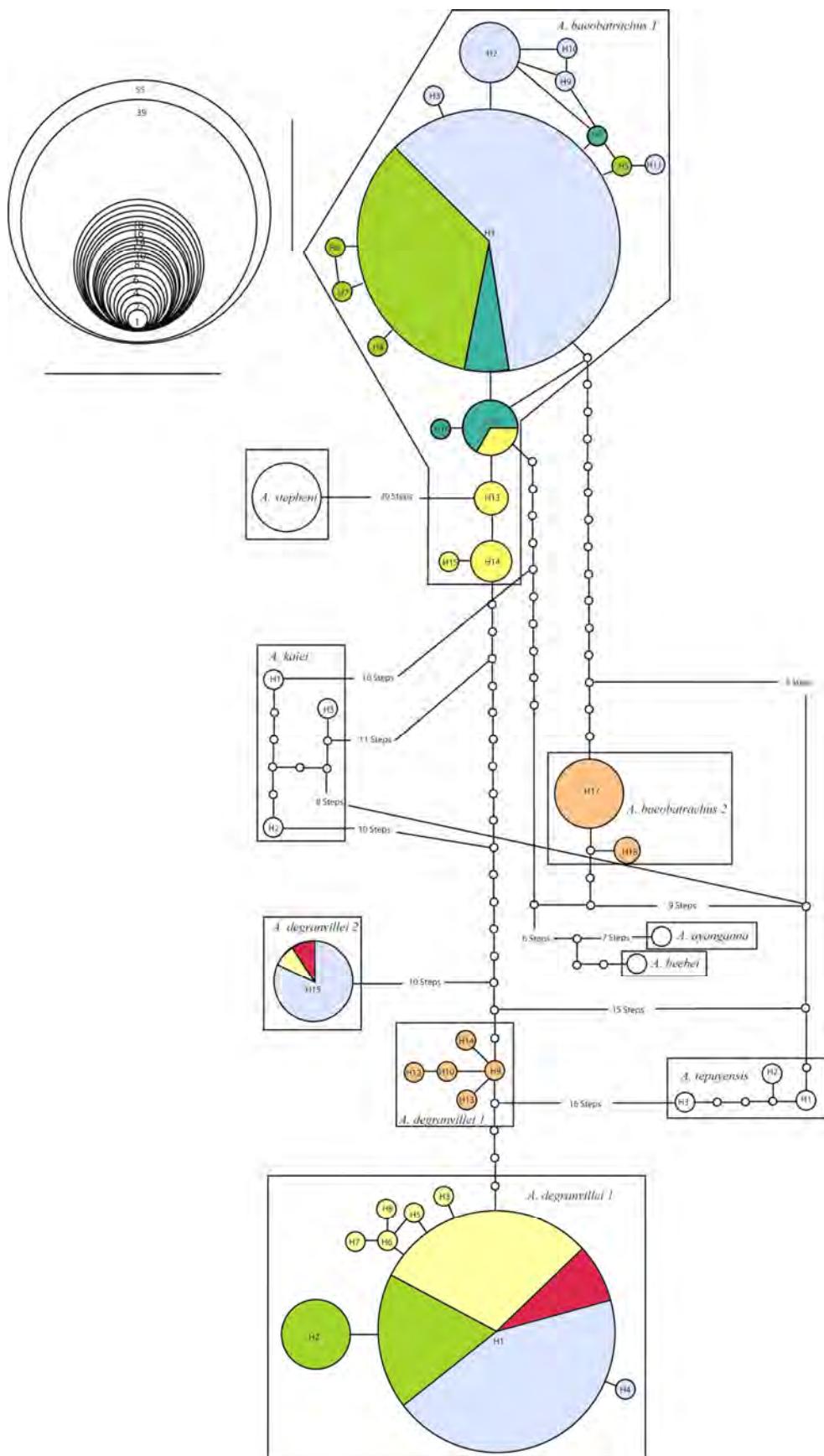
Fig. S5.27: nuDNA networks for the *Anomaloglossus* species (see legend page 200).
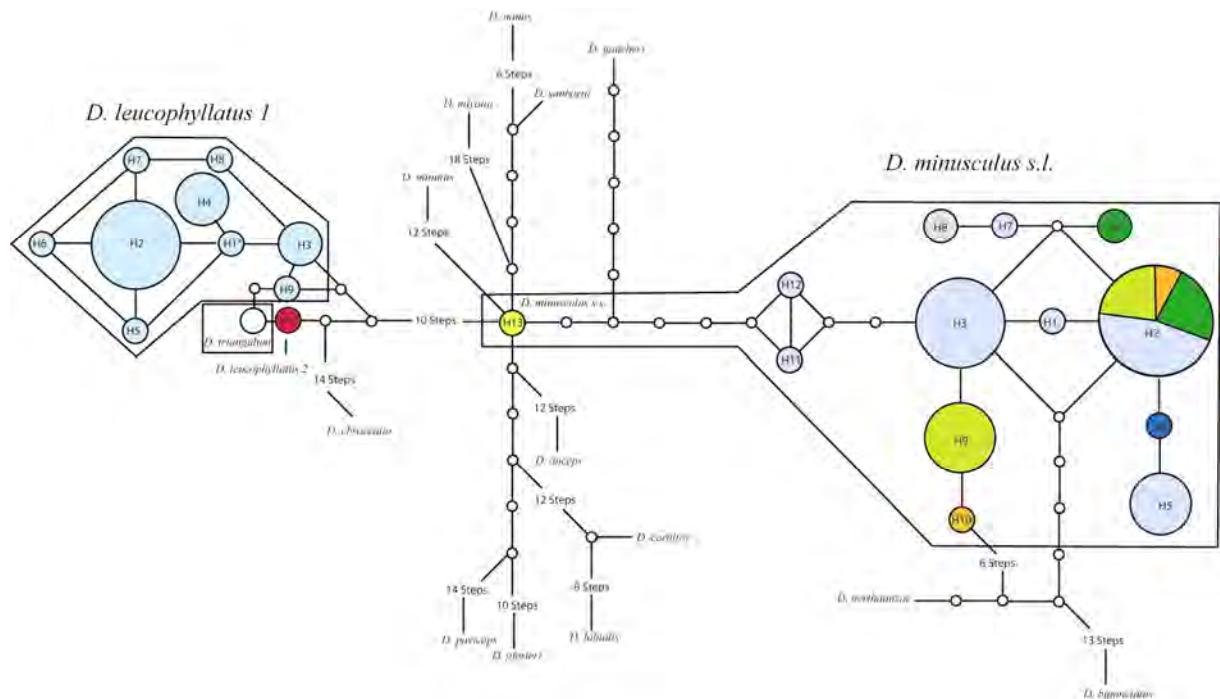
Fig. S5.28: nuDNA networks for the *Dendropsophus* species (see legend page 200).
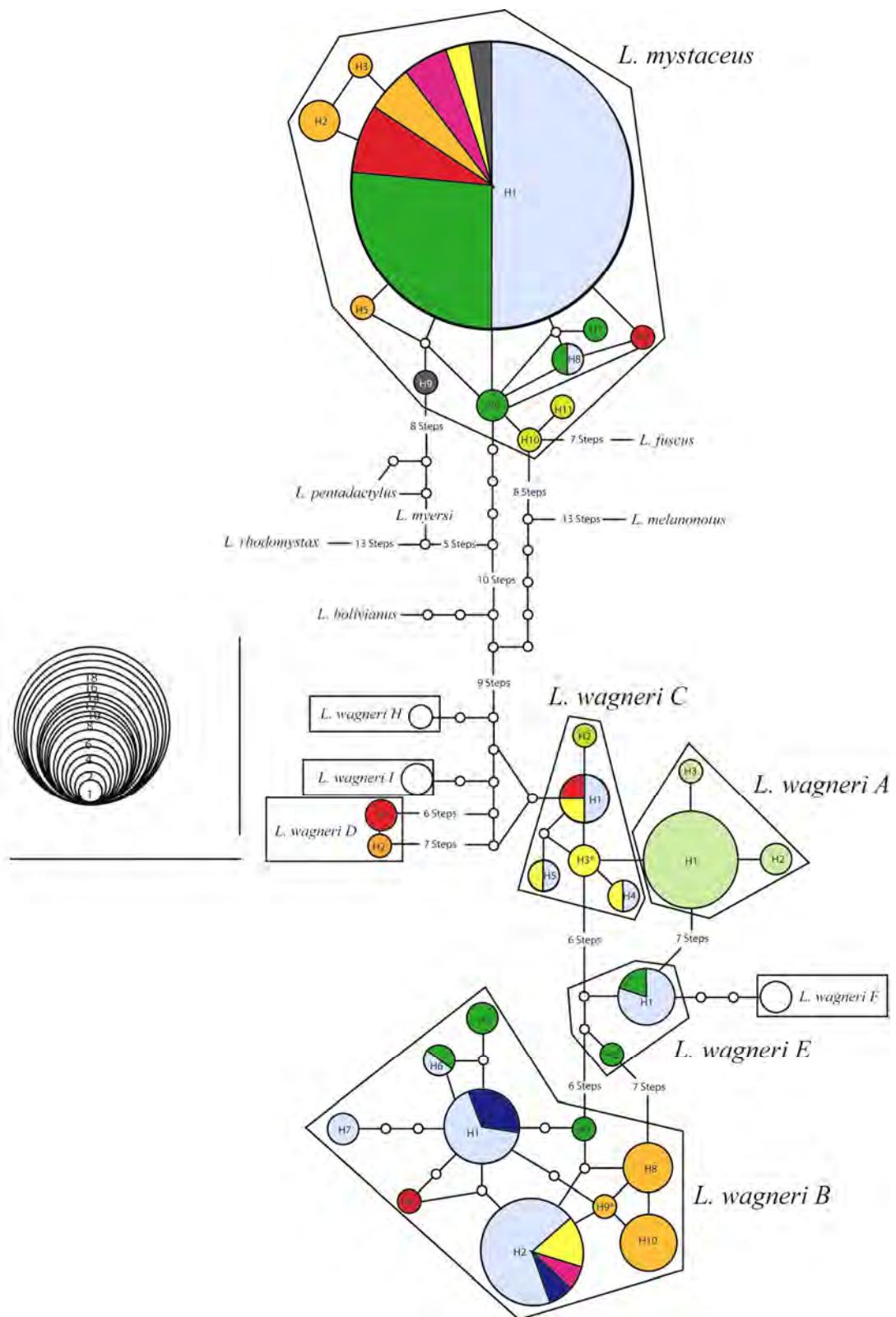
Fig. S5.29: nuDNA networks for the *Leptodactylus* species (see legend page 200).

197
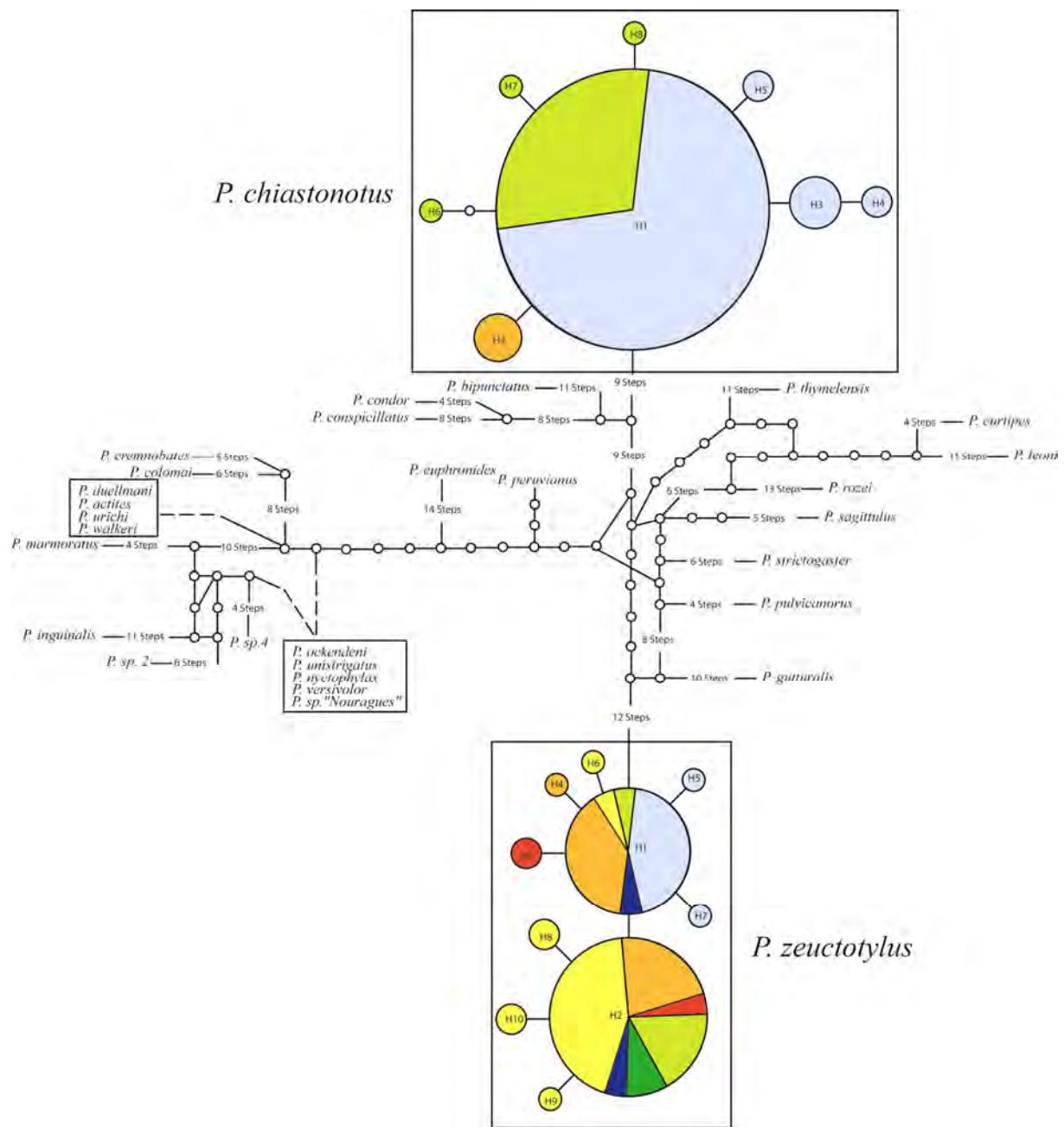
Fig. S5.30: nuDNA networks for the *Pristimantis* species (see legend page 200).
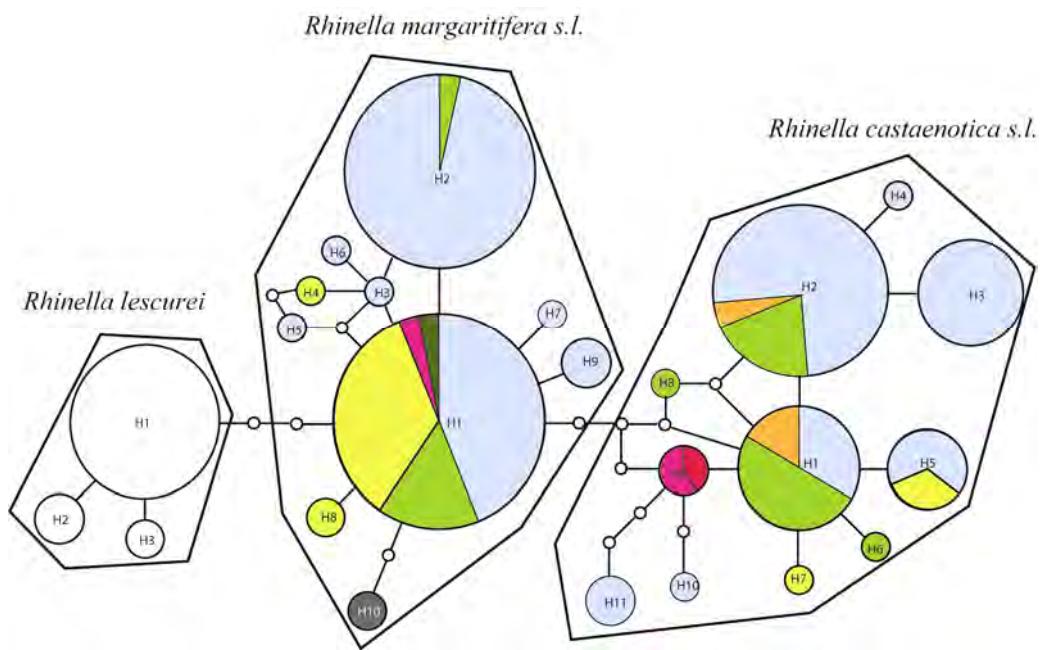
Fig. S5.31: nuDNA networks for the *Rhinella* species (see legend page 200).
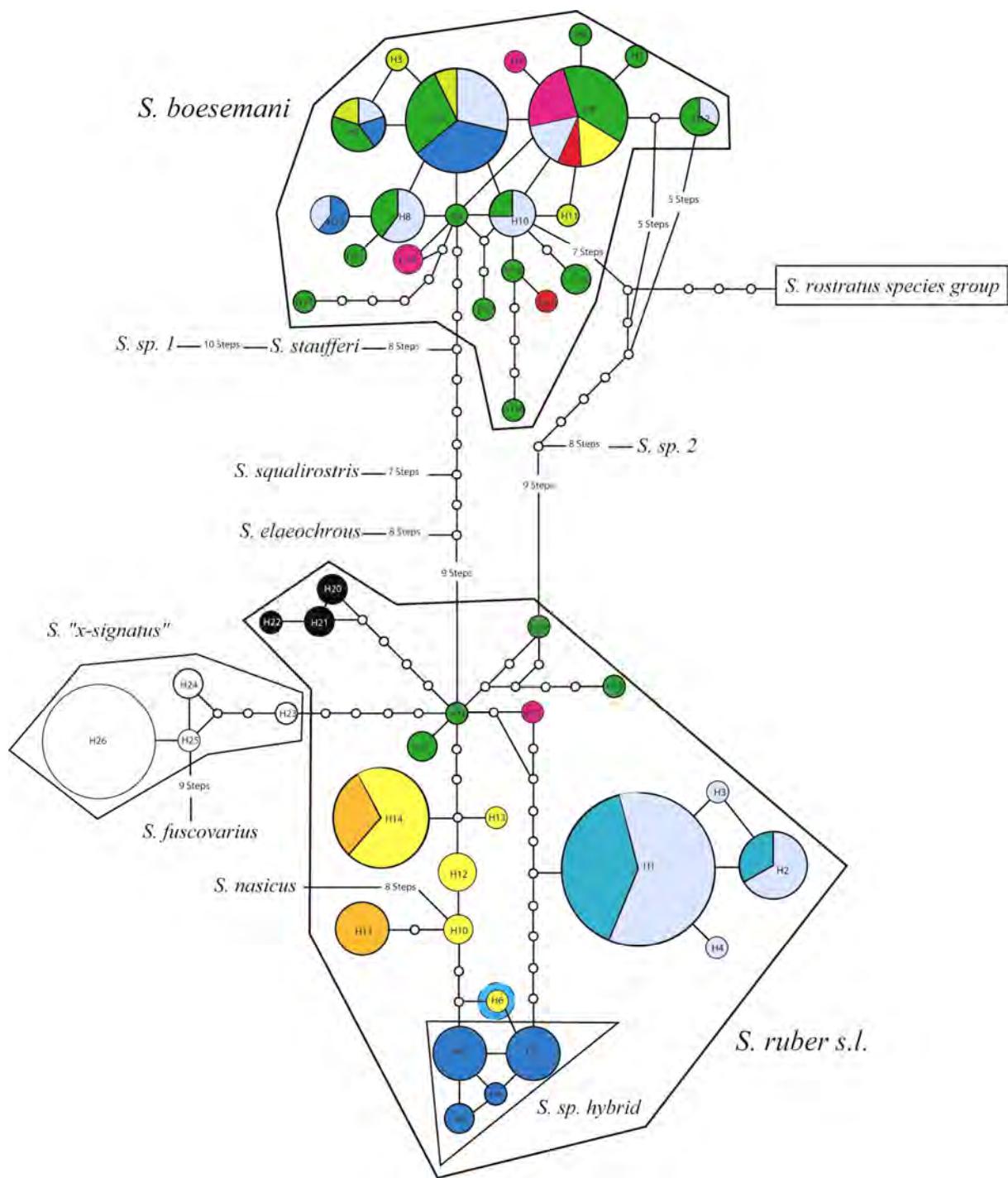
Fig. S5.32: nuDNA networks for the *Scinax* species (see legend below).

Fig. S5.25-32: nuDNA networks for each genus. The size of the circle representing haplotypes is proportional to the number of individuals. Corresponding mtDNA lineages are indicated with coresponding colouration (same colour code has been used in full trees (Fig. S5.1-8) and statistical parsimony networks (Fig. S5.9-16) and maps (Fig. 17-24)). A putative hybrid individual is indicated in *Scinax ruber* by dashed line circle.

Table 2.1: *Scinax* species occurring in French Guiana and their groupings after Lescure and Marty (2000).

S. ruber	
S. boesemani	
S. cruentommus	*S. ruber* **species group**
S. x-signatus	
S. sp. 1	
S. proboscideus	
S. jolyi	*S. rostratus* **species group**
S. nebulosus	

Table 2.2: Summary of genetic divergences among lineages (above the diagonal: mean uncorrected pairwise divergences among mtDNA and tyrosinase haplotypes among different lineages and species of *Scinax* (a) and *Rhinella* (b), not considering putative introgressed specimens or hybrids) and of geographical co-occurrence and haplotype sharing (HS) among them. The upper percentage value for each pairwise comparison gives rDNA distances, the lower value gives tyrosinase distances. SD computed with 1000 bootstrap pseudoreplicates are given. ?

(a)

	Scinax ruber A	*Scinax x-signatus*	*Scinax ruber* B	*Scinax ruber* C	*Scinax ruber* D	*Scinax ruber* E
SRA	---	0.6±0.3	1.3±0.4	3±0.6	4.9±0.8	13.9±1.2
		1.6±0.6	**0±0**	1.8±0.6	2.1±0.6	2.7±0.8
SX	sympatric		1.3±0.4	3.4±0.6	5±0.8	14±1.2
	no mtHS/no ncHS		1.6±0.5	1.4±0.5	2.1±0.6	2.7±0.8
SRB	syntopic	sympatric	---	3.7±0.7	4.8±0.8	13.6±1.2
	no mtHS/ **ncHS**	no mtHS/no ncHS		1.6±0.5	2.1±0.6	2.7±0.8
SRC	syntopic	sympatric	allopatric?	---	5.8±0.9	14.3±1.2
	no mtHS/no ncHS	**mtHS**/no ncHS	No mtHS/no ncHS		2±0.6	2.6±0.7
SRD	allopatric	allopatric	allopatric	allopatric	---	14.1±1.2
	no mtHS/no ncHS	no mtHS/no ncHS	no mtHS/no ncHS	no mtHS/no ncHS		2.7±0.8
SRE	syntopic	allopatric ?	syntopic	allopatric ?	allopatric ?	---
	no mtHS/no ncHS	no mtHS/no ncHS	no mtHS/no ncHS	no mtHS/no ncHS	no mtHS/no ncHS	

(b)

	Rhinella margaritifera A	*Rhinella margaritifear* B	*Rhinella margaritifera* C	*Rhinella margaritifera* D	*Rhinella margaritifera* E
RMA	---	1±0.3	2±0.5	3.8±0.6	4.9±0.7
		0±0	**0±0**	0.9±0.5	0.9±0.5
RMB	sympatric	---	2.3±0.5	4±0.7	5±0.7
	no mtHS/ **ncHS**		**0±0**	0.9±0.5	0.9±0.5
RMC	allopatric ?	allopatric ?	---	4.1±0.7	5±0.7
	No mtHS/ **ncHS**	No mtHS/ **ncHS**		0.9±0.5	0.9±0.5
RMD	syntopic	allopatric?	allopatric?	---	5.1±0.7
	no mtHS/no ncHS	No mtHS/no ncHS	No mtHS/no ncHS		1.8±0.7
RME	sympatric	sympatric	allopatric?	sympatric	---
	no mtHS/no ncHS	no mtHS/no ncHS	No mtHS/no ncHS	no mtHS/no ncHS	

Table S2.1: Catalogue numbers of voucher specimens, sampling localities, and Genbank accession numbers. Asterisks indicate discordant assignments for nuclear and mitochondrial data. Museum acronyms are as follows: MNHN, Muséum National d'Histoire Naturelle, Paris, France; MVZ, Museum of Vertebrate Zoology, Berkeley, USA; QZAC, Museo de Zoologia de la pontificia universidad catolica del Ecuador, MC, Christian Marty field numbers, BM, Michel Blanc field numbers, PG, Philippe Gaucher field numbers, RMNH, National Museum of Natural history of Netherlands, IWK, Field numbers used by Maureen A. Donnelly (to be accessioned in the herpetological collection of the Florida international university, MACN, Museo Argentino de ciencias naturales "Bernardino Rivadavia", Buenos Aires, Argentina; JF, Julian Faivovich field numbers; UTA, University of Texas at Arlington; KU, Kansas University, Museum of Natural History, Lawrence, KS; LSUMZ, Louisiana State University Museum of Zoology; USNM, National Museum of Natural History Smithsonian Institution; MZUSP, Museu de Zoologia da Universidade da São Paulo; MLPA, Museo de La Plata, La Plata, Argentina; MCP, Museu de Ciências e tecnologia da pontificia Universidade Catòlica de Rio Grande do Sul, Brazil; CFBH, Collection Célio F.B. Haddad, Universidade Estadual Paulista, Rio Claro, São Paulo, Brazil; ZUEC, Museu de Historia Natural, Univesidade de Campinas, Campinas, São Paulo, Brazil. Locality numbers refers to the Fig. 1. HN corresponds to haplotypes numbers.

S. ruber A	Catalog #	Country	Locality	N°	18S	tyr	HN tyr	12S	16S	HNmt	cytb	HN cytb
	30 mc	FG	Kaw	1		EF364168	AB1	EF217430	EF217473	A1	EF364235	A1
	9 bm	FG	Kaw	1		EF364163	AB1	EF217430	EF217473	A1	EF364235	A1
	59 bm	FG	Compté	2		EF364164	AB1	EF217430	EF217473	A1	EF364235	A1
	114 bm	FG	Cacao	3		EF364165	AB1	EF217430	EF217473	A1	EF364235	A1
	115 bm	FG	Cacao	3		EF364166	AB1	EF217430	EF217473	A1	EF364235	A1
	RMNH 35591	FG	Nouragues	4		EF364162	AB1	EF217430	EF217473	A1	EF364235	A1
	193mc	FG	Saül	5		EF364176	AB1	EF217430	EF217473	A1	EF364235	A1
	194mc	FG	Saül	5		EF364177	AB1	EF217430	EF217473	A1	EF364235	A1
	83 mc	FG	Montjoly	6		EF364172	AB1	EF217430	EF217473	A1	EF364236	A2
	70 mc	FG	Camopi	7		EF364169	AB1	EF217430	EF217473	A1	EF364239	A5
	177 mc	FG	Ouanary	8		EF364175	AB1	EF217431	EF217474	A2	EF364238	A4
	166 mc	FG	St Laurent	9		EF364173	AB1	EF217432	EF217475	A3	EF364237	A3
	176 mc	FG	Ouanary	8		EF364174	AB1	EF217432	EF217475	A3	EF364237	A3
	137 bm	FG	Cacao	3		EF364167	AB1	EF217433	EF217476	A4	EF364235	A1
	71 mc	FG	Trois-saut	10		EF364170	AB1	EF217434	EF217477	A5	EF364240	A6
	74 mc	FG	Montagne d'Argent	11	EF364227	EF364171	AB1	EF217435	EF217478	A6	EF364237	A3
S. ruber B												
	151 mc	FG	Guatemala	12	EF364228	EF364184	AB1	EF217438	EF217481	B1	EF364244	B4
	116 bm	FG	Cacao	3		EF364178	AB1	EF217438	EF217481	B1	EF364241	B1
	249mc	FG	Kaw	1				EF217438	EF217481	B1	EF364241	B1
	250mc	FG	Kaw	1		EF364185	AB1	EF217438	EF217481	B1	EF364241	B1
	150bm	FG	Road CSG Sinnamary	14		EF364183	AB1	EF217438	EF217481	B1	EF364241	B1
	141bm	FG	Petit saut	13		EF364180	AB1	EF217439	EF217482	B2	EF364242	B2
	148bm	FG	Road CSG Sinnamary	14		EF364181	AB1	EF217440	EF217483	B3	EF364243	B3
	130 bm	FG	Kourou	12		EF364179	AB1	EF217441	EF217484	B4	EF364241	B1
	149bm	FG	Road CSG Sinnamary	14		EF364182	AB1	EF217442	EF217485	B5	EF364245	B5
	282mc	FG	Montsinnery	15		EF364186	AB1	EF217443	EF217486	B6		
S. x-signatus												
	22bm	FG	Road 8/pk6	1		EF364144	X1	EF217436	EF217479	X1	EF364258	X1
	45bm	FG	Road 8/pk6	1		EF364145	X1	EF217436	EF217479	X1	EF364258	X1
	259mc	FG	Kaw	1		EF364150	X1	EF217436	EF217479	X1	EF364258	X1
	145bm	FG	Camp caiman	1		EF364149	X1	EF217436	EF217479	X1	EF364258	X1
	142bm	FG	Camp caiman	1		EF364146	X1	EF217436	EF217479	X1	EF364258	X1
	189mc	FG	Kaw	1		EF364153	X2	EF217436	EF217479	X1	EF364258	X1
	144bm	FG	Camp caiman	1	EF364229	EF364148	X3	EF217436	EF217479	X1		
	143bm	FG	Camp caiman	1		EF364147	X1	EF217436	EF217479	X1		
	86 mc	FG	Kaw	1		EF364152	X2	EF217436	EF217479	X1	EF364258	X1
	190mc	FG	Kaw	1		EF364154	X1	EF217436	EF217479	X1	EF364258	X1
	260mc	FG	Arataï	4		EF364151	X1	EF217437	EF217480	X2		
	18 mc*	FG	Antecum Pata	16		5:EF376147	X4	5:EF376041	6:AF467264	C1*	EF364246	C1
S. ruber C												
	178 mc	FG	Ouanary	8	EF364230	EF364159	C1	5:EF376041	5:EF376073	C1	EF364247	C2
	218mc	FG	Apatou	17		EF364160	C3	5:EF376041	5:EF376073	C1	EF364249	C4
	40 mc	FG	Grand Santi	19		5:EF376148	C2	5:EF376041	5:EF376073	C2	EF364248	C3
	IWK 109	Guyana	Iwokrama, Muri scrub camp			3:AY844181			2:AY549365			

Species	Code	Country	Locality									
S. ruber Peru	KU 207622	Peru	Madre de Dios, Cuzco Amazonico					4:AY326034				
S. ruber D	QCAZ 18217	Ecuador	Estacion Biologica Jatun sacha, Parroquia Ahuano, Canton Tena,Napo			EF364158	D1	EF217444	EF217487	D1		
	QCAZ 18219	Ecuador	Estacion Biologica Jatun sacha, Parroquia Ahuano, Canton Tena,Napo Province					EF217444	EF217487	D1		
	QCAZ 25275	Ecuador	AUCA 14 road, Parroquia Dayuma, Canton Coca, Orellana Province			EF364157	D3	EF217444	EF217487	D1		
	QCAZ 25874	Ecuador	Comunidad serena, North Side river Napo, Parroquia talag, Canton Tena,Napo Province			EF364156	D2	EF217444	EF217487	D1		
	QCAZ 25301	Ecuador	Comunidad serena, North Side river Napo, Parroquia talag, Canton Tena,Napo Province			EF364155	D2	EF217444	EF217487	D1		
S. ruber E												
	35 mc	FG	Montjoly	6		EF364139	E1	EF217447	EF217490	E1	EF372235	E1
	75 mc	FG	Mont Ravel	6		EF364140	E1	EF217447	EF217490	E1	EF372235	E1
	76 mc	FG	Mont Ravel	6	EF364231	EF364141	E1	EF217447	EF217490	E1	EF372235	E1
	3 bm	FG	Kourou	12		EF364135	E1	EF217447	EF217490	E1	EF372234	E2
	138bm	FG	Kourou	12		EF364136	E1	EF217447	EF217490	E1	EF372235	E1
	139bm	FG	Kourou	12		EF364137	E2	EF217447	EF217490	E1	EF372235	E1
	140bm	FG	Kourou	12		EF364138	E1	EF217447	EF217490	E1	EF372235	E1
	1 bm	FG	Kourou	12		EF364134	E1	EF217445	EF217488	E2	EF372235	E1
	210mc	FG	Ile royale	20		EF364142	E1	EF217446	EF217489	E3	EF372235	E1
S. sp 1 I												
	26 bm	FG	Crique grand leblond	21	EF364232	EF364216	I1	EF217448	EF217491	I1	EF364256	I2
	86 bm	FG	Crique grand leblond	21		EF364217	I2	EF217448	EF217491	I1	EF364255	I1
	174bm	FG	Crique grand leblond	21		EF364222	I1	EF217448	EF217491	I1		
	173bm	FG	Crique grand leblond	21		EF364221	I1	EF217450	EF217493	I2		
	257mc	FG	Aratai	4		EF364220	I1	EF217449	EF217492	I3	EF364255	I1
	256mc	FG	Aratai	4		EF364219	I1	EF217451	EF217494	I4	EF364255	I1
	255mc	FG	Aratai	4		EF364218	I1	EF217452	EF217495	I5	EF364257	I3
S. boesmani G												
	198mc	FG	Grand santi	19		EF364215	FG1*	EF217460	EF217503	G1		
	39mc	FG	Grand santi	19	5:EF376108	5:EF376146	FG2*	5:EF376040	5:EF376072	G2		
S. boesmani F												
	136bm	FG	Road 8/pk7	22		EF364208	FG5	EF217453	EF217496	F1		
	152bm	FG	Savane roche virginie	23		EF364210	FG3	EF217455	EF217498	F2		
	153bm	FG	Savane roche virginie	23		EF364211	FG6	EF217455	EF217498	F2		
	151bm	FG	Savane roche virginie	23		EF364209	FG4	EF217457	EF217500	F3		
	233mc	FG	Grand santi	19		EF364214	FG3	EF217459	EF217502	F4		
	232mc	FG	Grand santi	19		EF364213	FG4	EF217454	EF217497	F5		
	147mc	FG	Guatemala	19	EF364225	EF364212	FG3	EF217458	EF217501	F6		
	124bm	FG	Road 8/pk6	22		EF364207	FG5	EF217456	EF217499	F7		
S. elaeochrous												
	MVZ149785	Costa rica	Swamp on E edge of Cahuita Limon		5:EF376113	5:EF376151		5:EF376045	5:EF376076			
S. cruentommus H												
	PG 62	FG	Patawa	1		EF364201	H2	EF217463	EF217506	H1		
	PG 68	FG	Patawa	1		EF364204	H2	EF217463	EF217506	H1		
	PG 134	FG	Patawa	1		EF364205	H1	EF217463	EF217506	H1		
	PG 135	FG	Patawa	1		EF364206	H2	EF217463	EF217506	H1		
	126 mc	FG	Kaw	1				EF217463	EF217506	H1	EF364250	H1
	54 bm	FG	Crique grand leblond	21		EF364188	H2	EF217463	EF217506	H1	EF364250	H1
	79 bm	FG	Crique grand leblond	21				EF217463	EF217506	H1	EF364254	H5
	154bm	FG	Road 1/pk 91, 8	23		EF364191	H1	EF217463	EF217506	H1	EF364251	H2
	155bm	FG	Road 1/pk 91, 8	23		EF364192	H1	EF217463	EF217506	H1	EF364252	H3
	156bm	FG	Road 1/pk 91, 8	23		EF364193	H2	EF217463	EF217506	H1	EF364250	H1
	56 bm	FG	Kaw	1		EF364196	H2	EF217461	EF217504	H2	EF364250	H1
	PG 63	FG	Patawa	1		EF364202	H2	EF217461	EF217504	H2		
	120 mc	FG	Kaw	1		EF364199	H1	EF217461	EF217504	H2	EF364250	H1
	24 bm	FG	Kaw	1		EF364187	H2	EF217464	EF217507	H3	EF364250	H1
	121 mc	FG	Kaw	1		EF364200	H1	EF217464	EF217507	H3	EF364250	H1
	55 bm	FG	Kaw	1		EF364189	H3	EF217466	EF217509	H4	EF364250	H1
	PG 67	FG	Patawa	1		EF364203	H1	EF217465	EF217508	H5		
	29 mc	FG	Kaw	1		EF364198	H2	5:EF376043	5:EF376074	H6	EF364250	H1
	157bm	FG	Road 1/pk 91, 8	23		EF364194	H4	EF217467	EF217510	H7	EF364250	H1
	65 bm	FG	Kaw	1		EF364190	H3	EF217462	EF217505	H8	EF364250	H1
	8 mc	FG	Kaw	1	EF364233	EF364197	H2	5:EF376044	6:AF467263	H9	EF364253	H4
	193bm	FG	Crique grand leblond	21		EF364195	H1					
S. nasicus	MACN 38650	Argentina	Buenos Aires, Baradero, Estancia: "El retoño"			3:AY844180		3:AY843759			3:AY844004	
S. fuscovarius	JF1973	Argentina	Misiones, Guarani, San Vicente, Campo anexo INTA			3:AY844179		3:AY843758				
S. staufferi	UTA-A50749	Guatemala	Zacapa, 2.9Km S teculutan on road to Huit			3:AY844183		3:AY843761				
S. squalirostris	MACN38241	Argentina	Entre Rios, Depto. Islas del Ibicuy, Ruta 12 vieja, entre brasos largo y arroyo luciano			3:AY844182		3:AY843760				
S. nebulosus												
	24mc	FG	Road Régina-St. georges	18	5:EF376106	5:EF376144	H1	5:EF376038	6:AF467262			
	126bm	FG	Road 8/pk6	22			H3	EF217471	EF217514			
	258mc	FG	Mana	24			H2	EF217470	EF217513			
S. jolyi												
	3mc	FG	Kaw	1	5:EF376103	5:EF376141		5:EF376035	6:AF467261			
	4mc	FG	Gabrielle	1				5:EF376036	6:AF467261			
S. proboscideus												
	34mc	FG	Kaw	1	5:EF376105	5:EF376143	H1	5:EF376037	5:EF376070			
	208mc	FG	Kaw	1			H2	EF217468	EF217511			
S. rostratus												
	247mc	Venezuela	Rio caura		5:EF376107	5:EF376145		5:EF376039	5:EF376071			
S. sp. 2	AA	Colombia	Municipality of Orocué, Casanare, 4.83187°N; -71.27214°W		EF364234	EF364224		EF217469	EF217512			
S. boulengeri	MVZ207215	Costa Rica	Guanacaste, ca. 0.2Km W Hyw 1 on fst paved rd 10Km N entrance Santa Rosa NPark			3:AY844177		3:AY843755				
S. garbei	KU202764	Ecuador	Chimborazo, 6.7Km E Riobamba					4:AY326033				

Species	Voucher	Country	Locality	#						
S. acuminatus	**MACN38649**	Argentina	Corientes, Paso de la patria			3:AY844176			3:AY843753	
S. berthae	**MLPA2137**	Argentina	Buenso Aires, Atalaya						3:AY843754	
S. catharinae	**MCP3734**	Brazil	Rio grande do Sul, Pro-Mata						3:AY843756	
S.(Hyla) uruguayus	**CFBH5788**	Brazil	Rio grande do Sul, Canbara do Sul						3:AY843681	
D. nanus	**84mc**	FG	Kaw	28	5:EF376094	5:EF376132		5:EF376026	5:EF376062	
D. leucophyllatus	**36mc**	FG	Kaw	24	5:EF376091	5:EF376129		5:EF376023	5:EF376059	
S. lacteus	**85mc**	FG	Kaw	5	EF364226	EF364223		EF217472	EF217515	
R. margaritifera A										
	108 mc	FG	Kaw	1		EF364333	AB6	EF364266	EF364292	A1
	136 mc	FG	Crique Margot	9		EF364335	ABC1	EF364266	EF364292	A1
	225mc	FG	Road St. élie	25		EF364330	AB6	EF364266	EF364292	A1
	195mc	FG	Kaw	1		EF364325	AB6	EF364266	EF364292	A1
	158bm	FG	Guatemala	12		EF364315	ABC1	EF364266	EF364292	A1
	159bm	FG	Guatemala	12		EF364316	AB6	EF364266	EF364292	A1
	160bm	FG	Guatemala	12		EF364317	AB6	EF364266	EF364292	A1
	161bm	FG	Guatemala	12		EF364318	AB6	EF364266	EF364292	A1
	162bm	FG	Guatemala	12		EF364319	AB6	EF364266	EF364292	A1
	163bm	FG	Guatemala	12		EF364320	A3	EF364266	EF364292	A1
	284mc	FG	St. élie	25		EF364336	ABC1	EF364266	EF364292	A1
	164bm	FG	Montagne des singes	26		EF364321	AB6	EF364266	EF364292	A1
	165bm	FG	Montagne des singes	26		EF364322	ABC1	EF364266	EF364292	A1
	176bm	FG	Crique grand leblond	21		EF364323	AB6	EF364266	EF364292	A1
	217mc	FG	Grand santi	19		EF364329	AB6	EF364267	EF364299	A2
	203mc	FG	Saül	5		EF364327	ABC1	EF364269	EF364295	A3
	204mc	FG	Saül	5	EF364365	EF364328	AB6	EF364269	EF364295	A3
	2 bm	FG	Cisame	27		EF364313	AB6	EF364267	EF364293	A4
	137 mc	FG	Crique Margot	9				EF364268	EF364294	A5
	286mc	FG	St. élie	25		EF364332	AB6	EF364270	EF364296	A6
	196mc	FG	Kaw	1		EF364326	A4	EF364272	EF364298	A7
	66 mc	FG	Mont Barka	28		EF364334	A4	EF364272	EF364298	A7
	178bm	FG	Crique grand leblond	21		EF364324	AB6	EF364271	EF364297	A8
	92 bm	FG	Cisame	27		EF364314	A5	EF364275	EF364301	A9
	285mc	FG	St. élie	25		EF364331	ABC1	EF364274	EF364300	A10
R. margaritifera B										
	PG 143	FG	Patawa	1		EF364311	AB6	EF364276	EF364302	B1
	PG 144	FG	Patawa	1	EF364367	EF364312	ABC1	EF364276	EF364302	B1
R. margaritifera C										
	156 mc	FG	Trijonction	29	EF364363	EF364337	ABC1*	EF364277	EF364303	C1
	157 mc	FG	Trijonction	29		EF364338	ABC1*	EF364277	EF364303	C1
R. margaritifera D										
	112 bm	FG	Litany	30		EF364343	D1	EF364279	EF364305	D2
	121 bm	FG	Saül	5		EF364341	D2	EF364278	EF364304	D1
	5 mc	FG	Cisame	27	EF364366	EF364342	D1	EF364278	EF364304	D1
	PG 103	FG	Saül	5		EF364339	D2	EF364278	EF364304	D1
	PG 104	FG	Saül	5		EF364340	D2	EF364278	EF364304	D1
R. margaritifera E										
	128 bm	FG	Mataroni	23				EF364263	EF364289	E1
	129 bm	FG	Mataroni	23				EF364263	EF364289	E1
	133 bm	FG	Mataroni	23		EF364345	E5	EF364263	EF364289	E1
	135 bm	FG	Saül	5		EF364346	E3	EF364263	EF364289	E1
	145 mc	FG	Kaw	1		EF364356	E1	EF364263	EF364289	E1
	65 mc	FG	Mont Barka	28		EF364354	E3	EF364263	EF364289	E1
	186bm	FG	Crique grand leblond	21		EF364348	E5	EF364263	EF364289	E1
	198bm	FG	Crique grand leblond	21		EF364349	E1	EF364263	EF364289	E1
	248mc	FG	Kaw	1		EF364358	E4	EF364263	EF364289	E1
	104 mc	FG	Tibourou	1		EF364355	E1	EF364263	EF364289	E1
	211mc	FG	Montagne des singes	26		EF364350	E1	EF364264	EF364290	E2
	212mc	FG	Montagne des singes	26		EF364351	E1	EF364264	EF364290	E2
	161 mc	FG	Ouanary	8		EF364357	E1	EF364262	EF364288	E3
	254mc	FG	Camopi	7		EF364352	E1	EF364260	EF364286	E4
	PG 110	FG	Trois Sauts	10		EF364353	E2	EF364259	EF364285	E5
	169 mc	FG	Tibourou	1		EF364347	E1	EF364265	EF364291	E6
	131 bm	FG	Mataroni	23	EF364364	EF364344	E1	EF364261	EF364287	E7
	132 bm	FG	Mataroni	23				EF364261	EF364287	E7
R. cf. margaritifera 1	**QCAZ 10601**	Ecuador	Francisco de Orellana, Parque Nacional Yasuní				7:DQ158470			
R. cf. margaritifera 2	**QCAZ 13896**	Ecuador	Cañar, Manta Real				7:DQ158471			
R. cf. margaritifera 3	**QCAZ 11597**	Ecuador	Provincia Esmeraldas, Bosque Protector, 30 km from San Lorenz by way of Ibarra				7:DQ158472			
R. cf. margaritifera 4	**USNM 268828**	Peru	Madre de Dios				7:DQ158490			
R. cf. margaritifera 5	**KU 215145**	Peru	Madre de Dios				7:DQ158491			
R. cf. margaritifera 6	**ZUEC DCC3392**	Brazil	Rio de Janeiro				1:AY680260			
R. dapsilis	**QCAZ 3509**	Ecuador	Pichincha, Bosque Protector La Perla, 5 km E La Concordia				7:DQ158448			
R. castaneotica	**LSUMZ 17429**	Brazil	Para: 100 km S Santarem				7:DQ158440			
"Bufo" ocellatus	**MZUSP 103261**	Brazil	Peixe Tocantins				7:DQ158479			
Rhaebo guttatus	**144mc**	FG	Crique margot	9		EF364370	EF364361	EF364281	EF364307	
Chaunus granulosus	**235mc**	FG	Mana	24				EF364280	EF364306	
Chaunus marinus	**KU205236**	Peru	Madre de Dios, Cuzco Amazonico							
Pedostibes hosei	**NA**	Malaysia	Pahang, Pehang main research field station ~13Km NW Kuala Krau at confluence Krau and Lompat rivers				4:AY325993			
D.minutus	**98bm**	FG	Mont Arawa			EF364371	EF364362	EF364284	EF364310	
Ateopus flavecsens	**25bm**	FG	Trois pitons	8		EF364368	EF364359	EF364282	EF364308	
Atelopus barbotini	**63bm**	FG	Mont bakra	28	EF364369	EF364360		EF364283	EF364309	

#sequences published in: 1: Pauly et al., 2005; 2: Faivovitch et al., 2004; 3: 2005; 4: Darst and Cannatella, 2004; 5: Salducci et al., 2005; 6: 2003; 7: Pramuk, 2006.

Text S3.1: Additional details about materials and methods.

1. Except for seven species purportedly endemic to the Guianas (*Dendrobates tinctorius*, *Anomaloglossus degranvillei*, *Anomaloglossus baeobatrachus*, *Allobates granti*, *Chiasmocleis hudsoni*, *Adenomera heyeri* and *Eleutherodactylus chiastonotus*), all the selected species are believed to be widely distributed across the Guianas and Amazonia (88.3%).

2. If 104 species are supposed to occur in French Guiana according to Lescure and Marty (2000) and Boistel et al. (2006), we only counted 102: Three species of the *Leptodactylus wagneri* species group (*L.* gr. *wagneri*) are supposed to occur in French Guiana (*L. leptodactyloïdes*, *L. petersi* and *L. pallidirostris*). We have been unable to accurately identify morphologically these species in French Guiana. There are no published sequences for these species except for *L. leptodactyloïdes*. Consequently, they are treated here as a single species. We are conscious that it biased the analyses but we think it was the most parsimonious way to deal with this group. Moreover, not to take this group into account would not have changed the results and their interpretation.

3. Heyer (2005) clarified the species boundaries in the *Leptodactylus pentadactylus* species group during the writing of the manuscript. Consequently the different *L. pentadactylus* lineages used herein represent different species than described in Heyer (2005).

Heyer, W. R. (2005). Variation and taxonomic clarification of the large species of the *Leptodactylus pentadactylus* species group (Amphibia: Leptodactylidae) from Middle America, Northern South America and Amazonia. *Arquivos de Zoologia do Estado de São Paulo*, **37**(3), 269–348

4. One sequence attributed to *Adenomera andreae* published by Faivovich et al. (2005) unambiguously clustered in the *Leptodactylus wagneri* species group in preliminary phylogenetic analyses. This result is likely due to misidentification of the specimen. We called this taxon *Leptodactylus gr. wagneri* J.

5. We chose to keep the genera *Leptodactylus*, *Adenomera* and *Lithodytes* because we found arguments in Frost et al. (2006) for their synonymy to be ambiguous. Frost et al. (2006) based this recommendation on the work of Heyer (1998) in which the genus *Adenomera* is represented by only one species, its position, analysed with morphology and vocalisation, is not fully resolved and is not the main purpose of the article. Moreover, see comment 4 above.

Heyer, W.R. 1998. The relationships of *Leptodactylus diedrus*. *Alytes*, **16**(1-2), 1–24.

Recent works published during the writing of this manuscript also support taxonomic modifications for the genera *Eleutherodactylus* (Heinicke et al., 2007) and *Chaunus* (Pramuk et al., 2007).

Heinicke, M.P., Duellman, W.E., Hedges, S.B. 2007. Major Caribbean and Central American frog faunas originated by ancient oceanic dispersal. *Proceedings of the National Academy of Sciences of the United States of America*, **104**(24), 10092–10097.

Pramuk, J.B., Robertson, T., Sites, Jr. J.W., Noonan, B.P. 2008. Around the world in 10 million years: biogeography of the nearly cosmopolitan true toads (Anura: Bufonidae). *Global Ecology and Biogeography*, **17**(1), 72–83.

6. We also sampled and sequenced all other congeneric species supposedly occuring in French Guiana (23 species except *Chaunus marinus*, *Dendropsophus marmoratus*) according to Lescure and Marty (2000) for the same 16S fragment to avoid any misidentification of the specimens collected (data not shown, see Table S3.1). As there were no additional intraspecific data available inside or outside French Guiana these species have not been taken into account for the intraspecific analyses.

7. Such a selection was conducted to represent the geographical range of the lineages and because, (1) an evaluation of the diversity existing within each lineage requires extensive sampling and was not the purpose of this work; (2) the number of pairwise distances below 0.01 would be highly correlated by the number of individuals included within each lineages thus these data would have biased the analyses.

8. To test the monophyly of each species we selected in GenBank available sequences of additional species that were potentially nesting within species. To select these additional species, we used available data for taxa which displayed close relationship with the previously selected species according to previous work and using the Blast option with all the previously selected sequences. We chose the first hit if this sequence had not been already selected as a conspecific sequence. With this method we probably missed available data producing paraphyletic positions within species but our goal was not to evaluate the frequency of this phenomenon because the taxonomic representation of the available sequences would not allow us to evaluate it anyway, but only to show its appreciable presence and to be able to evaluate at which distances it occurs.

The following references are only used in supplementary materials as sources for the sequence information.

Austin, J.D., Lougheed, S.C., Tanner, K., Chek, A.A., Bogart, J.P., Boag, P.T. 2002. A molecular perspective on the evolutionary affinities of an enigmatic Neotropical frog, *Allophryne ruthveni*. *Zoological journal of the Linnean Society*, **134**(3), 335–346.

Biju, S.D., Bossuyt, F. 2003. New frog family from India reveals an ancient biogeographical link with the Seychelles. *Nature*, **425**, 711–714.

Camargo, A., de Sá, R.O., Heyer, W.R. 2006. Phylogenetic analyses of mtDNA sequences reveal three cryptic lineages in the widespread Neotropical frog *Leptodactylus fuscus* (Schneider, 1799) (Anura, Leptodactylidae). *Biological Journal of the Linnean Society*, **87**, 325–341.

Clough, M., Summers, K. 2000. Phylogenetic systematics and biogeography of the poison frogs: evidence from mitochondrial DNA sequences. *Biological Journal of the Linnean Society*, **70**, 515–540.

Darst, C.R., Cannatella, D.C. 2004. Novel relationships among hyloid frogs inferred from 12S and 16S mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, **31**, 462–75.

de Sá R.O., Heyer W.R., Camargo A. 2005. Are *Leptodactylus didymus* and *L. mystaceus* phylogenetically sibling species (Amphibia, Anura, Leptodactylidae)? In: Ananjeva N. and Tsinenko O., (eds.) Herpetologica Petropolitana-Proceedings of the 12th Ordinary General Meeting of the Societas Europaea Herpetologica, August 12-16, 2003, St. Petersburg, Russia. *Russian Journal of Herpetology*, **12**(Supplement), 90–92.

de Sá, R.O., Heyer, W.R., Camargo, A. 2005. A phylogenetic analysis of *Vanzolinius* Heyer, 1974 (Amphibia, Anura, Leptodactylidae): Taxonomic and life history implications. *Arquivos do Museu Nacional, Rio de Janeiro*, **63**, 707–726.

Faivovich, J., Garcia, P.C.A., Ananias, F., Lanari, L., Basso, N.G., Wheeler, W.C. 2004. A molecular perspective on the phylogeny of the *Hyla pulchella* species group (Anura, Hylidae). *Molecular Phylogenetics and Evolution*, **32**, 938–950.

Frost, D.R., Grant, T., Faivovich, J., Bain, R.H., Haas, A., Haddad, C.F.B., de Sá, R.O., Channing, A., Wilkinson, M., Donnellan, S.C., Raxworthy, C.J., Campbell, J.A., Blotto, B.L., Moler, P., Drewes, R.C., Nussbaum, R.A., Lynch, J.D., Green, D.M., Wheeler, W.C. 2006. The amphibian tree of life. *Bulletin of the American Museum of Natural History*, **297**, pp.370.

Heyer, W.R., de Sá, R.O., Rettig, A. 2005. Sibling species, advertisement calls, and reproductive isolation in frogs of the *Leptodactylus pentadactylus* species cluster (Amphibia, Leptodactylidae). In: Ananjeva N. and Tsinenko O., (eds.). Herpetologica

Petropolitana-Proceedings of the 12th Ordinary General Meeting of the Societas Europaea Herpetologica, August 12-16, 2003, St. Petersburg, Russia. *Russian Journal of Herpetology*, **12**(Supplement), 35–39.

Heyer, W.R. 2005. Variation and taxonomic clarification of the large species of the *Leptodactylus pentadactylus* species group (Amphibia: Leptodactylidae) from Middle America, Northern South America and Amazonia. *Arquivos de Zoologia do Estado de São Paulo*, **37**(3), 269–348

Heyer, W.R. 1998. The relationships of *Leptodactylus diedrus* Alytes, **16**(1-2), 1–24.

Hillis, D.M., Wilcox, T.P. 2005. Phylogeny of the New World true frogs (*Rana*). *Molecular Phylogenetics and Evolution*, **34**, 299–314.

Hull, D.L. 1977. The ontological status of species as evolutionary units. In: Butts R. and Hintikka J., (eds.) *Foundational problems in the special sciences*, D. Reidel Publishing Company, pp. 91–102.

Lougheed, S.C., Gascon, C., Jones, D.A., Bogart, J.P., Boag, P.T. 1999. Ridges and rivers: a test of competing hypotheses of Amazonian diversification using a dart-poison frog (*Epipedobates femoralis*). *Proceedings of the Royal Society of London Series B-Biological Sciences*, **266**, 1829–1835.

Loetters, S., Vences, M. 2000. Bemerkungen zur Nomenklatur und Taxonomie peruanischer Pfeilgiftfrösche. *Salamandra*, **36**, 247–260.

Pauly, G.B., Hillis, D.M., Cannatella, D.C. 2004. The history of a Nearctic colonization: molecular phylogenetics and biogeography of the Nearctic toads (*Bufo*). *Evolution*, **58**, 2517–2535.

Pramuk, J.B. 2006. Phylogeny of South American *Bufo* (Anura: Bufonidae) inferred from combined evidence. *Zoological Journal of the Linnean Society*, **146**, 407–452.

Pramuk, J.B., Hass, C.A., Hedges, S.B. 2001. Molecular phylogeny and biogeography of West Indian toads (Anura: Bufonidae). *Molecular Phylogenetics and Evolution*, **20**, 294–301.

Roberts, J.L., Brown, J.L., Schutle, R., Wilfredo, A., Summers, K. 2006. Rapid diversification of colouration among populations of a poison frog isolated on sky peninsulas in the central cordilleras of Peru. *Journal of Biogeography*, **34**(3), 417–426.

Roelants, K., Bossuyt, F. 2005. Archaeobatrachian paraphyly and pangaean diversification of crown-group frogs. *Systematic Biology*, **54**, 111–126.

Ron, S.R., Santos, J.C., Cannatella , D.C. 2006. Phylogeny of the tungara frog genus *Engystomops* (=*Physalaemus pustulosus* species group, Anura: Leptodactylidae). *Molecular Phylogenetics and Evolution*, **39**, 392–403.

Ruvinsky, I., Maxson, L.R. 1996. Phylogenetic relationships among bufonid frogs (Anura: Neobatrachia) inferred from mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, **5**, 533–547.

Salducci, M.-D., Marty, C., Chappaz, R., Gilles, A. 2002. Molecular phylogeny of French Guiana Hylinae: implications for the systematic and biodiversity of the Neotropical frogs. *Comptes Rendus Biologies*, **325**(2), 141–153.

Santos, J.C., Coloma, L.A., Cannatella, D.C. 2003. Multiple, recurring origins of aposematism and diet specialization in poison frogs. *Proceedings of the National Academy of Sciences of the United States of America*, **100**(22), 12792–12797.

Summers, K., Clough, M.E. 2001. The evolution of coloration and toxicity in the poison frog family (Dendrobatidae). *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 6227–6232.

Summers, K., Symula, R., Schulte, R. 2001. Molecular phylogenetic evidence for a mimetic radiation in Peruvian poison frogs supports a Mullerian mimicry hypothesis. *Proceedings of the Royal Society B-Biological Sciences*, **268**(1484), 2415–2421.

Summers, K., Weigt, L.A., Boag, P., Bermingham, E. 1999. The evolution of female parental care in poison frogs of the genus *Dendrobates*: Evidence from mitochondrial DNA sequences. *Herpetologica*, **55**, 254–270.

Symula, R., Schulte, R., Summers, K. 2003. Molecular systematics and phylogeography of Amazonian poison frogs of the genus *Dendrobates*. *Molecular Phylogenetics and Evolution*, **26**, 452–475.

Vences, M., Kosuch, J., Boistel, R., Haddad, C.F.B., La Marca, E., Lotters, S., Veith, M. 2003. Convergent evolution of aposematic coloration in Neotropical poison frogs: a molecular phylogenetic perspective. *Organisms Diversity and Evolution*, **3**, 215–226.

Table S3.1: Sample details and accession numbers. Names in grey correspond to additional species used in the figure to illustrate paraphyletic positions. X and O are used to indicate which sequences have been discarded from the analyses.

Species/lineage	voucher number	Accession # 16S		Countries	Locality	References	Coordinates
Adenomera andreae A	32mc	EU201044	X	French Guiana	Montjoly	New	04 55 00 N 52 16 00 W
Adenomera andreae B	216mc	EU201046	X	French Guiana	Saül	New	03 37 32 N 53 12 26 W
Adenomera andreae B	105AF	EU201047	X	Suriname	Road to Apura	New	05 11 00 N 55 39 00 W
Adenomera andreae C	87bm	EU201048	X	French Guiana	Mt Arawa	New	02 48 59 N 53 21 59 W
Adenomera andreae D	199bm	EU201045	X	French Guiana	Trinité	New	04 35 00 N 53 21 00 W
Adenomera andreae E	121AF	EU201049	X	Suriname	Brownsberg	New	04 56 31 N 55 10 33 W
Adenomera heyeri A	221mc	EU201050	X	French Guiana	Montagne des singes	New	05 04 00 N 52 43 00 W
Adenomera heyeri B	46PG	EU201051	X	French Guiana	Piton baron	New	03 17 00 N 53 04 00 W
Adenomera hylaedactyla A	272mc	EU201054	X	French Guiana	Kaw	New	04 42 00 N 52 18 00 W
Adenomera hylaedactyla B	92mc	EU201052	X	French Guiana	Montagne d'argent	New	04 23 00 N 51 42 00 W
Adenomera hylaedactyla C	1235BPN	EU201053	X	Guyana	Imbaimadai	New	05 44 23 N 60 17 51 W
Adenomera hylaedactyla D	MJH 3669	DQ283063	X	Peru	Huanuco, Rio Llullapichis, Panguana	Frost et al., 2006	09 23 02 S 75 52 57 W
Adenomera hylaedactyla E	MZUSP 70958	AY943240	X	Brazil	Alter do Chão	de Sà et al., 2005	02 32 00 S 54 58 00 W
Allobates femoralisA	56AF	EU201064	X	French Guiana	Petit,saut	New	05 04 00 N 53 03 00 W
Allobates femoralisB	303MC	EU201065	X	French Guiana	Toponowini	New	03 03 10 N 52 42 37 W
Allobates femoralisC	LSUMZ 17552	DQ283045	X	Brazil	Rondonia, Rio Formoso, Parque Guajira,Mirim, approx. 90 km N Nova Mamore	Frost et al., 2006	10 19 17 S 64 33 47 W
Allobates femoralisD	OMNH 34568	DQ502089	O	Brazil	Para, 101 km S and 15 km E Santarem (near Rio Curua,Una)	Grant et al., 2006	03 09 00 S 54 50 00 W
Allobates femoralisD	OMNH 34572	DQ502090	O	Brazil	Para, 101 km S and 15 km E Santarem (near Rio Curua,Una)	Grant et al., 2006	03 09 00 S 54 50 00 W
Allobates femoralisD	MPEG 12021	DQ502220	X	Brazil	Para, 101 km S and 15 km E Santarem (near Rio Curua,Una)	Grant et al., 2006	03 09 00 S 54 50 00 W
Allobates femoralisD	MPEG 13415	DQ502088	O	Brazil	Rondonia, Parque Estadual Guajara,Mirim	Grant et al., 2006	10 19 17 S 64 33 47 W
Allobates femoralisE	MJH 3976	DQ502113	X	Brazil	Amazonas, Reserva Florestal Adolfo Ducke	Grant et al., 2006	02 58 51 S 59 55 16 W
Allobates femoralisE	AF124106	AF124106	O	Brazil	?	Vences et al., 2003	
Allobates femoralisF	MJH 7354	DQ502117	X	Peru	Huanuco, Rio Llullapichis, Panguana	Grant et al., 2006	09 23 02 S 75 52 57 W
Allobates femoralisF	AfemRSucv4a	DQ523023	O	Peru	Rio Sucusari Iquitos, Loreto	Grant et al., 2006	03 14 26 N 72 55 42 W
Allobates femoralisF	AfemTahuiv1b	DQ523025	O	Peru	Tahuayo River Iquitos, Loreto,	Grant et al., 2006	04 11 13 S 73 06 16 W
Allobates femoralisF	AfemShucv3a	DQ523072	O	Peru	Shucshuyacu Yurimaguas, Loreto,	Roberts et al., 2006	06 00 59 S 75 50 40 W
Allobates femoralisG	OMNH 34102	DQ502093	O	Ecuador	Sucumbios, Estacion de Universidad Catolica near Reserva Faunistica Cuyabeno	Grant et al., 2006	00 00 00 S 76 10 00 W
Allobates femoralisG	OMNH 34104	DQ502094	O	Ecuador	Sucumbios, Estacion de Universidad Catolica near Reserva Faunistica Cuyabeno	Grant et al., 2006	00 00 00 S 76 10 00 W
Allobates femoralisG	LSU 12798	DQ502228	O	Ecuador	Sucumbios, Estacion de Universidad Catolica near Reserva Faunistica Cuyabeno	Grant et al., 2006	00 00 00 S 76 10 00 W
Allobates femoralisG	QCAZ16484	AY364543	X	Ecuador	?	Santos et al., 2003	
Allobates femoralisG		AF128572	O	Ecuador	Cuyabeno	Vences et al., 2003	00 15 19 S 75 53 24 W
Allobates femoralisH	WED 55470; KU 205291	AY326026	X	Peru	Madre de Dios, Cusco Amazonico	Darst and Cannatella, 2003	11 39 00 S 70 33 35 W
Allobates femoralisH	WED 55560; KU 205292	AY326027	O	Peru	Madre de Dios, Cusco Amazonico	Darst and Cannatella, 2003	11 39 00 S 70 33 35 W
Allobates femoralisH	KU 215179	DQ501990	O	Peru	Madre de Dios, Cusco Amazonico, 15 km E Puerto Maldonado, 200 m	Grant et al., 2006	11 39 00 S 70 33 35 W
Allobates femoralisH	KU 215177	DQ502014	O	Peru	Madre de Dios, Cusco Amazonico, 15 km E Puerto Maldonado, 200 m	Grant et al., 2006	11 39 00 S 70 33 35 W
Allobates femoralisH	KU 215180	DQ502015	O	Peru	Madre de Dios, Cusco Amazonico, 15 km E Puerto Maldonado, 200 m	Grant et al., 2006	11 39 00 S 70 33 35 W
Allobates femoralisH	AfemBocMan22	DQ523069	O	Peru	Boca Manu Cuzco,	Roberts et al., 2006	12 16 32 S 70 56 49 W
Allobates femoralisI	OMNH 36066	DQ502091	O	Brazil	Acre, Porto Walter	Grant et al., 2006	08 15 31 S 72 46 37 W
Allobates femoralisI	OMNH 36070	DQ502092	X	Brazil	Acre, Porto Walter	Grant et al., 2006	08 15 31 S 72 46 37 W
Allobates femoralisI	OMNH 36073	DQ502231	O	Brazil	Acre, Porto Walter	Grant et al., 2006	08 15 31 S 72 46 37 W
Allobates femoralisJ	AfemRManv12	DQ523040	X	Peru	Rio Manati Iquitos, Loreto	Roberts et al., 2006	
Allobates femoralisK	AfemItaya2ii	DQ523062	O	Peru	Itaya River Iquitos, Loreto	Roberts et al., 2006	04 27 00 S 73 34 11 W
Allobates femoralisK	AfemNautv5a	DQ523059	X	Peru	Nauta Road Iquitos, Loreto	Roberts et al., 2006	04 34 14 S 73 46 00 W
Allobates femoralisL	AfemMazukovi	DQ523055	X	Peru	Mazuko Madre de Dios	Roberts et al., 2006	
Allobates femoralisM	AfemSapoiv10	DQ523082	X	Peru	Saposoa Tarapoto, San Martin,	Roberts et al., 2006	06 46 15 S 76 56 28 W
Allobates femoralisN	UTA A56478	DQ502246	X	Suriname	Sipaliwini, in the vicinity of Kayser airstrip	Grant et al., 2006	03 05 70 S 56 28 30 W
Allobates granti A	38RB	EU201067	X	French Guiana	St Eugene	New	04 51 00 N 53 04 00 W

Species	Specimen	GenBank	O/X	Country	Locality	Reference	Coordinates
Allobates granti A	MNHN????	AY263233	O	French Guiana	Saül	Vences et al., 2003	03 37 32 N 53 12 26 W
Allobates granti B	185mc	EU201066	X	French Guiana	Trijonction	New	02 20 00 N 54 36 00 W
Allobates granti C	148AF	EU201068	X	Suriname	Brownsberg	New	04 56 31 N 55 10 33 W
Allobates granti D	49BM	EU201069	X	French Guiana	Saül	New	03 37 32 N 53 12 26 W
Allobates granti D	MNHN2000-651	AY263230	O	French Guiana	Saül	Vences et al., 2003	03 37 32 N 53 12 26 W
Allobates granti D	MNHN2000-653	AY263232	O	French Guiana	Saül	Vences et al., 2003	03 37 32 N 53 12 26 W
Allobates sp.PEG-M3	MPEG 13385	DQ502191		Brazil	Rondonia, Parque Estadual Guajara,Mirim	Grant et al., 2006	10 19 17 S 64 33 47 W
Allobates zaparo	QCAZ16601	AY364578		Ecuador		Santos et al., 2003	
Allophryne ruthveni A	205mc	EU201098	X	French Guiana	Cacao	New	04 34 00 N 52 28 00 W
Allophryne ruthveni B	MAD 1512	AY843564	X	Guyana	Kabocali camp, 101 m	Faivovich et al., 2005	04 17 10 N 58 30 56 W
Allophryne ruthveni C	?	AF364512	X	Brazil	eastern Amazon near Rio Xingu,	Austin et al., 2001	07 39 00 S 51 21 00 W
Ameerega hahneli A	MNHN 2000-656	AY263247	X	French Guiana	Trinité	Vences et al., 2003	04 35 00 N 53 21 00 W
Ameerega hahneli B	OMNH 36090	DQ502085	O	Brazil	Acre, Porto Walter	Grant et al., 2006	08 15 31 S 72 46 37 W
Ameerega hahneli B	OMNH 37443	DQ502081	O	Brazil	Amazonas, Castanho, ca. 40 km S Manaus,at km 12 on road to Autazes	Grant et al., 2006	03 37 10 S 59 86 78 W
Ameerega hahneli B	MPEG 13849	DQ502086	O	Brazil	Amazonas, Castanho, ca. 40 km S Manaus,at km 12 on road to Autazes	Grant et al., 2006	03 37 10 S 59 86 78 W
Ameerega hahneli B	OMNH 37444	DQ502087	X	Brazil	Amazonas, Castanho, ca. 40 km S Manaus,at km 12 on road to Autazes	Grant et al., 2006	03 37 10 S 59 86 78 W
Ameerega hahneli B	MPEG 13844	DQ502226	O	Brazil	Amazonas, Castanho, ca. 40 km S Manaus,at km 12 on road to Autazes	Grant et al., 2006	03 37 10 S 59 86 78 W
Ameerega hahneli B	EhahnAmazvii1b	DQ523063	O	Brazil	Amazonas	Roberts et al., 2006	
Ameerega hahneli B	EhahnAmaz1E	DQ523067	O	Brazil	Amazonas	Roberts et al., 2006	
Ameerega hahneli C	OMNH 36088	DQ502077	X	Brazil	Acre, Porto Walter	Grant et al., 2006	08 15 31 S 72 46 37 W
Ameerega hahneli C	MPEG 12420	DQ502083	O	Brazil	Acre, Porto Walter	Grant et al., 2006	08 15 31 S 72 46 37 W
Ameerega hahneli D	OMNH 36092	DQ502084	O	Brazil	Acre, Porto Walter	Grant et al., 2006	08 15 31 S 72 46 37 W
Ameerega hahneli D	EhahnPWvii1a	DQ523064	O	Brazil	Acre Porto Walter	Roberts et al., 2006	08 15 31 S 72 46 37 W
Ameerega hahneli E		AF282246	X	Bolivia	Cobija	Loetters and Vences, 2000	11 01 12 S 68 46 00 W
Ameerega hahneli E	KU 215183	DQ501991	O	Peru	Madre de Dios, Cusco Amazonico, 15 km E Puerto Maldonado, 200 m	Grant et al., 2006	11 39 00 S 70 33 35 W
Ameerega hahneli E	KU 215185	DQ501996	X	Peru	Madre de Dios, Cusco Amazonico, 15 km E Puerto Maldonado, 200 m	Grant et al., 2006	11 39 00 S 70 33 35 W
Ameerega hahneli E	KU 215184	DQ501997	O	Peru	Madre de Dios, Cusco Amazonico, 15 km E Puerto Maldonado, 200 m	Grant et al., 2006	11 39 00 S 70 33 35 W
Ameerega hahneli E	EhahnAP8iii9b	DQ523034	O	Peru	Alto Purus River Ucayali	Roberts et al., 2006	09 24 05 S 73 15 29 W
Ameerega hahneli E	EhahnAPR8iii1c	DQ523041	O	Peru	Alto Purus River Ucayali	Roberts et al., 2006	09 24 05 S 73 15 29 W
Ameerega hahneli E	EhahnAP8iii9a	DQ523081	O	Peru	Alto Purus River Ucayali	Roberts et al., 2006	09 24 05 S 73 15 29 W
Ameerega hahneli E	EhahnBocMan	DQ523027	O	Peru	Boca Manu Cuzco	Roberts et al., 2006	12 16 32 S 70 56 49 W
Ameerega hahneli E	EhahnRAmigosix	DQ523056	O	Peru	Rio Amigos Madre de Dios	Roberts et al., 2006	
Ameerega hahneli F		AF282248	X	Peru	Huanuco, Rio Llullapichis,Panguana	Loetters and Vences, 2000	09 23 02 S 75 52 57 W
Ameerega hahneli G	QCAZ13325	AY364573	X	Ecuador		Santos et al., 2003	
Ameerega hahneli H	ICN 50410	DQ502270	X	Colombia	Amazonas, Leticia, Lago Yahuarcaca	Grant et al., 2006	04 10 06 S 69 54 41 W
Ameerega hahneli H	EhahnConvviii4	DQ523032	O	Peru	Convento Tarapoto, San Martin	Roberts et al., 2006	06 15 03 S 76 18 52 W
Ameerega hahneli H	EhahnItayaiii2	DQ523033	X	Peru	Itaya River Iquitos, Loreto	Roberts et al., 2006	04 27 00 S 73 34 11 W
Ameerega hahneli H	EhahnItaya2iii	DQ523061	O	Peru	Itaya River Iquitos, Loreto	Roberts et al., 2006	04 27 00 S 73 34 11 W
Ameerega hahneli I	EhahnIvochviii	DQ523038	X	Peru	Ivochote Cuzco	Roberts et al., 2006	12 28 15 S 72 59 37 W
Ameerega hahneli J	EhahnAguamiii3	DQ523037	X	Peru	Aguamo,Muyuma Tarapoto, San Martin	Roberts et al., 2006	06 30 42 S 76 28 54 W
Ameerega hahneli K	EhahnSapoiii9d	DQ523086	X	Peru	Saposoa Tarapoto, San Martin	Roberts et al., 2006	06 46 15 S 76 56 28 W
Ameerega hahneli L		DQ523022	O	Peru	Cachiyacu Road Tarapoto, San Martin	Roberts et al., 2006	06 30 42 S 76 28 54 W
Ameerega hahneli L	EhahnTCRdi6a	DQ523026	X	Peru	Cachiyacu Road Tarapoto, San Martin	Roberts et al., 2006	06 28 39 S 76 19 21 W
Ameerega hahneli L	EhahnTCRd1	DQ523078	O	Peru	Cachiyacu Road Tarapoto, San Martin	Roberts et al., 2006	06 28 39 S 76 19 21 W
Ameerega hahneli L	EhahnChaz2B	DQ523051	O	Peru	Near Chazuta Tarapoto, San Martin	Roberts et al., 2006	06 58 00 S 76 15 00 W
Ameerega hahneli L	TSRdviii2	DQ523079	O	Peru	Road to Sisa Tarapoto, San Martin	Roberts et al., 2006	
Ameerega hahneli L	EhahnVSAiv3a	DQ523049	O	Peru	Valle San Antonio Tarapoto, San Martin	Roberts et al., 2006	
Ameerega hahneli M	EhahnRManv9a	DQ523075	X	Peru	Loreto, Iquitos Rio Manati	Roberts et al., 2006	
Ameerega trivittata A	MPEG 12504	DQ502079	X	Brazil	Acre, Porto Walter	Grant et al., 2006	08 15 31 S 72 46 37 W
Ameerega trivittata A	EtrivAmazvii1d	DQ523065	O	Brazil	Amazonas	Grant et al., 2006	
Ameerega trivittata A	MJH 3907	DQ502112	O	Brazil	Amazonas, Base 2 island in reservoir of Uatuma river, 8km NW Balbina	Grant et al., 2006	01 50 40 S 59 33 43 W
Ameerega trivittata A	OMNH 37453	DQ502148	X	Brazil	Amazonas, Castanho, ca. 40 km S Manaus, at km 12 on road to Autazes	Grant et al., 2006	03 37 10 S 59 86 78 W
Ameerega trivittata A	OMNH 37455	DQ502147	O	Brazil	Amazonas, Castanho, ca. 40 km S Manaus, at km 12 on road to Autazes	Roberts et al., 2006	03 37 10 S 59 86 78 W

Ameerega trivittata A	???????????	DQ523077	X	French Guiana	?????????????????????	Roberts et al., 2006	
Ameerega trivittata A	BPN 910	DQ502250	X	Suriname	Road to Apura	Grant et al., 2006	05 11 00 N 55 37 00 W
Ameerega trivittata B	USNM 268846	DQ502021	X	Peru	Puerto Maldonado, Explorer's Inn, 30 km (airline) SSW of Tambopata Reserve	Grant et al., 2006	12 35 60 S 69 10 60 W
Ameerega trivittata B	USNM 269052	DQ502023	O	Peru	Puerto Maldonado, Explorer's Inn, 30 km (airline) SSW of Tambopata Reserve	Grant et al., 2006	12 35 60 S 69 10 60 W
Ameerega trivittata C		AF098750	O	?	?	Summers et al., 1999	
Ameerega trivittata C	ZFMK 69880	AF124128	O	captive	?	Vences et al., 2003	
Ameerega trivittata C		DQ523068	X	Peru	Cordillera Oriental Amazonas,	Roberts et al., 2006	10 26 00 S 74 31 00 W
Ameerega trivittata C		DQ523021	O	Peru	Shilcayo Valley Tarapoto, San Martin	Roberts et al., 2006	
Ameerega trivittata C		AF128569	O	Peru,	Yurimaguas	Vences et al., 2003	05 55 05 S 76 05 40 W
Ameerega trivittata D	MPEG 12450	DQ502082	O	Brazil	Acre, Porto Walter	Grant et al., 2006	08 15 31 S 72 46 37 W
Ameerega trivittata D	MPEG 12447	DQ502219	O	Brazil	Acre, Porto Walter	Grant et al., 2006	08 15 31 S 72 46 37 W
Ameerega trivittata D	MPEG 12468	DQ502227	X	Brazil	Acre, Porto Walter	Grant et al., 2006	08 15 31 S 72 46 37 W
Ameerega trivittata D		DQ523029	O	Brazil	Acre, Porto Walter	Roberts et al., 2006	08 15 31 S 72 46 37 W
Ameerega trivittata D	ICN 50437	DQ502267	X	Colombia	Amazonas, Leticia, Km 11 (Leticia,Tarapaca)	Grant et al., 2006	04 10 06 S 69 54 41 W
Ameerega trivittata D		DQ523028	O	Peru	Alto Purus River Ucayali,	Roberts et al., 2006	09 24 05 S 73 15 29 W
Ameerega trivittata D		DQ523030	O	Peru	Chumilla San Martin,	Roberts et al., 2006	05 51 23 S 77 02 10 W
Ameerega trivittata D		DQ523050	X	Peru	Cordillera Azul San Martin,	Roberts et al., 2006	07 26 24 S 76 57 03 W
Ameerega trivittata D		DQ523046	O	Peru	Iscozazin Pasco	Roberts et al., 2006	10 11 19 S 75 09 37 W
Ameerega trivittata D		DQ523054	O	Peru	Near Bonilla Tarapoto, San Martin	Roberts et al., 2006	07 02 46 S 76 47 00 W
Ameerega trivittata D		DQ523071	O	Peru	Near Chazuta Tarapoto, San Martin	Roberts et al., 2006	06 58 00 S 76 15 00 W
Ameerega trivittata D		DQ523031	O	Peru	Rio Manati Iquitos, Loreto	Roberts et al., 2006	
Ameerega trivittata D		DQ523058	O	Peru	Road to Barranquita Tarapoto, San Martin,	Roberts et al., 2006	
Ameerega trivittata D		DQ523047	O	Peru	Santa Rosa Huanuco	Roberts et al., 2006	08 50 12 S 74 34 17 W
Ameerega trivittata D		DQ523035	O	Peru	Tahuayo River Iquitos, Loreto,	Roberts et al., 2006	04 11 13 S 73 06 16 W
Ameerega trivittata D		DQ523052	O	Peru	Tahuayo River Iquitos, Loreto,	Roberts et al., 2006	04 11 13 S 73 06 16 W
Ameerega trivittata D		DQ523066	O	Peru	Tahuayo River Iquitos, Loreto,	Roberts et al., 2006	04 11 13 S 73 06 16 W
Ameerega trivittata D	LM 739-A	U39973	O	Peru,	Huanuco, Rio Llullapichis,Panguana	Ruvinski and maxson, 1996	09 23 02 S 75 52 57 W
Ameerega trivittata E		DQ523036	X	Peru	Rio Sucusari Iquitos, Loreto	Roberts et al., 2006	03 14 26 N 72 55 42 W
Ameerega trivittata F	MJH 7483	DQ502111	X	Peru	Huanuco, Rio Llullapichis, Panguana	Grant et al., 2006	09 23 02 S 75 52 57 W
Amerega macero	LR 742	DQ502155		Peru	Madre de Dios, Parque Nacional del Manu	Grant et al., 2006	12 15 00 S 71 45 00 W
Anomaloglossus baeobatrachus A	220MC	EU201070	X	French Guiana	Saül	New	03 37 32 N 53 12 26 W
Anomaloglossus baeobatrachus A	MNHN1995-9454	AY263236	O	French Guiana	Aratai	Vences et al., 2003	05 10 00 N 54 20 00 W
Anomaloglossus baeobatrachus A	MNHN2000-0654	AY263231	O	French Guiana	Saül	Vences et al., 2003	03 37 32 N 53 12 26 W
Anomaloglossus baeobatrachus B	148mc	EU201072	X	French Guiana	Trijonction	New	02 20 00 N 54 36 00 W
Anomaloglossus baeobatrachus C	182mc	EU201071	X	French Guiana	Trijonction	New	02 20 00 N 54 36 00 W
Anomaloglossus baeobatrachus D	149AF		X	Suriname	Brownsberg	New	04 56 31 N 55 10 33 W
Anomaloglossus degranvillei A	17RB	EU201076	X	French Guiana	St Eugene	New	04 51 00 N 53 04 00 W
Anomaloglossus degranvillei B	355MC	EU201075	X	French Guiana	Lucifer	New	04 46 00 N 53 55 00 W
Anomaloglossus degranvillei C	68MC	EU201073	X	French Guiana	Monts Bakra	New	03 18 08 N 52 56 73 W
Anomaloglossus degranvillei D	125BM	EU201074	X	French Guiana	Saül	New	03 37 32 N 53 12 26 W
Anomaloglossus degranvillei D	MNHN2000-0655	AY263234	O	French Guiana	Saül	Vences et al., 2003	03 37 32 N 53 12 26 W
Anomaloglossus degranvillei E	143AF	EU201078	X	Suriname	Brownsberg	New	04 56 31 N 55 10 33 W
Anomaloglossus degranvillei F	3025T	EU201077	X	French Guiana	Mitaraka	New	02 16 00 N 54 31 00 W
Anomaloglossus degranvillei G	113MC	EU201079	X	French Guiana	Tibourou	New	04 25 00 N 52 18 00 W
Anomaloglossus degranvillei H	230MC	EU201080	X	French Guiana	Saül	New	03 37 32 N 53 12 26 W
Anomaloglossus degranvillei I	38AF	EU201081	X	French Guiana	Saül	New	03 37 32 N 53 12 26 W
Anomaloglossus degranvillei J	278	DQ502019	X	Guyana	Mereme Mountains	Grant et al., 2006	
Anomaloglossus degranvillei K	CPI 10209	DQ502257	X	Guyana	Mazaruni,Potoro, Mt. Roraima, 1075 m	Grant et al., 2006	01 49 19 N 61 52 15 W
Anomaloglossus sp. "ayanganna"	ROM39639	DQ502129		Guyana	Mt Ayanganna	Grant et al., 2006	5 23 00 N 59 59 00 W
Anomaloglossus sp. Tafelberg	UTA A55758	DQ502247		Suriname	Sipaliwini, ca. 4.0 km N of Tafelberg airstrip	Grant et al., 2006	03 47 00 N 56 09 00 W
Anomaloglossus sp.Brownsberg D	UTA A56469	DQ502249		Suriname	Brokopondo, Brownsberg Nature Park	Grant et al., 2006	04 43 00 N 56 13 00 W
Chaunus granulosus A	USNM302451	AY680261	O	Brazil	Roraima, Caracarann	Pauly et al., 2004	03 50 00 N 59 47 00 W
Chaunus granulosus A	USNM302450	DQ158457	X	Brazil	Roraima	Pramuk, 2007	03 50 00 N 59 47 00 W

Chaunus granulosus A	235mc	EF364306	X	French Guiana	Mana		Fouquet et al., 2007	05 39 00 N 53 47 00 W
Chaunus granulosus A	AMNH A139020	DQ283332	X	Guyana	Southern Rupununi Savanna, Aishalton (onKubabawau Creek), 150 m		Frost et al., 2006	02 28 31 N 59 19 16 W
Chaunus granulosus A	185AF	EU201056	X	Suriname	Brownsberg		New	04 43 00 N 56 13 00 W
Chaunus granulosus B	LM 1493	AY028483	X	Brazil	Rondonia, Porto Velho		Pramuk, 2001	08 44 38 S 64 04 59 N
Chaunus granulosus B	LM 1493	AY028496	O	Brazil	Rondonia, Porto Velho		Pramuk, 2001	08 44 38 S 64 04 59 N
Chaunus granulosus C	AF0093	DQ158458	X	Brazil	Roraima		Pramuk, 2006	03 50 00 N 59 47 00 W
Chiasmocleis hudsoni A	28bm	EU201099	X	French Guiana	Monts Bakra		New	03 18 08 N 52 56 73 W
Chiasmocleis hudsoni B	439PG	EU201100	X	French Guiana	Kotika		New	03 56 05 N 54 12 17 W
Ctenophryne geayi	21bm	EU201103	X	French Guiana	Trinité		New	04 35 00 N 53 21 00 W
Ctenophryne geayi	AMNH A166444	DQ283383	X	Guyana	Berbice River camp at ca. 18 mi (linear) SW Kwakwani		Frost et al., 2006	05 05 06 N 58 14 14 W
Dendrobates azureus	CFBH 4203	AY263250		Brazil	uncertain possibly Alto rio trombetas		Vences et al., 2003	
Dendrobates tinctorius A	1mc	EU201082	X	French Guiana	Ouanary		New	04 15 00 N 51 40 00 W
Dendrobates tinctorius B	UTA A56495	DQ502248	X	Suriname	Sipaliwini, ca. 1.0 km N of Tafelberg airstrip		Grant et al., 2006	03 47 00 N 56 09 00 W
Dendrophryniscus minutus A	98bm	EF364310	X	French Guiana	Mt Arawa		Fouquet et al., 2007	02 48 59 N 53 21 59 W
Dendrophryniscus minutus B	3035T	EU201057	X	French Guiana	Mitaraka		New	02 16 00 N 54 31 00 W
Dendrophryniscus minutus C	QCAZ13965	AF375516	X	Ecuador	?		Gluesenkamp, unpub.	
Dendrophryniscus minutus D	QCAZ 883	DQ158420	X	Ecuador	?		Pramuk, 2006	
Dendrophryniscus minutus E	MJH7095	AY843582	X	Peru	Huanuco, Rio Llullapichis, Panguana		Faivovich et al., 2005	09 23 02 S 75 52 57 W
Dendropsophus brevifrons	28mc	EF376058	X	French Guiana	Kaw		Salducci et al., 2005	04 42 00 N 52 18 00 W
Dendropsophus brevifrons	MJH 7101	AY843611	X	Peru	Huanuco, Rio Llullapichis, Panguana		Faivovich et al., 2005	09 23 02 S 75 52 57 W
Dendropsophus leucophyllatus A	Man-95231	AF308091	O	Brazil	Manaus, Amazonas		Chek et al., 2001	02 28 00 S 60 00 57 W
Dendropsophus leucophyllatus A	Man-95232	AF308092	X	Brazil	Manaus, Amazonas		Chek et al., 2001	02 28 00 S 60 00 57 W
Dendropsophus leucophyllatus A	SdN-95143	AF308087	O	Brazil	Serra do Navio, Amapà		Chek et al., 2001	00 55 05 N 52 00 10 W
Dendropsophus leucophyllatus A	SdN-95156	AF308088	X	Brazil	Serra do Navio, Amapà		Chek et al., 2001	00 55 05 N 52 00 10 W
Dendropsophus leucophyllatus A	95161	DQ393416	O	Brazil	Alter do Chão		Lougheed et al., 2006	02 32 00 S 54 58 00 W
Dendropsophus leucophyllatus A	95232	DQ393427	O	Brazil	approx. 100 km north of Manaus, Amazonas		Lougheed et al., 2006	02 28 00 S 60 00 57 W
Dendropsophus leucophyllatus A	95193	DQ393428	O	Brazil	approx. 100 km north of Manaus, Amazonas		Lougheed et al., 2006	02 28 00 S 60 00 57 W
Dendropsophus leucophyllatus A	95143	DQ393417	O	Brazil	Serra do Navio, Amapà		Lougheed et al., 2006	00 55 05 N 52 00 10 W
Dendropsophus leucophyllatus A	36mc	EF376059	X	French Guiana	Kaw		Salducci et al., 2005	04 42 00 N 52 18 00 W
Dendropsophus leucophyllatus B	R.Bran-95253	AF308097	O	Brazil	Rio Branco, Acre		Chek et al., 2001	09 58 00 S 67 48 00 W
Dendropsophus leucophyllatus B	93044	DQ393421	X	Brazil	approx. 200km west of Redenção, Para		Lougheed et al., 2006	07 40 00 S 51 22 00 W
Dendropsophus leucophyllatus B	95253	DQ393432	X	Brazil	Rio Branco, Acre		Lougheed et al., 2006	09 58 00 S 67 48 00 W
Dendropsophus leucophyllatus B	95254	DQ393433	O	Brazil	Rio Branco, Acre		Lougheed et al., 2006	09 58 00 S 67 48 00 W
Dendropsophus leucophyllatus C	AdC-95163	AF308089	X	Brazil	Alter do Chão		Chek et al., 2001	02 33 00 S 54 59 00 W
Dendropsophus leucophyllatus C	95163	DQ393419	O	Brazil	Alter do Chão		Lougheed et al., 2006	02 32 00 S 54 58 00 W
Dendropsophus leucophyllatus D	95162	DQ393422	X	Brazil	Alter do Chão		Lougheed et al., 2006	02 32 00 S 54 58 00 W
Dendropsophus leucophyllatus E	Aukre-93045	AF308085	X	Brazil	A,Ukre, Para		Chek et al., 2001	07 40 00 S 51 22 00 W
Dendropsophus leucophyllatus E	Aukre-93046	AF308086	O	Brazil	A,Ukre, Para		Chek et al., 2001	07 40 00 S 51 22 00 W
Dendropsophus leucophyllatus E	93042, 93043	DQ393418	O	Brazil	approx. 200km west of Redenção, Para		Lougheed et al., 2006	07 40 00 S 51 22 00 W
Dendropsophus leucophyllatus F	93049	DQ393420	X	Brazil	approx. 200km west of Redenção, Para		Lougheed et al., 2006	07 40 00 S 51 22 00 W
Dendropsophus leucophyllatus G	Jur-4483 INPA4483	AF308096	O	Brazil	Nova Vida, Acre		Chek et al., 2001	08 35 00 S 72 50 00 W
Dendropsophus leucophyllatus G	Obd-95176	AF308090	X	Brazil	Obidos, Pará		Chek et al., 2001	01 55 00 S 55 31 00 W
Dendropsophus leucophyllatus G	Jur-4273 INPA4273	AF308095	X	Brazil	Porongaba, Acre		Chek et al., 2001	08 41 00 S 72 48 00 W
Dendropsophus leucophyllatus G	Tab-96056	AF308094	O	Brazil	Tabatinga, Amazonas		Chek et al., 2001	04 16 00 S 69 58 00 W
Dendropsophus leucophyllatus G	4273	DQ393431	O	Brazil	Igarapé Porongaba, Acre		Lougheed et al., 2006	08 40 00 S 72 47 00 W
Dendropsophus leucophyllatus G	4483	DQ393430	O	Brazil	Nova Vida, Acre		Lougheed et al., 2006	08 22 00 S 72 49 00 W
Dendropsophus leucophyllatus G	95175	DQ393423	O	Brazil	Obidos, Pará		Lougheed et al., 2006	01 55 00 S 55 31 00 W
Dendropsophus leucophyllatus G	95176	DQ393424	O	Brazil	Obidos, Pará		Lougheed et al., 2006	01 55 00 S 55 31 00 W
Dendropsophus leucophyllatus G	95178	DQ393425	O	Brazil	Obidos, Pará		Lougheed et al., 2006	01 55 00 S 55 31 00 W
Dendropsophus leucophyllatus G	95172	DQ393426	O	Brazil	Obidos, Pará		Lougheed et al., 2006	01 55 00 S 55 31 00 W
Dendropsophus leucophyllatus G	Tab-96018	AF308093	O	Brazil	Tabatinga, Amazonas		Lougheed et al., 2006	04 16 00 S 69 58 00 W
Dendropsophus leucophyllatus G	96023	DQ393429	O	Brazil	Tabatinga, Amazonas		Lougheed et al., 2006	04 16 00 S 69 58 00 W
Dendropsophus leucophyllatus G	96034	DQ393434	O	Brazil	Tabatinga, Amazonas		Lougheed et al., 2006	04 16 00 S 69 58 00 W

Species	Voucher	GenBank		Country	Locality	Reference	Coordinates
Dendropsophus leucophyllatus G	96009, 96018	DQ393435	O	Brazil	Tabatinga, Amazonas	Lougheed et al., 2006	04 16 00 S 69 58 00 W
Dendropsophus leucophyllatus G	96019, 96020	DQ393436	O	Brazil	Tabatinga, Amazonas	Lougheed et al., 2006	04 16 00 S 69 58 00 W
Dendropsophus minutus A	114mc	EF376063	X	French Guiana	Kaw	Salducci et al., 2005	04 42 00 S 52 18 00 W
Dendropsophus minutus B	MZUSP70297	AF308112	O	Brazil	A,Ukre, Para	Chek et al 01	07 40 00 S 51 22 00 W
Dendropsophus minutus B	MZUSP70296	AF308113	X	Brazil	A,Ukre, Para	Chek et al 01	07 40 00 S 51 22 00 W
Dendropsophus minutus C	MACN 33799	AY549345	X	Argentina	Misiones, Guarani, San Vicente, Campo Anexo INTA 'Cuartel Rio Victoria	Faivovich et al., 2004	26 56 00 S 54 24 00 W
Dendropsophus nanus A	170bm	EU201104	X	French Guiana	Kaw	New	04 42 00 S 52 18 00 W
Dendropsophus nanus A	84mc	EF376063	O	French Guiana	Kaw	Salducci et al., 2005	04 42 00 S 52 18 00 W
Dendropsophus nanus B	MACN 37785	AY549346	X	Argentina	Entre Rios, Dto. Islas del Ibicuy	Faivovich et al., 2004	32 07 02 S 59 18 15 W
Dendropsophus triangulum	KU202745	AY326053		Ecuador	Napo, Misahualli, 600 m	Darst and Cannatella, 2003	01 02 00 S 77 40 13 W
Dendropsophus walfordi	MJH 129	AY843683		Brazil	?	Faivovich et al., 2005	
Elachistocleis ovalis	82mc	EU201101	X	French Guiana	Montjoly	New	04 55 00 N 52 16 00 W
Elachistocleis ovalis	AMNH A141136	DQ283405	X	Guyana	Dubulay Ranch on the Berbice River, 200ft	Frost et al 06	05 40 55 N 57 51 32 W
Eleutherodactylus chiastonotus A	101mc	EU201060	X	French Guiana	Tibourou	New	04 25 00 N 52 18 00 W
Eleutherodactylus chiastonotus B	162AF	EU201061	X	Suriname	Brownsberg	New	04 56 31 N 55 10 33 W
Eleutherodactylus marmoratus A	110bm	EU201063	X	French Guiana	Kaw	New	04 42 00 N 52 18 00 W
Eleutherodactylus marmoratus B	77mc	EU201062	X	French Guiana	Trois saut	New	02 14 00 N 52 52 00 W
Eleutherodactylus zeuctotylus A	95mc	EF376083	X	French Guiana	Tibourou	Salducci et al., 2005	04 25 00 N 52 18 00 W
Eleutherodactylus zeuctotylus B	100AF	EU201059	X	Suriname	Road to Apura	New	05 11 00 N 55 39 00 W
Engystomops petersi	QCAZ 11965	DQ337231	O	Ecuador	Napo, Cando	Ron et al., 2006	
Engystomops petersi	QCAZ 14723	DQ337232	O	Ecuador	Napo, Napo,Galeras, Ishquiñambi	Ron et al., 2006	
Engystomops petersi	QCAZ 12128	DQ337233	O	Ecuador	Orellana, Estación Científica Yasuní, Universidad Católica del Ecuador	Ron et al., 2006	00 40 00 S 76 23 00 W
Engystomops petersi A	108bm	EU201097	X	French Guiana	Trinité	New	04 35 00 N 53 21 00 W
Engystomops petersi B	QCAZ 23976	DQ337234	X	Ecuador	Sucumbíos, La Selva	Ron et al., 2006	00 00 33 N 76 35 23 W
Engystomops petersi C	QCAZ 26210	DQ337230	X	Ecuador	Pastaza, El Puyo	Ron et al., 2006	01 29 04 S 78 00 38 W
Hamptophryne boliviana A		AF215370	O	?????	?????????????????????????????????	Vences, 2000	
Hamptophryne boliviana A	104bm	EU201102	X	French Guiana	Trinité	New	04 35 00 N 53 21 00 W
Hamptophryne boliviana B	Rafael de Sa	DQ283438	X	Peru	?	Frost et al., 2006	
Hypsiboas boans A	43mc	EU201105	X	French Guiana	Kaw	New	04 42 00 N 52 18 00 W
Hypsiboas boans A	99bm	EF376055		French Guiana	Monts Bakra	Salducci et al., 2005	03 18 08 N 52 56 73 W
Hypsiboas boans A	RWM 17746	AY843610	X	Venezuela	Amazonas, Cano Agua Blanca, 3.5Km SE Neblina Camp on Rio Mawarinuma	Faivovich et al., 2005	00 49 50 N 66 09 40 W
Hypsiboas calcaratus A	131mc	EF376064	X	French Guiana	Crique margot	Salducci et al., 2005	05 28 00 N 53 57 00 W
Hypsiboas calcaratus B	NMP6V 71250	AY843613	X	Peru	Anguilla, 50 km W of Iquitos	Faivovich et al., 2005	03 43 47 S 73 49 51 W
Hypsiboas calcaratus C	WED 54086; KU 202911	AY326056	X	Ecuador	Napo, Misahualli, 600 m	Darst and Cannatella, 2003	01 02 00 S 77 40 13 W
Hypsiboas crepitans A	95bm	EU201107	X	French Guiana	Mont St Marcel	New	02 23 09 N 53 00 68 W
Hypsiboas crepitans B	CFBH2966	AY843621	X	Brazil	Alagoas, Municipio de Piranhas, Represa de Xingo	Faivovich et al., 2005	09 39 22 S 36 42 08 W
Hypsiboas fasciatus A	229mc	EU201108	X	French Guiana	Saül	New	03 37 32 N 53 12 26 W
Hypsiboas fasciatus A	AMNH-A 164081	AY549335	X	Guyana	Iwokrama, Cowfly camp	Faivovich et al., 2004	04 40 17 N 58 41 06 W
Hypsiboas fasciatus A	97AF	EU201109	X	Suriname	Road to Apura	New	05 11 00 N 55 39 00 W
Hypsiboas fasciatus B	168mc	EF376065	X	French Guiana	Guatemala	Salducci et al., 2005	05 09 00 N 52 38 00 W
Hypsiboas geographicus A	33mc	EF376054	X	French Guiana	Grand,Santi	Salducci et al., 2005	04 20 00 N 54 15 00 W
Hypsiboas geographicus A	AMNH-A141054;AMCC101481	AY843628	X	Guyana	Warniabo Creek, 4 mi (by rd) SW Dubulay Ranch house	Faivovich et al., 2005	05 37 56 N 57 53 55 W
Hypsiboas geographicus B	171bm	EU201106	X	French Guiana	Trinité	New	04 35 00 N 53 21 00 W
Hypsiboas granosus A	189bm	EU201113	X	French Guiana	Trinité	New	04 35 00 N 53 21 00 W
Hypsiboas granosus B	AMNH-A 164105	AY549336	X	Guyana	Iwokrama, Muri Scrub camp	Faivovich et al., 2004	04 40 17 N 58 41 06 W
Hypsiboas multifasciatus A	241mc	EU201111	X	French Guiana	Saül	New	03 37 32 N 53 12 26 W
Hypsiboas multifasciatus A	38mc	EF376057		French Guiana	Kaw	Salducci et al., 2005	04 42 00 N 52 18 00 W
Hypsiboas multifasciatus B	47AF	EU201110	X	French Guiana	Petit,saut	New	05 04 00 N 53 03 00 W
Hypsiboas multifasciatus B	AMNH A141040;AMCC101446	AY843648	X	Guyana	Demerara, Ceiba Station, Madewini River, ca 3 mi (linear) E Timehri Airport	Faivovich et al., 2005	06 28 24 N 58 03 16 W
Hypsiboas punctatus A	193AF	EU201112	X	French Guiana	Mana	New	05 39 00 N 53 47 00 W
Hypsiboas punctatus B	MACN 37792	AY549353	X	Argentina	Chaco, Resistencia, Camino a Isla del Cerrito	Faivovich et al., 2004	27 14 01 S 58 37 00 W
Hypsiboas raniceps A	15mc	AF467269	X	French Guiana	Crique yiyi	Salducci et al., 2002	05 29 00 N 53 09 00 W
Hypsiboas raniceps B	MACN 37795	AY843657	X	Argentina	Santa Fe, Vera, Ea. 'Las Gamas'	Faivovich et al., 2005	29 28 01 S 60 12 08 W

Species	Voucher	Accession		Country	Locality	Reference	Coordinates
Hypsiboas semilineatus	CFBH 5424	AY843779		Brazil	Rio de Janeiro, Duque de Caxias	Faivovich et al., 2005	22 47 00 S 43 15 49 W
Leptodactylus fuscus E	USNM284551	AY911279	X	Brazil	Pernambuco	Camargo et al., 2005	
Leptodactylus gr. wagneri A	81mc	EU201128	X	French Guiana	Montjoly	New	04 55 00 N 52 16 00 W
Leptodactylus gr. wagneri B	51bm	EU201125	X	French Guiana	Kaw	New	04 42 00 N 52 18 00 W
Leptodactylus gr. wagneri C	170mc	EU201126	X	French Guiana	Apatou	New	05 10 00 N 54 20 00 W
Leptodactylus gr. wagneri D	66bm	EU201127	X	French Guiana	Mt Arawa	New	02 48 59 N 53 21 59 W
Leptodactylus gr. wagneri E	215mc	EU201129	X	French Guiana	Apatou	New	05 10 00 N 54 20 00 W
Leptodactylus gr. wagneri F	78bm	EU201130	X	French Guiana	Trinité	New	04 35 00 N 53 21 00 W
Leptodactylus gr. wagneri G	183af	EU201131	X	Suriname	Road to Apura	New	05 11 00 N 55 39 00 W
Leptodactylus gr. wagneri H	155mc	EU201132	X	French Guiana	Kaw	New	04 42 00 N 52 18 00 W
Leptodactylus gr. wagneri I	129af	EU201133	X	Suriname	Brownsberg	New	04 56 31 N 55 10 33 W
Leptodactylus gr. wagneri J *Adenomera sp.*	AMNH-A 166312	AY843561	X	Guyana	Berebice River camp at ca 18 mi SWKwakwani, ca. 2 mi downriver from Kurundi River	Faivovich et al., 2005	05 05 06 N 58 14 14 W
Leptodactylus knudseni A	52AF	EU201135	X	French Guiana	Petit,saut	New	05 04 00 N 53 03 00 W
Leptodactylus knudseni B	QCAZ13077	AY947863	X	Ecuador	Francisco de Orellana, Parque Nacional Yasuní, Napo	Heyer et al., 2005	00 26 56 S 77 00 55 W
Leptodactylus leptodactyloides	MZUSP 70969	AY943236	X	Brazil	Para, Serra de Kokoinhokren	de Sà et al., 2005	07 46 00 S 51 57 00 W
Leptodactylus longirostris A	76bm	EU201119	X	French Guiana	Mont arawa	New	02 48 59 N 53 21 59 W
Leptodactylus longirostris B	199mc	EU201120	X	French Guiana	Grand santi	New	04 20 00 N 54 15 00 W
Leptodactylus longirostris B	103AF	EU201121	X	Suriname	Road to Apura	New	05 11 00 N 55 39 00 W
Leptodactylus mystaceus A	134MC	EU201117	X	French Guiana	Crique margot	New	05 28 00 N 53 57 00 W
Leptodactylus mystaceus B	115AF	EU201116	X	Suriname	Brownsberg	New	04 56 31 N 55 10 33 W
Leptodactylus mystaceus C	73AF	EU201118	X	French Guiana	St georges	New	03 52 00 N 51 48 00 W
Leptodactylus mystaceus D	167mc	EU201115	X	French Guiana	Kaw	New	04 42 00 N 52 18 00 W
Leptodactylus mystaceus E	1126BPN	EU201114	X	Guyana	Imbaimadai	New	05 44 23 N 60 17 51 W
Leptodactylus mystaceus F	MZUSP 70371	AY911286	X	Brazil	Pará, Serra de Kukoinhokren	Camargo et al., 2005	07 46 00 S 51 57 00 W
Leptodactylus ocellatus A	45mc	EU201124	X	French Guiana	Guatemala	New	05 09 00 N 52 38 00 W
Leptodactylus ocellatus A	MACN 38648	AY843688	X	Argentina	Buenos Aires, Escobar, Loma Verde,Ea. 'Los Cipreses'	Faivovich et al., 2005	35 16 56 S 58 25 18 W
Leptodactylus ocellatus B	KU 289191	DQ158417	X	Paraguay	Parque Nacional San Rafael	Pramuk, 2006	26 25 00 S 55 45 00 W
Leptodactylus ocellatus C	MZUSP 68993	AY162395	X	Brazil	SANTA CATARINA, Campeche	Nuin, 2002	27 40 17 S 48 28 33 W
Leptodactylus pentadactylus A	USNM 303466	AY947868	X	Brazil	Para, near Cachoeira do Espelho, ca. 50 km (airline) S of Altamira	Heyer et al., 2005	03 37 03 S 52 10 26 W
Leptodactylus pentadactylus A	MZUSP 70917	AY947867	O	Brazil	Pará, Serra de Kukoinhokren.	Heyer et al., 2005	07 46 00 S 51 57 00 W
Leptodactylus pentadactylus A	181mc	EU201134	X	French Guiana	Tibourou	New	04 25 00 N 52 18 00 W
Leptodactylus pentadactylus B	MZUSP 70023	AY947856	X	Brazil	Pará, Aldeia A,Ukre	Heyer et al., 2005	03 37 23 S 49 20 32 W
Leptodactylus pentadactylus B	MZUSP 70075	AY947857	O	Brazil	Pará, Rio Vermelho	Heyer et al., 2005	
Leptodactylus pentadactylus C	QCAZ 17056	AY947864	X	Ecuador	Esmeraldas, Alto Tambo.	Heyer et al., 2005	00 54 05 N 78 32 39 W
Leptodactylus pentadactylus C	QCAZ 19859	AY947865	O	Ecuador	Esmeraldas, Bosque Protector La Perla	Heyer et al., 2005	00 00 26 S 78 23 02 W
Leptodactylus pentadactylus D	C13095; MVZ 233238	AY326017	X	Costa Rica	Limon, Rio Penitencia, 2 mi N Tortuguero	Darst and Cannatella, 2003	10 35 31 N 83 31 40 W
Leptodactylus pentadactylus D	USNM 534219	AY947862	O	Honduras	Colon, Quebrada Machin	Heyer et al., 2005	15 33 18 N 85 42 45 W
Leptodactylus pentadactylus D	USNM 347153	AY943238	O	Panama	Bocas del Toro, Isla Popa	Heyer et al., 2005	09 09 09 N 82 07 57 W
Leptodactylus pentadactylus D	USNM 298079	AY947866	O	Panama	Bocas del Toro, Isla Popa	Heyer et al., 2005	09 09 09 N 82 07 57 W
Leptodactylus rhodomystax A	213mc	EU201122	X	French Guiana	Montagne des singes	New	05 04 00 N 52 43 00 W
Leptodactylus rhodomystax B	1248BPN	EU201123	X	Guyana	Imbaimadai	New	05 44 23 N 60 17 51 W
Leptodactylus rhodomystax C	MZUSP 70375	AY947855	X	Brazil	Pará, Serra de Kukoinhokren.	Heyer et al., 2005	07 46 00 S 51 57 00 W
Leptodactylusfuscus A	MZUSP67073	AY911264	X	Brazil	Roraima, Caracaranã, near Normandia	Camargo et al., 2005	03 50 00 N 59 47 00 W
Leptodactylusfuscus A	USNM291363	AY911273	X	French Guiana	Cayenne, Sinnamary	Camargo et al., 2005	05 23 00 N 52 57 00 W
Leptodactylusfuscus A	USNM497739	AY911284	O	Guyana	East Berbice, Region 10 cty.	Camargo et al., 2005	06 17 26 N 57 51 34 W
Leptodactylusfuscus A	AMNH A139088	DQ283404	X	Guyana	Southern Rupununi Savanna, Aishalton (onKubabawau Creek), 150 m	Frost et al., 2006	02 28 31 N 59 19 16 W
Leptodactylusfuscus B	USNM306189	AY911269	X	Panamá	Tocumen, Panamá City	Camargo et al., 2005	09 02 40 N 79 22 57 W
Leptodactylusfuscus C	USNM306067	AY911265	O	Tobago	Saint Paul, Roxborough	Camargo et al., 2005	11 15 00 N 60 35 00 W
Leptodactylusfuscus C	USNM306149	AY911276	O	Trinidad	Saint George, Arima,	Camargo et al., 2005	10 38 03 N 61 16 49 W
Leptodactylusfuscus C	USNM306123	AY911270	O	Trinidad	Manzanilla Mayaro Road, Nariva	Camargo et al., 2005	10 22 24 N 61 09 28 W
Leptodactylusfuscus C	USNM287012	AY911272	X	Trinidad	Saint Patrick, Icacos Point	Camargo et al., 2005	10 07 22 N 61 40 47 W
Leptodactylusfuscus D	MZUSP67039	AY911277	O	Brazil	Roraima, Bôa Vista	Camargo et al., 2005	02 44 14 N 60 42 40 W

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Species	Voucher	Accession		Country	Locality	Reference	Coordinates
Leptodactylusfuscus D	MZUSP76019	AY911278	X	Brazil	Roraima, Igarapé Cocal	Camargo et al., 2005	03 45 00 N 61 44 00 W
Leptodactylusfuscus D		AY263226	O	Venezuela	Canaima	Vences et al., 2003	06 13 58 N 62 50 59 W
Leptodactylusfuscus E	FML04789	AY911274	X	Argentina	Salta, Embarcación	Camargo et al., 2005	23 12 48 S 64 08 27 W
Leptodactylusfuscus E	USNMFS174020	AY911267	X	Bolivia	La Paz, Palos Blancos	Camargo et al., 2005	15 34 00 S 67 16 00 W
Leptodactylusfuscus F	USNM303149	AY911266	O	Brazil	São Paulo, Luiz Antonio	Camargo et al., 2005	
Leptodactylusfuscus F	USNM303154	AY911280	O	Brazil	São Paulo, Luiz Antonio	Camargo et al., 2005	
Leptodactylusfuscus F	USNM303155	AY911281	O	Brazil	São Paulo, Luiz Antonio	Camargo et al., 2005	
Leptodactylusfuscus F	USNM303156	AY911282	O	Brazil	São Paulo, Luiz Antonio	Camargo et al., 2005	
Leptodactylusfuscus F	USNM303157	AY911283	X	Brazil	São Paulo, Luiz Antonio	Camargo et al., 2005	
Leptodactylusfuscus G	FML04788	AY911271	X	Argentina	Salta, Joaquín V. González	Camargo et al., 2005	24 48 33 S 65 21 47 W
Leptodactylusfuscus H	CBF02908	AY911275	X	Bolivia	Beni Biosphere Reserve	Camargo et al., 2005	13 24 01 N 64 33 20 W
Leptodactylusfuscus I	MZUSP66954	AY911268	X	Brazil	Pará, Serra de Kukoinhoken, Kenpore	Camargo et al., 2005	07 46 00 S 51 57 00 W
Lithobates palmipes A	KU 202896	AY779211	X	Ecuador	Napo, Misahualli, 600 m	Hillis and Wilcox, 2005	01 02 00 N 77 40 13 W
Lithobates palmipes A	10mc	AF467266;AF467265	X	French Guiana	Trois saut	Salducci et al., 2004	02 14 00 N 52 52 00 W
Lithobates palmipes A	AMNH A166454	DQ283384	X	Guyana	Magdalen's Creek camp, 300 yds NW bank of Konawaruk River ca. 25 mi (linear) WSW Mabura Hill, 400 ft	Frost et al., 2006	05 13 70 N 59 02 43 W
Lithobates palmipes B	AMNH A-118801	AY779210	X	Venezuela	Amazonas, Neblina Base Camp on Río Mawarinuma	Hillis and Wilcox, 2005	00 49 50 N 66 09 40 W
Lithodytes lineatus A	55mc	EU201136	X	French Guiana	Grand,Santi	New	04 20 00 N 54 15 00 W
Lithodytes lineatus A	AMNH-A 166426	AY843690	X	Guyana	Berebice River camp at ca 18 mi (linear) SW	Faivovich et al., 2005	05 05 06 N 58 14 14 W
Lithodytes lineatus B	N. Basso; USP 968438	AY326012	X	Brazil	Mato grosso, Apiacas	Darst and Cannatella, 2003	09 39 09 S 57 23 36 W
Lithodytes lineatus B	MZUSP 80874	AY943241	O	Brazil	Mato grosso, Apiacas	de Sà et al., 2005	09 39 09 S 57 23 36 W
Lithodytes lineatus C	LM 269	U39988	O	Peru	?	Ruvinski and maxson, 1996	
Osteocephalus cabrerai	JPC 13178; LSUMZ H-13720	AY843705	X	Brazil	Acre, Porto Walter	Faivovich et al., 2005	08 15 31 S 72 46 37 W
Osteocephalus cabrerai	14mc	AF467267	X	French Guiana	Kaw	Salducci et al., 2004	04 42 00 N 52 18 00 W
Osteocephalus leprieurii A	141mc	EF376066	X	French Guiana	Crique margot	Salducci et al., 2005	05 28 00 N 53 57 00 W
Osteocephalus leprieurii B	AMNH-A 1312546	AY549361	X	Venezuela	Amazonas, Neblina Base Camp on Rio Mawarinuma (=Rio Baria), 140 M	Faivovich et al., 2004	00 49 50 N 66 09 40 W
Osteocephalus leprieurii B	AMNH A-131254	AY843707	O	Venezuela	Amazonas, Neblina Base Camp on Rio Mawarinuma (=Rio Baria), 140 M	Faivovich et al., 2005	00 49 50 N 66 09 40 W
Osteocephalus taurinus A	214mc	EF376067	X	French Guiana	Saül	Salducci et al., 2005	03 37 32 N 53 12 26 W
Osteocephalus taurinus B	AMNH-A 131245	AY843709	X	Venezuela	Amazonas, Neblina Base Camp on Rio Mawarinuma (=Rio Baria), 140 M	Faivovich et al., 2005	00 49 50 N 66 09 40 W
Osteocephalus taurinus C	WED 55452; KU 205406	AY326041	X	Peru	Madre de Dios, Cusco Amazonico	Darst and Cannatella, 2003	11 39 00 S 70 33 35 W
Phyllomedusa hypochondrialis	49mc	EF376079	X	French Guiana	Grand,Santi	Salducci et al., 2005	04 20 00 N 54 15 00 W
Phyllomedusa hypochondrialis	MNH-A 141109; AMCC 101463	AY843724	X	Guyana	Dubulay Ranch on the Berbice River, 200ft	Faivovich et al., 2005	05 40 55 N 57 51 32 W
Phyllomedusa hypochondrialis	109AF	EU201085	X	Suriname	Brownsberg	New	04 56 31 N 55 10 33 W
Phyllomedusa tomopterna A	53mc	EF376077	X	French Guiana	Kaw	Salducci et al., 2005	04 42 00 N 52 18 00 W
Phyllomedusa tomopterna B	181AF	EU201086	X	Suriname	Brownsberg	New	04 56 31 N 55 10 33 W
Phyllomedusa tomopterna C	WED 55380; KU 205428	AY326045	X	Peru	Madre de Dios, Cusco Amazonico	Darst and Cannatella, 2003	11 39 00 S 70 33 35 W
Phyllomedusa tomopterna D	MJH 7076	AY843728	X	Peru	Huanuco, Rio Llullapichis, Panguana	Faivovich et al., 2005	09 23 02 S 75 52 57 W
Phyllomedusa vaillanti	84bm	EU201087	X	French Guiana	Petit,saut	New	05 04 00 N 53 03 00 W
Phyllomedusa vaillanti	AMNH-A 1662888	AY549363	X	Guyana	Berbice River camp at ca.18 mi (linear)SW Kwakwan	Faivovich et al., 2004	05 05 06 N 58 14 14 W
Pipa pipa A	11mc	EU201058	X	French Guiana	Guatemala	New	05 09 00 N 52 38 00 W
Pipa pipa B	KU 205801	AY581621	X	Peru	Madre de Dios, Cusco Amazonico 15 km E of Puerto Maldonado	Evans et al., 2004	12 34 48 S 69 03 51 W
Pipa pipa C	USNM 546385	DQ283053	X	Venezuela	Amazonas, Depto. Rio Negro, Neblina Base Camp on the Rio Baria, 140 m	Frost et al., 2006	00 49 50 N 66 09 40 W
Ranitomeya amazonica	DamaAema	AF482785		Peru	Almendras, Loreto, Peru	Symula et al., 2003	03 48 00 S 73 25 00 W
Ranitomeya variabilis	DvTY26b	AF412492		Peru	26 km NE Tarapoto, San Martin,	Summers et al., 2001	06 21 37 S 76 24 45 W
Ranitomeya ventrimaculata	MNHN2000-0659	AY263248	O	French Guiana	Nouragues	Vences et al., 2003	04 05 00 N 52 41 00 W
Ranitomeya ventrimaculata A	105mc	EU201084	X	French Guiana	Tibourou	New	04 25 00 N 52 18 00 W
Ranitomeya ventrimaculata B	75bm	EU201083	X	French Guiana	Pic coudreau	New	03 18 02 N 52 56 77 W
Ranitomeya ventrimaculata B	BPN737	DQ163076	O	French Guiana	Kaw	Noonan and Wray, 2006	04 42 00 N 52 18 00 W
Ranitomeya ventrimaculata B	BPN741	DQ163077	O	French Guiana	Maripa	Noonan and Wray, 2006	03 48 52 N 51 53 06 W
Ranitomeya ventrimaculata B	BPN742	DQ163078	O	French Guiana	Maripa	Noonan and Wray, 2006	03 48 52 N 51 53 06 W

Ranitomeya ventrimaculata B	BPN744	DQ163080	O	French Guiana	Maripa	Noonan and Wray, 2006	03 48 52 N 51 53 06 W
Ranitomeya ventrimaculata B	BPN664	DQ163075	O	French Guiana	Pic Matecho	Noonan and Wray, 2006	03 45 00 N 53 02 00 W
Ranitomeya ventrimaculata B	BPN762	DQ163081	O	French Guiana	Saül	Noonan and Wray, 2006	03 37 32 N 53 12 26 W
Ranitomeya ventrimaculata C	JDL 24489	DQ502266	X	Colombia	Amazonas,Leticia,Km11(Leticia,Tarapaca)	Grant et al., 2006	04 10 06 S 69 54 41 W
Ranitomeya ventrimaculata D	OMNH 37440	DQ502232	O	Brazil	Amazonas, Castanho, ca. 40 km S Manaus,at km 12 on road to Autazes	Grant et al., 2006	03 37 10 S 59 86 78 W
Ranitomeya ventrimaculata D	DvenBraz1	AF482797	X	Brazil	Porto Walter, Acre, Brazil	Symula et al., 2003	08 15 31 S 72 46 37 W
Ranitomeya ventrimaculata E	OMNH 36666	DQ502071	X	Brazil	Amazonas, Rio Ituxi, Scheffer Madeireira	Grant et al., 2006	08 28 45 S 65 42 59 W
Ranitomeya ventrimaculata E	OMNH 36667	DQ502072	O	Brazil	Amazonas, Rio Ituxi, Scheffer Madeireira	Grant et al., 2006	08 28 45 S 65 42 59 W
Ranitomeya ventrimaculata E	LSUMZ H-3092	DQ163079	O	Brazil	Rio Ituxi, Amazonas	Noonan and Wray, 2006	08 28 45 S 65 42 59 W
Ranitomeya ventrimaculata F	?	AF128619	O	Ecuador	Pompeya	Clough and Summers, 2000	00 00 03 N 76 36 28 W
Ranitomeya ventrimaculata F	OMNH 34091	DQ502069	O	Ecuador	Sucumbios, Estacion Universidad Catolica near Reserva Faunistica Cuyabeno	Grant et al., 2006	00 00 00 S 76 10 00 W
Ranitomeya ventrimaculata F	QCAZ16566	AY364570	O	Ecuador	?	Santos et al., 2003	
Ranitomeya ventrimaculata F	DvenEcuador	AF482795	X	Ecuador	Pompeya, Sucumbios	Symula et al., 2003	00 00 03 N 76 36 28 W
Ranitomeya ventrimaculata G	DvnNBon2	AF412494	X	Peru	Bonilla, San Martin, Peru	Symula et al., 2003	06 12 36 S 76 16 20 W
Ranitomeya ventrimaculata H	DvenNAPO	AF482796	X	Peru	N. Bank Napo R., Loreto	Symula et al., 2003	
Ranitomeya ventrimaculata I	Dvenorama	AF482791	X	Peru	Allpahuayo, Loreto, Peru	Symula et al., 2003	03 52 52 S 73 26 02 W
Ranitomeya ventrimaculata J	OMNH 36062	DQ502233	O	Brazil	Acre, Porto Walter	Grant et al., 2006	08 15 31 S 72 46 37 W
Ranitomeya ventrimaculata J	MPEG 12394	DQ502070	X	Brazil	Acre, Porto Walter	Grant et al., 2006	08 15 31 S 72 46 37 W
Ranitomeya ventrimaculata K	DvnNBon1	AF412493	O	Peru	Bonilla, San Martin, Peru	Symula et al., 2003	07 02 46 S 76 47 00 W
Ranitomeya ventrimaculata L	DvenITYB8a2	AF482799	O	Peru	Nauta Road Iquitos, Loreto	Symula et al., 2003	04 34 14 S 73 46 00 W
Rhaebo guttatus A	144mc	EF364307	X	French Guiana	Crique margot	Fouquet et al., 2007	05 28 00 N 53 57 00 W
Rhaebo guttatus A	AMNH A141058	DQ283375	X	Guyana	Dubulay Ranch on the Berbice River, 200ft	Frost et al., 2006	05 40 55 N 57 51 32 W
Rhaebo guttatus B	LSUMZ 17418	DQ158459	X	Brazil	Rondonia	Pramuk, 2006	
Rhinella castaneotica	LSUMZ 17429	DQ158440		Brazil	Para, 100 km S Santarem	Pramuk, 2006	03 09 00 S 54 50 00 W
Rhinella cf.margaritifera F	QCAZ 13896	DQ158471	X	Ecuador	Cañar, Manta Real	Pramuk, 2006	02 30 44 S 79 04 56 W
Rhinella cf.margaritifera F	QCAZ 11597	DQ158472	O	Ecuador	Prov. Esmeraldas, Bosque Protector, 30km from San Lorenzo by way of Ibarra	Pramuk, 2006	01 16 47 N 78 42 29 W
Rhinella cf.margaritifera G	QCAZ 10601	DQ158470	X	Ecuador	Francisco de Orellana, Parque Nacional Yasuní, Napo	Pramuk, 2006	00 26 56 S 77 00 55 W
Rhinella cf.margaritifera I	USNM 268828	DQ158490	X	Peru	Madre de Dios	Pramuk, 2006	11 39 00 S 70 33 35 W
Rhinella cf.margaritifera J	KU 215145	DQ158491	X	Peru	Madre de Dios	Pramuk, 2006	11 39 00 S 70 33 35 W
Rhinella dapsilis	QCAZ 3509	DQ158448		Ecuador	Pichincha, Bosque Protector La Perla, 5 km E La Concordia	Pramuk, 2006	00 00 01 S 79 22 59 W
Rhinella margaritifera A	204mc	EF364295	X	French Guiana	Saül	Fouquet et al., 2007	03 37 32 N 53 12 26 W
Rhinella margaritifera A 24 add.			O	French Guiana		Fouquet et al., 2007	
Rhinella margaritifera B	143PG	EF364302	O	French Guiana	Kaw	Fouquet et al., 2007	04 42 00 N 52 18 00 W
Rhinella margaritifera B	144PG	EF364302	X	French Guiana	Kaw	Fouquet et al., 2009	04 42 00 N 52 18 00 W
Rhinella margaritifera C	157mc	EF364303	O	French Guiana	Tri jonction	Fouquet et al., 2007	02 20 00 N 54 36 00 W
Rhinella margaritifera C	156mc	EF364303	X	French Guiana	Tri jonction	Fouquet et al., 2011	02 20 00 N 54 36 00 W
Rhinella margaritifera D	5mc	EF364304	X	French Guiana	Cisame	Fouquet et al., 2007	04 11 00 N 52 22 00 W
Rhinella margaritifera D 4 additional			O	French Guiana		Fouquet et al., 2007	
Rhinella margaritifera E	131bm	EF364287	X	French Guiana	Mataroni	Fouquet et al., 2015	04 12 00 N 52 10 00 W
Rhinella margaritifera E 17 add.			O	French Guiana		Fouquet et al., 2007	
Rhinella margaritifera G	AGG172 (QCAZ)	AF375514	O	Ecuador	Volcan Sumaco, Provincia Napo	Gluesenkamp, unpub.	00 27 51 S 77 35 30 W
Rhinella margaritifera H	ZUEC (DCC 3393)	AY680262	X	Brazil	Rio de Janeiro, Mage´, Campo de Escouteiras, Santo Aleixo	Pauly et al., 2004	22 33 54 S 43 04 00 W
Scinax boesemani A	147mc	EF217501	X	French Guiana	Guatemala	Fouquet et al., 2007	05 09 00 N 52 38 00 W
Scinax boesemani A 7 additional			O	French Guiana		Fouquet et al., 2007	
Scinax boesemani B	932BPN	EU201090	X	Suriname	Road to Apura	New	05 11 00 N 55 37 00 W
Scinax boesemani C	1022BPN	EU201089	X	Suriname	Sipilawini	New	02 02 00 N 56 07 00 W
Scinax boesemani D	198mc	EF217503	X	French Guiana	Grand Santi	Fouquet et al., 2007	04 20 00 N 54 15 00 W
Scinax boesemani D	39mc	EF376072	O	French Guiana	Grand Santi	Salducci et al., 2005	04 20 00 N 54 15 00 W
Scinax boesemani E	1169BPN	EU201088	X	Guyana	Mazaruni,Potaro Imbaimadai	New	05 44 23 N 60 17 51 W
Scinax cf. cruentommus A	8mc	AF467263	X	French Guiana	Kaw	Salducci et al., 2004	04 42 00 N 52 18 00 W
Scinax cf. cruentommus A 20 add.			O	French Guiana		Fouquet et al., 2007	
Scinax cf. cruentommus B	324mc	EU201093	X	French Guiana	Antecum,Pata	New	03 19 00 N 54 04 00 W

Species	Voucher	GenBank		Country	Locality	Reference	Coordinates
Scinax fuscovarius	MACN 38647	AY843758	X	Argentina	Misiones, Guarani, San Vicente, Campo Anexo INTA 'Cuartel Rio Victoria	Faivovich et al., 2005	26 56 00 S 54 24 00 W
Scinax nasicus	MACN 38650	AY843759	X	Argentina	Buenos Aires, Baradero, Estancia 'El Retonio'	Faivovich et al., 2005	33 48 44 S 59 30 25 W
Scinax nebulosus B	394BPN	EU201094	X	Brazil	State of Pernambuco, Timbaúba, Engenho Água Azul	New	06 38 05 S 37 54 02 W
Scinax nebulosus A	24mc	AF467262	X	French Guiana	Régina,St Georges Road	Salducci et al., 2004	04 03 00 N 52 01 00 W
Scinax nebulosus A 2 additional			O	French Guiana		Fouquet et al., 2007	
Scinax nebulosus D	AA900	EU201095	X	Guyana	Barima,Waini Mabaruma	New	08 12 00 N 59 46 48 W
Scinax nebulosus C	CE581	EU201096	X	Brazil	Ceará State, Ibiapina, Sítio Pimentas, Vivenda Santa Rosa	New	03 55 00 N 40 53 00 W
Scinax ruber A	74mc	EF217478	X	French Guiana	Montagne d'argent	Fouquet et al., 2007	04 23 00 N 51 42 00 W
Scinax ruber A 15 additional			O	French Guiana		Fouquet et al., 2007	
Scinax ruber B	151mc	EF217481	X	French Guiana	Guatemala	Fouquet et al., 2007	05 09 00 N 52 38 00 W
Scinax ruber B 10 additional			O	French Guiana		Fouquet et al., 2007	
Scinax ruber C	WED 56265; KU 207622	AY326034	X	Peru	Madre de Dios, Cusco Amazonico	Darst and cannatella, 2003	11 39 00 S 70 33 35 W
Scinax ruber D	40mc	EF376073	O	French Guiana		Fouquet et al., 2007	
Scinax ruber D	178mc	EF376073	X	French Guiana	Ouanary	Salducci et al., 2005	04 15 00 N 51 40 00 W
Scinax ruber D	164AF	EU201092	X	Suriname	Brownsberg	New	04 56 31 N 55 10 33 W
Scinax ruber D 3 additional			O	French Guiana		Fouquet et al., 2007	
Scinax ruber E	IWK 109	AY549365	X	Guyana	Iwokrama, Muri Scrub camp	Faivovich et al., 2004	04 40 17 N 58 41 06 W
Scinax ruber F	76mc	EF217490	X	French Guiana	Mont Ravel	Fouquet et al., 2007	04 54 42 N 52 15 39 W
Scinax ruber F 9 additional			O	French Guiana		Fouquet et al., 2007	
Scinax ruber G	360mc	EU201091	X	French Guiana	Mont Ravel	New	04 54 42 N 52 15 39 W
Scinax ruber H	QCAZ25275	EF217487	X	Ecuador	AUCA14road,parroquia Dayuma,canton coca,Orellana	Fouquet et al., 2007	01 04 03 S 77 36 55 W
Scinax ruber H 3 additional			O	Ecuador		Fouquet et al., 2007	
Scinax x-signatus	144bm	EF217479	X	French Guiana	Kaw	Fouquet et al., 2007	04 42 00 N 52 18 00 W
Sphaenorhynchus lacteus	85mc	EF217515	X	French Guiana	Kaw	Fouquet et al., 2007	04 42 00 N 52 18 00 W
Sphaenorhynchus lacteus	USNM 268930	AY549367	X	Peru	Madre de Dios, Tambopata Reserve	Faivovich et al., 2004	14 13 25 S 69 10 36 W
Trachycephalus hadroceps	MNHN 2001.0814	AY843717		French Guiana	Kaw	Faivovich et al., 2005	04 42 00 N 52 18 00 W
Trachycephalus resinifictrix	AMNH-A 131201; AMCC 101463	AY843719		Venezuela	Amazonas, Neblina Base Camp on Rio Mawarinuma, 140 m	Faivovich et al., 2005	00 49 50 N 66 09 40 W
Trachycephalus venulosus A	163mc	EF376069	X	French Guiana	Guatemala	Salducci et al., 2005	05 09 00 N 52 38 00 W
Trachycephalus venulosus A	AMNH-A 1411427	AY549362	X	Guyana	Dubulay Ranch on the Berbice River, 200ft	Faivovich et al., 2004	05 40 55 N 57 51 32 W
Trachycephalus venulosus B	DCC 3069; TNHC 62490	AY326048	X	Ecuador	?	Darst and cannatella, 2003	
Trachycephalus venulosus C	?	AY364350	O	?	?	Biju and Bossuyt, 2003	
Trachycephalus venulosus C	VUB 0987	AY364371	X	?	?	Biju and Bossuyt, 2003	

Table 4.1: Morphometric measurements. Abbreviations are explained in the text. Means and standard deviations (sd) are presented my lineages and sexes. From the "/SVL" line the following measurements are divided through SVL (snout-vent length).

	R. margaritifera A				R. martyi nov. sp .C				R. lescurei nov. sp. D				R. sp. E			
	Males (n=18)	sd	Females (n=9)	sd	Males (n=3)	sd	Females (n=4)	sd	Males (n=7)	sd	Females (n=2)	sd	Males (n=18)	sd	Females (n=5)	sd
SVL	**46.91**	5.861	**59.42**	10.115	**52.33**	4.924	**62.85**	3.131	**34.57**	4.359	**43.70**	0.849	**31.04**	2.282	**34.77**	2.835
ESD	5.67	0.783	7.12	1.341	6.93	0.473	7.71	0.397	5.15	0.486	6.00	0.141	4.51	0.341	5.01	0.442
FML	19.34	3.636	24.17	4.059	20.63	2.122	26.53	1.212	14.00	1.587	17.90	0.424	12.39	1.340	14.05	1.411
FTL	11.15	1.810	14.61	2.312	12.50	1.300	15.30	0.560	7.30	0.931	9.65	0.354	6.78	1.037	7.22	1.244
HL	15.80	2.297	20.53	3.796	17.97	1.447	21.93	0.650	11.99	1.308	15.15	0.071	10.25	0.685	11.80	1.059
HW	19.34	3.072	25.41	5.057	22.43	2.214	28.15	0.947	13.24	1.674	15.95	0.212	11.59	1.127	13.00	1.544
TIBL	19.74	2.729	23.51	3.800	21.30	2.252	25.43	0.903	14.07	1.620	18.45	0.636	12.07	1.189	13.00	1.241
IND	2.47	0.391	2.95	0.592	3.17	0.321	3.55	0.238	1.92	0.400	2.05	0.212	1.86	0.222	1.95	0.235
UEW	3.61	0.488	4.00	0.610	4.43	0.551	4.25	0.545	3.37	0.538	3.53	0.530	2.47	0.246	2.91	0.301
IOD	6.86	0.996	8.30	2.050	7.37	0.351	7.70	2.708	4.64	0.492	5.90	0.141	4.36	0.480	5.13	0.428
EN	3.96	0.538	5.12	1.021	4.57	0.231	5.13	0.330	3.24	0.435	4.23	0.106	3.14	0.262	3.57	0.418
ED	6.71	0.758	7.72	1.269	7.30	0.872	8.25	0.265	5.19	0.606	6.30	0.141	4.48	0.398	5.18	0.319
ETD	0.82	0.253	1.13	0.187	0.93	0.351	1.05	0.387	0.69	0.219	0.90	0.424	0.41	0.119	0.60	0.255
FL1	5.27	1.104	7.33	1.475	6.00	0.100	8.63	0.718	3.94	0.508	4.90	0.707	3.07	0.417	3.54	0.373
FL3	12.46	1.875	15.55	2.668	13.60	0.854	16.83	1.001	8.41	1.024	10.93	0.389	7.52	0.858	8.46	1.163
TL4	17.13	2.714	21.31	3.788	19.13	2.055	22.28	0.780	11.50	1.356	14.90	0.566	10.85	1.488	11.80	1.554
TD	3.93	0.602	4.94	1.034	4.33	1.060	4.93	0.465	2.67	0.702	3.15	0.212	2.28	0.384	2.50	0.321
ML	14.20	2.003	18.46	3.314	16.07	1.429	19.93	0.695	9.89	1.090	12.90	0.141	8.80	0.796	10.00	0.836
SOCH	8.83	1.141	11.74	2.173	9.20	1.058	11.50	0.346	6.38	0.794	7.85	0.071	5.27	0.403	6.05	0.517
STCD	17.22	2.380	24.08	4.114	17.70	1.229	23.53	1.578	12.41	1.286	15.68	0.530	11.02	0.928	12.43	1.180
STCH	9.89	1.797	16.08	4.343	9.83	1.002	14.63	1.613	6.03	0.574	7.83	0.460	5.26	0.325	5.94	0.716
/SVL																
ESD	0.12	0.009	0.12	0.010	0.13	0.006	0.12	0.006	0.15	0.007	0.14	0.006	0.15	0.008	0.14	0.006
FML	0.41	0.042	0.41	0.018	0.39	0.008	0.42	0.008	0.41	0.018	0.41	0.018	0.40	0.022	0.40	0.022
FTL	0.24	0.014	0.25	0.037	0.24	0.008	0.24	0.011	0.21	0.006	0.22	0.004	0.22	0.021	0.21	0.020
HL	0.34	0.013	0.34	0.017	0.34	0.008	0.35	0.014	0.35	0.008	0.35	0.008	0.33	0.013	0.34	0.008
HW	0.41	0.019	0.43	0.024	0.43	0.007	0.45	0.018	0.38	0.010	0.37	0.012	0.37	0.017	0.37	0.017
TIBL	0.42	0.012	0.40	0.007	0.41	0.013	0.40	0.010	0.41	0.012	0.42	0.006	0.39	0.018	0.37	0.009
IND	0.05	0.004	0.05	0.006	0.06	0.003	0.06	0.005	0.06	0.006	0.05	0.004	0.06	0.005	0.06	0.003
UEW	0.08	0.010	0.07	0.008	0.08	0.008	0.07	0.008	0.10	0.005	0.08	0.011	0.08	0.009	0.08	0.010
IOD	0.15	0.008	0.14	0.020	0.14	0.007	0.12	0.046	0.13	0.006	0.14	0.001	0.14	0.008	0.15	0.005
EN	0.08	0.006	0.09	0.006	0.09	0.011	0.08	0.006	0.09	0.003	0.10	0.001	0.10	0.008	0.10	0.006
ED	0.14	0.010	0.13	0.008	0.14	0.005	0.13	0.005	0.15	0.004	0.14	0.006	0.14	0.009	0.15	0.013
ETD	0.02	0.005	0.02	0.003	0.02	0.005	0.02	0.006	0.02	0.005	0.02	0.009	0.01	0.004	0.02	0.006
FL1	0.11	0.012	0.12	0.010	0.12	0.010	0.14	0.013	0.10	0.043	0.11	0.014	0.10	0.011	0.10	0.004
FL3	0.27	0.015	0.26	0.016	0.26	0.016	0.27	0.018	0.24	0.006	0.25	0.004	0.24	0.018	0.24	0.022
TL4	0.36	0.019	0.36	0.011	0.37	0.026	0.35	0.012	0.33	0.011	0.34	0.006	0.35	0.028	0.34	0.024
TD	0.08	0.008	0.08	0.009	0.08	0.013	0.08	0.010	0.08	0.014	0.07	0.003	0.07	0.010	0.07	0.011
ML	0.30	0.012	0.31	0.016	0.31	0.002	0.32	0.009	0.29	0.009	0.30	0.009	0.28	0.013	0.29	0.006
SOCH	0.19	0.008	0.20	0.011	0.18	0.009	0.18	0.008	0.18	0.005	0.18	0.002	0.17	0.010	0.17	0.008
STCD	0.37	0.019	0.41	0.025	0.34	0.015	0.37	0.019	0.36	0.013	0.36	0.019	0.36	0.016	0.36	0.008
STCH	0.21	0.017	0.27	0.049	0.19	0.009	0.23	0.023	0.18	0.008	0.18	0.014	0.17	0.008	0.17	0.009

Table 4.2: Acoustic measurements. Means followed by sampling size (n) and standard deviation (sd) are presented.

	R. margaritifera (clade A)	*R. martyi* (clade C)	*R. lescurei* (clade D)	*Rhinella* sp. (clade E)	remarks
calls/minute	69	81	1 to 10	90	too few data for D
	n = 2; sd = 4.24	n = 2; sd = 21.21	/	n = 2; sd = 0	
call duration (ms)	287.975	295.125	30 ms / pulse-group	273	
	n = 4; sd = 45.40	n = 4; sd = 13.09	n = 10; sd = 0	n = 4; sd = 9.69	
peak frequency/pulse group	1.265	1.169	1.161	1.407	increasing slightly within each call for A,C,E
	n = 27; sd = 0.035	n = 24; sd = 0.04	n = 7; sd = 0.015	n = 24; sd = 0.037	
pulse-groups/call	6,75	6	480 / min	6	
	n = 4; sd = 0.957	n = 4; sd = 0	/	n = 4; sd = 0	
pulses/pulse-group	2 (3.25 last one)	2 (4.75 last one)	4.83	2 (4.5 last one)	last pulse group with more pulses for representatives of clades A,C,E
	n = 23; sd = 0 (n = 4; sd = 0.5)	n = 20; sd = 0 (n = 4; sd = 0.96)	n = 7; sd = 0.787	n = 20; sd = 0 (n = 4; sd = 0.577)	
pulse duration (ms)	8.44	9.55	3.45	8.54	
	n = 24; sd = 0.726	n = 24; sd = 1.179	n = 6; sd = 0.164	n = 24; sd = 1.184	
inter pulse-groups duration (ms)	25.94	25.56	97.2	28.85	decreasing by half within each call for representatives of clades A,C,E
	n = 23; sd = 6.868	n = 20; sd = 3.583	n = 5; sd = 17.754	n = 20; sd = 3.911	

Text S5.1: Taxonomic and distributional considerations

Preliminary results and previous studies (Fouquet et al., 2007a-c, Chapters 2-4) suggested the existence of distinct not closely related species within what is considered *Allobates granti* (n=2), *Dendropsophus leucophyllatus* (n=2), *Leptodactylus gr. wagneri* (n=9), *Scinax ruber* (n=3) and *Rhinella margaritifera* (n=8). Consequently, we focused our analyses to the species or lineages for which the phylogeographical pattern can be examined in the Guiana Shield.

We considered:

• The most widely distributed lineage of *Allobates granti* which is likely to correspond to the nominal species recently described by Kok (2006) and pers. obs.

• Two lineages within the *Leptodactylus wagneri* species complex (*L. wagneri* B and *L. wagneri* C) which are forestrial and occur in the Guiana Shield as opposed to *L. gr. wagneri* A and E which also occur in the Guiana Shield but seem restricted to open areas, *L. gr. wagneri* D which has been found in Suriname and Guyana but in only a few specimens and the 4 additional species occurring outside the Guiana Shield in Amazonia,

• The widely distributed lineage of *Scinax ruber* which occur in patches of open vegetation within the forest and open habitat, as opposed to the exclusive coastal open habitat species probably corresponding to *S. x-signatus* or a close relative and to one misidentified species from the Atlantic forest of Brazil which is actually clustering with *Scinax catharinae* species group.

• The lineages within the *Rhinella margaritifera* species complex which occur in the Guiana Shield as opposed to the newly described *R. lescurei* (Fouquet et al., 2007c, Chapter 4) from French Guiana and the lineages occurring elsewhere in South America.

• The lineage of *Dendropsophus leucophyllatus* occurring in the Guiana Shield as opposed to the highly divergent Amazonian lineages (Check et al, 2001; Lougheed et al. 2006; Fouquet et al., 2007b, Chapter 3).

On the contrary, we grouped several putative species under one name:

• We grouped *Rhinella margaritifera* lineages from the Guiana Shield, *Rhinella martyi* (Fouquet et al., 2007c, Chapter 4) and the closest Amazonian lineages because they appeared allopatric in the Guiana Shield and/or phylogenetically close enough to be included in the same group.

- For similar reasons we also grouped under the name *Rhinella castaneotica* data from Amazonia of this species and material from either an undescribed species or a synonym species from the Guiana Shield (Fouquet et al., 2007c, Chapter 4).

- *Dendropsophus minusculus* inhabits the swamps of the costal region of the Guiana Shield. It probably represents a distinct species from the forestrial species called *Hyla* sp. 1 by Lescure and Marty (2000). However, Salducci et al. (2005) suggested they have very close relationships and they are indeed confused across their range (R. Ernst pers. com. and pers. obs.). We consequently considered the two species under the name *D. minusculus*.

- We also grouped *Scinax ruber* lineage from the Guiana Shield with a still undescribed species of *Scinax* (*S.* sp. hybrid) (Fouquet el al., 2007a, Chapter 2), which was previously called *S. x-signatus* (Lescure and Marty, 2000), because its mitochondrial lineages shares a recent history with *Scinax ruber*.

Due to the confusion surrounding species delineation in several species like in the *Leptodactylus wagneri* species group we mapped the ranges of most Amazonian species according to the GAA supposedly occurring in the Guiana Shield and additional species (see Figures S21b).

We also mapped the observed and supposed ranges of *Anomaloglossus stepheni* because it appeared to have a contact zone with *Anomaloglossus baeobatrachus*. These two different species have similar ecology and reproductive behaviour and interestingly no overlap across their ranges is observed. We took this contact zone into account for the phylogeographic break analysis and used the range of both species as a whole.

On the contrary, *Anomaloglossus degranvillei* displays also two major lineages largely overlapping in central French Guiana and in the North West. However, these two lineages are not syntopic (pers. obs.). *Anomaloglossus degranvillei* 2 because we estimated that data are too scarce to recover any well oriented phylogeographic breaks.

We also mapped the *D. leucophyllatus* lineages for which 16S rDNA data were available from Chek et al. (2001) and Lougheed et al. (2006) but we did not take into account phylogeographic breaks among these Amazonian lineages.

Table S5.1: Sample details:

Group (Congeneric=CGsp, Outgroup=OGsp, Ingroup) / Genus name /Species name / Voucher and field number (AF=Antoine Fouquet, BM and AG=Michel Blanc, CM=Christian Marty, PG=Philippe Gaucher, BPN=Brice P. Noonan, MTR=Miguel Trefaut Rodrigues / 12SrDNA accession Number / 16SrDNA accession Number / mtDNA haplotype number / clades (same colour code has been used in full trees (Fig. S5.1-8) and statistical parsimony networks (Fig. S5.9-16; S5.25-32) and maps (Fig. 17-24)) / nuDNA accession Number / nuDNA haplotype number / location / country/geographical coordinates.

Group	Genus	species	Voucher #	12S Acces. #	16S Acces. #	mtDNA haplo. #	Clades					Tyrosinase Acces. #	nuDNA haplo. #	Locality	country	coordinates
OGsp	*Acris*	*crepitans*		AY843559								AY844019				
	Adenomera	*andreae*	300AF	#######	#######	Adan-H01	1-1	2-1	3-1	4-1	5-1	#######	Adan-H10	Matoury	French Guiana	04 51 48 N 52 21 28 W
	Adenomera	*andreae*	1AF	#######	#######	Adan-H01	1-1	2-1	3-1	4-1	5-1	#######	Adan-H10	Montjoly	French Guiana	04 55 00 N 52 16 00 W
	Adenomera	*andreae*	2AF	#######	#######	Adan-H02	1-1	2-1	3-1	4-1	5-1	#######	Adan-H05	Montjoly	French Guiana	04 55 00 N 52 16 00 W
	Adenomera	*andreae*	429CM	#######	#######	Adan-H06	1-4	2-2	3-1	4-1	5-1	#######	Adan-H34	Cacao	French Guiana	04 34 00 N 52 28 00 W
	Adenomera	*andreae*	327CM	#######	#######	Adan-H07	1-5	2-3	3-2	4-1	5-1	#######	Adan-H14	Montagne Petite Tortue	French Guiana	05 10 46 N 52 55 53 W
	Adenomera	*andreae*	292CM	#######	#######	Adan-H08	1-6	2-4	3-3	4-1	5-1	#######	Adan-H03	Camp Canopé	French Guiana	04 53 37 N 52 47 57 W
	Adenomera	*andreae*	273AF	#######	#######	Adan-H09	1-7	2-5	3-2	4-1	5-1	#######	Adan-H03	Nouragues2	French Guiana	04 05 30 N 52 42 00 W
	Adenomera	*andreae*	270AF	#######	#######	Adan-H10	1-7	2-5	3-2	4-1	5-1	#######	Adan-H02	Nouragues2	French Guiana	04 05 30 N 52 42 00 W
	Adenomera	*andreae*	241AF	#######	#######	Adan-H11	1-18	2-12	3-8	4-1	5-1	#######	Adan-H02	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
	Adenomera	*andreae*	251AF	#######	#######	Adan-H11	1-18	2-12	3-8	4-1	5-1	#######	Adan-H13	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
	Adenomera	*andreae*	239AF	#######	#######	Adan-H12	1-18	2-12	3-8	4-1	5-1	#######	Adan-H03	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
	Adenomera	*andreae*	240AF	#######	#######	Adan-H13	1-19	2-13	3-8	4-1	5-1	#######	Adan-H09	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
	Adenomera	*andreae*	ACM	#######	#######	Adan-H20	1-12	2-8	3-3	4-1	5-1	#######	Adan-H03	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Adenomera	*andreae*	297AF	#######	#######	Adan-H23	1-15	2-10	3-6	4-1	5-1	#######	Adan-H03	Kaw1	French Guiana	04 31 00 N 52 02 00 W
	Adenomera	*andreae*	59AF	#######	#######	Adan-H24	1-16	2-11	3-7	4-1	5-1	#######	Adan-H12	Petit-saut	French Guiana	05 04 00 N 53 03 00 W
	Adenomera	*andreae*	58AF	#######	#######	Adan-H25	1-17	2-11	3-7	4-1	5-1	#######	Adan-H03	Petit-saut	French Guiana	05 04 00 N 53 03 00 W
	Adenomera	*andreae*	212AF	#######	#######	Adan-H26	1-20	2-14	3-9	4-1	5-1	#######	Adan-H33	Angouleme	French Guiana	05 23 00 N 53 39 00 W
	Adenomera	*andreae*	219AF	#######	#######	Adan-H28	1-21	2-14	3-9	4-1	5-1	#######	Adan-H33	Angouleme	French Guiana	05 23 00 N 53 39 00 W
	Adenomera	*andreae*	232AF	#######	#######	Adan-H29	1-21	2-14	3-9	4-1	5-1	#######	Adan-H21	Angouleme	French Guiana	05 23 00 N 53 39 00 W
	Adenomera	*andreae*	200AF	#######	#######	Adan-H30	1-22	2-14	3-9	4-1	5-1	#######	Adan-H33	Angouleme	French Guiana	05 23 00 N 53 39 00 W
	Adenomera	*andreae*	5BM	#######	#######	Adan-H01	1-1	2-1	3-1	4-1	5-1	#######	Adan-H10	Montravel	French Guiana	04 54 42 N 52 15 39 W
	Adenomera	*andreae*	7BM	#######	#######	Adan-H01	1-1	2-1	3-1	4-1	5-1	#######	Adan-H10	Montravel	French Guiana	04 54 42 N 52 15 39 W
	Adenomera	*andreae*	35RB	#######	#######	Adan-H05	1-3	2-1	3-1	4-1	5-1	#######	Adan-H03	St Eugene	French Guiana	04 51 00 N 53 04 00 W
	Adenomera	*andreae*	267CM	#######	#######	Adan-H18	1-10	2-7	3-5	4-1	5-1	#######	Adan-H12	DZ5	French Guiana	04 03 00 N 52 01 00 W
	Adenomera	*andreae*	12AF	#######	#######	Adan-H01	1-1	2-1	3-1	4-1	5-1	#######	Adan-H11	Montjoly	French Guiana	04 55 00 N 52 16 00 W
	Adenomera	*andreae*	31CM	#######	#######	Adan-H04	1-2	2-1	3-1	4-1	5-1	#######	Adan-H05	Montjoly	French Guiana	04 55 00 N 52 16 00 W
	Adenomera	*andreae*	378CM	#######	#######	Adan-H14	1-8	2-6	3-4	4-1	5-1	#######	Adan-H10	Régina	French Guiana	04 18 00 N 52 07 00 W
	Adenomera	*andreae*	375CM	#######	#######	Adan-H15	1-9	2-6	3-4	4-1	5-1	#######	Adan-H02	Régina	French Guiana	04 18 00 N 52 07 00 W
	Adenomera	*andreae*	377CM	#######	#######	Adan-H16	1-9	2-6	3-4	4-1	5-1	#######	Adan-H10	Régina	French Guiana	04 18 00 N 52 07 00 W
	Adenomera	*andreae*	289AG	#######	#######	Adan-H19	1-11	2-7	3-5	4-1	5-1	#######	Adan-H03	St Georges	French Guiana	03 52 00 N 51 48 00 W
	Adenomera	*andreae*	219BM	#######	#######	Adan-H21	1-13	2-9	3-6	4-1	5-1	#######	Adan-H04	Kaw1	French Guiana	04 31 00 N 52 02 00 W
	Adenomera	*andreae*	221BM	#######	#######	Adan-H22	1-14	2-9	3-6	4-1	5-1	#######	Adan-H03	Kaw1	French Guiana	04 31 00 N 52 02 00 W
	Adenomera	*andreae*	T-4491	#######	#######	Adan-H27	1-21	2-14	3-9	4-1	5-1	#######	Adan-H15	Angoulème	French Guiana	05 23 00 N 53 39 00 W
	Adenomera	*andreae*	279CM	#######	#######	Adan-H17	1-8	2-6	3-4	4-1	5-1	#######	Adan-H02	Aratai	French Guiana	03 59 41 N 52 35 45 W
	Adenomera	*andreae*	1553BPN	#######	#######	Adan-H22	1-14	2-9	3-6	4-1	5-1	#######	Adan-H05	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Adenomera	*andreae*	T-2540	#######	#######	Adan-H49	1-36	2-22	3-15	4-5	5-1	#######	Adan-H10	Pic Matecho	French Guiana	03 45 00 N 53 02 00 W
	Adenomera	*andreae*	1689BPN	#######	#######	Adan-H48	1-36	2-22	3-15	4-5	5-1	#######	Adan-H03	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Adenomera	*andreae*	104AF	#######	#######	Adan-H46	1-35	2-21	3-15	4-5	5-1	#######	Adan-H28	Road to Apura	Suriname	05 11 00 N 55 37 00 W
	Adenomera	*andreae*	565PG	#######	#######	Adan-H44	1-33	2-20	3-14	4-5	5-1	#######	Adan-H02	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
	Adenomera	*andreae*	13964MTR	#######	#######	Adan-H42	1-31	2-19	3-13	4-5	5-1	#######	Adan-H03	Laranjal do Jari	Brazil	00 43 00 S 52 23 00 W
	Adenomera	*andreae*	13962MTR	#######	#######	Adan-H43	1-32	2-19	3-13	4-5	5-1	#######	Adan-H08	Laranjal do Jari	Brazil	00 43 00 S 52 23 00 W
	Adenomera	*andreae*	13961MTR	#######	#######	Adan-H43	1-32	2-19	3-13	4-5	5-1	#######	Adan-H10	Laranjal do Jari	Brazil	00 43 00 S 52 23 00 W
	Adenomera	*andreae*	13963MTR	#######	#######	Adan-H43	1-32	2-19	3-13	4-5	5-1	#######	Adan-H18	Laranjal do Jari	Brazil	00 43 00 S 52 23 00 W
	Adenomera	*andreae*	89PG	#######	#######	Adan-H52	1-39	2-23	3-16	4-4	5-2	#######	Adan-H31	Mont Saint Marcel	French Guiana	02 23 09 N 53 00 58 W
	Adenomera	*andreae*	235PG	#######	#######	Adan-H50	1-37	2-23	3-16	4-4	5-2	#######	Adan-H03	Haute Wanapi	French Guiana	02 30 57 N 53 49 56 W

Genus	species	Code			Haplotype							Haplotype	Locality	Country	Coordinates
Adenomera	andreae	416CM	#######	#######	Adan-H35	1-27	2-17	3-11	4-2	5-2	#######	Adan-H03	Lucifer	French Guiana	04 46 00 N 53 55 00 W
Adenomera	andreae	353CM	#######	#######	Adan-H36	1-27	2-17	3-11	4-2	5-2	#######	Adan-H02	Lucifer	French Guiana	04 46 00 N 53 55 00 W
Adenomera	andreae	352CM	#######	#######	Adan-H37	1-28	2-17	3-11	4-2	5-2	#######	Adan-H02	Lucifer	French Guiana	04 46 00 N 53 55 00 W
Adenomera	andreae	412CM	#######	#######	Adan-H37	1-28	2-17	3-11	4-2	5-2	#######	Adan-H22	Lucifer	French Guiana	04 46 00 N 53 55 00 W
Adenomera	andreae	61CM	#######	#######	Adan-H33	1-25	2-16	3-11	4-2	5-2	#######	Adan-H02	Monts Bakra	French Guiana	03 18 08 N 52 56 73 W
Adenomera	andreae	62CM	#######	#######	Adan-H34	1-26	2-16	3-11	4-2	5-2	#######	Adan-H32	Monts Bakra	French Guiana	03 18 08 N 52 56 73 W
Adenomera	andreae	398CM	#######	#######	Adan-H35	1-27	2-17	3-11	4-2	5-2	#######	Adan-H23	Lucifer	French Guiana	04 46 00 N 53 55 00 W
Adenomera	andreae	158PG	#######	#######	Adan-H32	1-24	2-15	3-10	4-2	5-2	#######	Adan-H03	Armontabo	French Guiana	03 48 16 N 52 17 17 W
Adenomera	andreae	13807MTR	#######	#######	Adan-H38	1-29	2-18	3-12	4-3	5-2	#######	Adan-H02	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
Adenomera	andreae	13762MTR	#######	#######	Adan-H38	1-29	2-18	3-12	4-3	5-2	#######	Adan-H07	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
Adenomera	andreae	13783MTR	#######	#######	Adan-H38	1-29	2-18	3-12	4-3	5-2	#######	Adan-H08	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
Adenomera	andreae	13784MTR	#######	#######	Adan-H38	1-29	2-18	3-12	4-3	5-2	#######	Adan-H19	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
Adenomera	andreae	13785MTR	#######	#######	Adan-H38	1-29	2-18	3-12	4-3	5-2	#######	Adan-H35	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
Adenomera	andreae	13794MTR	#######	#######	Adan-H39	1-29	2-18	3-12	4-3	5-2	#######	Adan-H19	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
Adenomera	andreae	13806MTR	#######	#######	Adan-H40	1-29	2-18	3-12	4-3	5-2	#######	Adan-H02	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
Adenomera	andreae	13758MTR	#######	#######	Adan-H41	1-30	2-18	3-12	4-3	5-2	#######	Adan-H02	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
Adenomera	andreae	119AF	#######	#######	Adan-H53	1-40	2-24	3-17	4-6	5-1	#######	Adan-H27	Brownsberg	Suriname	04 56 31 N 55 10 33 W
Adenomera	andreae	146AF	#######	#######	Adan-H53	1-40	2-24	3-17	4-6	5-1	#######	Adan-H28	Brownsberg	Suriname	04 56 31 N 55 10 33 W
Adenomera	andreae	123AF	#######	#######	Adan-H54	1-40	2-24	3-17	4-6	5-1	#######	Adan-H27	Brownsberg	Suriname	04 56 31 N 55 10 33 W
Adenomera	andreae	144AF	#######	#######	Adan-H54	1-40	2-24	3-17	4-6	5-1	#######	Adan-H28	Brownsberg	Suriname	04 56 31 N 55 10 33 W
Adenomera	andreae	120AF	#######	#######	Adan-H55	1-41	2-24	3-17	4-6	5-1	#######	Adan-H27	Brownsberg	Suriname	04 56 31 N 55 10 33 W
Adenomera	andreae	13845MTR	#######	#######	Adan-H57	1-42	2-25	3-18	4-7	5-1	#######	Adan-H26	Lourenço	Brazil	02 19 25 N 51 38 43 W
Adenomera	andreae	13866MTR	#######	#######	Adan-H58	1-42	2-25	3-18	4-7	5-1	#######	Adan-H06	Lourenço	Brazil	02 19 25 N 51 38 43 W
Adenomera	andreae	13880MTR	#######	#######	Adan-H59	1-43	2-25	3-18	4-7	5-1	#######	Adan-H06	Lourenço	Brazil	02 19 25 N 51 38 43 W
Adenomera	andreae	13867MTR	#######	#######	Adan-H60	1-44	2-25	3-18	4-7	5-1	#######	Adan-H02	Lourenço	Brazil	02 19 25 N 51 38 43 W
Adenomera	andreae	13865MTR	#######	#######	Adan-H61	1-43	2-25	3-18	4-7	5-1	#######	Adan-H17	Lourenço	Brazil	02 19 25 N 51 38 43 W
Adenomera	andreae	MTR10.060	#######	#######	Adan-H66	1-49	2-28	3-21	4-9	5-4	#######	Adan-H16	Santa Maria (Terra Preta)	Brazil	05 47 52 S 60 15 55 W
Adenomera	andreae	MTR10.023	#######	#######	Adan-H67	1-49	2-28	3-21	4-9	5-4	#######	Adan-H17	Santa Maria (Terra Preta)	Brazil	05 47 52 S 60 15 55 W
Adenomera	andreae	MTR10.024	#######	#######	Adan-H68	1-50	2-28	3-21	4-9	5-4	#######	Adan-H02	Santa Maria (Terra Preta)	Brazil	05 47 52 S 60 15 55 W
Adenomera	andreae	MTR10.008	#######	#######	Adan-H69	1-51	2-29	3-21	4-9	5-4	#######	Adan-H29	Lago Cipotuba	Brazil	05 48 05 S 60 13 16 W
Adenomera	andreae	MTR11095	#######	#######	Adan-H64	1-47	2-27	3-20	4-8	5-3	#######	Adan-H30	Floresta Nacional Tapajós	Brazil	03 30 00 S 55 04 00 W
Adenomera	andreae	MTR11094	#######	#######	Adan-H65	1-48	2-27	3-20	4-8	5-3	#######	Adan-H30	Floresta Nacional Tapajós	Brazil	03 30 00 S 55 04 00 W
Adenomera	andreae	MSH10219	#######	#######	Adan-H62	1-45	2-26	3-19	4-8	5-3	#######	Adan-H02	E.E. Anavilhanas- Base 2	Brazil	02 32 04 S 60 50 12 W
Adenomera	andreae	MSH10220	#######	#######	Adan-H63	1-46	2-26	3-19	4-8	5-3	#######	Adan-H20	E.E. Anavilhanas- Base 2	Brazil	02 32 04 S 60 50 12 W
Adenomera	andreae	199BM	#######	EU201045	Adan-H31	1-23	2-15	3-10	4-2	5-2	#######	Adan-H02	Trinité	French Guiana	04 35 00 N 53 21 00 W
Adenomera	andreae	20AF	#######	EU201046	Adan-H47	1-36	2-22	3-15	4-5	5-1	#######	Adan-H25	Saül1	French Guiana	03 37 32 N 53 12 26 W
Adenomera	andreae	T-2541	#######	EU201046	Adan-H47	1-36	2-22	3-15	4-5	5-1	#######	Adan-H01	Pic Matecho	French Guiana	03 45 00 N 53 02 00 W
Adenomera	andreae	216CM	#######	EU201046	Adan-H47	1-36	2-22	3-15	4-5	5-1	#######	Adan-H07	Saül1	French Guiana	03 37 32 N 53 12 26 W
Adenomera	andreae	1656BPN	#######	EU201046	Adan-H47	1-36	2-22	3-15	4-5	5-1	#######	Adan-H03	Saül1	French Guiana	03 37 32 N 53 12 26 W
Adenomera	andreae	1655BPN	#######	EU201046	Adan-H47	1-36	2-22	3-15	4-5	5-1	#######	Adan-H06	Saül1	French Guiana	03 37 32 N 53 12 26 W
Adenomera	andreae	105AF	#######	EU201047	Adan-H45	1-34	2-21	3-15	4-5	5-1	#######	Adan-H24	Road to Apura	Suriname	05 11 00 N 55 37 00 W
Adenomera	andreae	87BM	#######	EU201048	Adan-H51	1-38	2-23	3-16	4-4	5-2	#######	Adan-H03	Mont Arawa	French Guiana	02 48 59 N 53 21 59 W
Adenomera	andreae	121AF	#######	EU201049	Adan-H56	1-41	2-24	3-17	4-6	5-1	#######	Adan-H27	Brownsberg	Suriname	04 56 31 N 55 10 33 W
Adenomera	andreae	295AF			Adan-NA						#######	Adan-H01	Kaw2	French Guiana	04 43 00 N 52 08 00 W
Adenomera	andreae	238AF	#######	#######	Adan-H11	1-18	2-12	3-8	4-1	5-1		Adan-NA	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
Adenomera	andreae	16CM	#######	#######	Adan-H01	1-1	2-1	3-1	4-1	5-1		Adan-NA	Cayenne	French Guiana	04 56 00 N 52 20 00 W
Adenomera	andreae	32CM	#######	EU201044	Adan-H03	1-2	2-1	3-1	4-1	5-1		Adan-NA	Montjoly	French Guiana	04 55 00 N 52 16 00 W
Adenomera	heyeri	203AF	#######	#######	Adhe-H01	1-1	2-1	3-1			#######	Adhe-H08	Angouleme	French Guiana	05 23 00 N 53 39 00 W
Adenomera	heyeri	348CM	#######	#######	Adhe-H01	1-1	2-1	3-1			#######	Adhe-H02	Lucifer	French Guiana	04 46 00 N 53 55 00 W
Adenomera	heyeri	400CM	#######	#######	Adhe-H01	1-1	2-1	3-1			#######	Adhe-H07	Lucifer	French Guiana	04 46 00 N 53 55 00 W
Adenomera	heyeri	469PG	#######	#######	Adhe-H01	1-1	2-1	3-1			#######	Adhe-H04	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
Adenomera	heyeri	307AG	#######	#######	Adhe-H01	1-1	2-1	3-1			#######	Adhe-H02	Trinité	French Guiana	04 35 00 N 53 21 00 W
Adenomera	heyeri	G-648PG	#######	#######	Adhe-H03	1-2	2-1	3-1			#######	Adhe-H01	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
Adenomera	heyeri	242AF	#######	#######	Adhe-H03	1-2	2-1	3-1			#######	Adhe-H02	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
Adenomera	heyeri	T-2529	#######	#######	Adhe-H04	1-1	2-1	3-1			#######	Adhe-H02	Pic Matecho	French Guiana	03 45 00 N 53 02 00 W
Adenomera	heyeri	411CM	#######	#######	Adhe-H05	1-1	2-1	3-1			#######	Adhe-H05	Lucifer	French Guiana	04 46 00 N 53 55 00 W
Adenomera	heyeri	402CM	#######	#######	Adhe-H06	1-1	2-1	3-1			#######	Adhe-H06	Lucifer	French Guiana	04 46 00 N 53 55 00 W
Adenomera	heyeri	369CM	#######	#######	Adhe-H07	1-3	2-1	3-1			#######	Adhe-H02	Lucifer	French Guiana	04 46 00 N 53 55 00 W
Adenomera	heyeri	274AF	#######	#######	Adhe-H03	1-2	2-1	3-1			#######	Adhe-H01	Nouragues2	French Guiana	04 05 30 N 52 42 00 W
Adenomera	heyeri	269AF	#######	#######	Adhe-H08	1-4	2-2	3-1			#######	Adhe-H02	Nouragues2	French Guiana	04 05 30 N 52 42 00 W
Adenomera	heyeri	211AF	#######	#######	Adhe-H09	1-5	2-2	3-1			#######	Adhe-H08	Angouleme	French Guiana	05 23 00 N 53 39 00 W

	Genus	species	Code	GB1	GB2	Hap1	c1	c2	c3	c4	c5	GB3	Hap2	Locality	Country	Coordinates
	Adenomera	heyeri	175BM	#######	#######	Adhe-H01	1-1	2-1	3-1			#######	Adhe-H08	Trinité	French Guiana	04 35 00 N 53 21 00 W
	Adenomera	heyeri	1361BPN	#######	#######	Adhe-H03	1-2	2-1	3-1			#######	Adhe-H01	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Adenomera	heyeri	T-3036	#######	#######	Adhe-H12	1-8	2-4	3-2			#######	Adhe-H02	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
	Adenomera	heyeri	N30,2001.0354	#######	#######	Adhe-H12	1-8	2-4	3-2			#######	Adhe-H04	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
	Adenomera	heyeri	T-3039	#######	#######	Adhe-H12	1-8	2-4	3-2			#######	Adhe-H04	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
	Adenomera	heyeri	127AF	#######	#######	Adhe-H13	1-9	2-4	3-2			#######	Adhe-H01	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Adenomera	heyeri	126AF	#######	#######	Adhe-H14	1-9	2-4	3-2			#######	Adhe-H01	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Adenomera	heyeri	T-3021	#######	#######	Adhe-H12	1-8	2-4	3-2			#######	Adhe-H04	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
	Adenomera	heyeri	11963SMNS	#######	#######	Adhe-H15	1-10	2-4	3-2			#######	Adhe-H01	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Adenomera	heyeri	11966SMNS	#######	#######	Adhe-H15	1-10	2-4	3-2			#######	Adhe-H01	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Adenomera	heyeri	11964SMNS	#######	#######	Adhe-H16	1-10	2-4	3-2			#######	Adhe-H01	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Adenomera	heyeri	11965SMNS	#######	#######	Adhe-H17	1-10	2-4	3-2			#######	Adhe-H02	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Adenomera	heyeri	11967SMNS	#######	#######	Adhe-H17	1-10	2-4	3-2			#######	Adhe-H02	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Adenomera	heyeri	90PG	#######	#######	Adhe-H03	1-6	2-3	3-2			#######	Adhe-H03	Mont Saint Marcel	French Guiana	02 23 09 N 53 00 58 W
	Adenomera	heyeri	4BM	#######	EU201050	Adhe-H02	1-1	2-1	3-1			#######	Adhe-H02	Montagne des Singes	French Guiana	05 04 00 N 52 43 00 W
	Adenomera	heyeri	221CM	#######	EU201050	Adhe-H02	1-1	2-1	3-1			#######	Adhe-H02	Montagne des singes	French Guiana	05 04 00 N 52 43 00 W
	Adenomera	heyeri	264CM	#######	EU201050	Adhe-H02	1-1	2-1	3-1			#######	Adhe-H04	Montagne des singes	French Guiana	05 04 00 N 52 43 00 W
	Adenomera	heyeri	46PG,2001.0815MNHN	#######	EU201051	Adhe-H11	1-7	2-3	3-2			#######	Adhe-H08	Piton Baron	French Guiana	03 17 00 N 53 04 00 W
	Adenomera	hylaedactyla	80BM	#######	#######	Adhy-H05	1-1	2-1	3-1	4-1		#######	Adhy-H12	Savane Corossony	French Guiana	05 23 00 N 53 00 00 W
	Adenomera	hylaedactyla	309CM	#######	#######	Adhy-H02	1-1	2-1	3-1	4-1		#######	Adhy-H12	Tibourou	French Guiana	04 25 00 N 52 18 00 W
	Adenomera	hylaedactyla	58BM	#######	#######	Adhy-H04	1-1	2-1	3-1	4-1		#######	Adhy-H12	Kaw3	French Guiana	04 32 53 N 52 09 07 W
	Adenomera	hylaedactyla	140	#######	#######	Adhy-H03	1-1	2-1	3-1	4-1		#######	Adhy-H12	Cacao	French Guiana	04 34 00 N 52 28 00 W
	Adenomera	hylaedactyla	238BM	#######	#######	Adhy-H07	1-3	2-2	3-1	4-1		#######	Adhy-H13	St Georges	French Guiana	03 52 00 N 51 48 00 W
	Adenomera	hylaedactyla	69BM	#######	#######	Adhy-H08	1-2	2-2	3-1	4-1		#######	Adhy-H12	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Adenomera	hylaedactyla	220BM	#######	#######	Adhy-H06	1-2	2-2	3-1	4-1		#######	Adhy-H07	Kaw1	French Guiana	04 31 00 N 52 02 00 W
	Adenomera	hylaedactyla	218BM	#######	#######	Adhy-H06	1-2	2-2	3-1	4-1		#######	Adhy-H10	Kaw1	French Guiana	04 31 00 N 52 02 00 W
	Adenomera	hylaedactyla	13992MTR	#######	#######	Adhy-H10	1-5	2-4	3-2	4-1		#######	Adhy-H03	Macapa	Brazil	00 02 45 N 51 03 00 W
	Adenomera	hylaedactyla	13813MTR	#######	#######	Adhy-H11	1-6	2-4	3-2	4-1		#######	Adhy-H05	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Adenomera	hylaedactyla	13814MTR	#######	#######	Adhy-H11	1-6	2-4	3-2	4-1		#######	Adhy-H06	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Adenomera	hylaedactyla	13773MTR	#######	#######	Adhy-H11	1-6	2-4	3-2	4-1		#######	Adhy-H05	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Adenomera	hylaedactyla	977122MTR	#######	#######	Adhy-H16	1-11	2-8	3-5	4-3		#######	Adhy-H01	Juruena	Brazil	10 19 25 S 58 29 34 W
	Adenomera	hylaedactyla	977121MTR	#######	#######	Adhy-H15	1-10	2-7	3-4	4-3		#######	Adhy-H08	Juruena	Brazil	10 19 25 S 58 29 34 W
	Adenomera	hylaedactyla	13821MTR	#######	#######	Adhy-H13	1-8	2-6	3-3	4-2		#######	Adhy-H02	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Adenomera	hylaedactyla	13820MTR	#######	#######	Adhy-H13	1-8	2-6	3-3	4-2		#######	Adhy-H04	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Adenomera	hylaedactyla	13822MTR	#######	#######	Adhy-H13	1-8	2-6	3-3	4-2		#######	Adhy-H04	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Adenomera	hylaedactyla	13876MTR	#######	#######	Adhy-H14	1-9	2-6	3-3	4-2		#######	Adhy-H11	Lourenço	Brazil	02 19 25 N 51 38 43 W
	Adenomera	hylaedactyla	13830MTR	#######	#######	Adhy-H13	1-8	2-6	3-3	4-2		#######	Adhy-H05	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Adenomera	hylaedactyla	92CM	#######	EU201052	Adhy-H06	1-2	2-2	3-1	4-1		#######	Adhy-H10	Montagne d'Argent	French Guiana	04 23 00 N 51 42 00 W
	Adenomera	hylaedactyla	1235BPN	#######	EU201053	Adhy-H09	1-4	2-3	3-1	4-1		#######	Adhy-H09	Imbaimadai	Guyana	05 44 23 N 60 17 51 W
	Adenomera	hylaedactyla	1111BPN	#######	EU201053	Adhy-H09	1-4	2-3	3-1	4-1		#######	Adhy-H09	Imbaimadai	Guyana	05 44 23 N 60 17 51 W
	Adenomera	hylaedactyla	61BM	#######	EU201054	Adhy-H01	1-1	2-1	3-1	4-1		#######	Adhy-H13	Kaw3	French Guiana	04 32 53 N 52 09 07 W
	Adenomera	hylaedactyla	272CM	#######	EU201054	Adhy-H01	1-1	2-1	3-1	4-1		#######	Adhy-H13	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Adenomera	hylaedactyla	MJH3669	DQ283063	DQ283063	Adhy-H12	1-7	2-5	3-2	4-1			Adan-NA	Huanuco	Peru	09 23 02 S 75 52 57 W
CGsp	Adenomera	lutzi	1316BPN	#######	#######							#######		Imbaimadai	Guyana	05 44 23 N 60 17 51 W
CGsp	Allobates	alagoanus	MRT6031	DQ502126	DQ502126									Bahia, Sao Jose da Vitoria, Fazenda Unacau	Brazil	15 09 00 S 39 18 00 W
CGsp	Allobates	brunneus	OMNH34473	DQ502047	DQ502047									Para, 101 km S and 15 km E Santarem (near Rio Curua-Una)	Brazil	03 09 00 S 54 50 00 W
CGsp	Allobates	brunneus	OMNH34461	DQ502205	DQ502205									Para, 101 km S and 15 km E Santarem	Brazil	03 09 00 S 54 50 00 W
CGsp	Allobates	caeruleodactylus	OMNH37411	DQ502212	DQ502212									Amazonas, Castanho, ca. 40 km S Manaus, at km 12 on road to Autazes	Brazil	03 37 10 S 59 86 00 W
CGsp	Allobates	conspicuus	OMNH35997	DQ502135	DQ502135									Acre, Porto Walter	Brazil	08 15 31 S 72 46 37 W
CGsp	Allobates	sp. "Curua_Una"	MJH3973	DQ502110	DQ502110									Para, Rio Curua-Una	Brazil	
	Allobates	femoralis	VOGT2050	#######	#######	Alfe-H12	1-9	2-8	3-5	4-3	5-1	#######	Alfe-H17	Boca do Juma - M.E. Aripuanã	Brazil	06 00 53 S 60 10 45 W
	Allobates	femoralis	MTR11096	#######	#######	Alfe-H20	1-12	2-9	3-6	4-2	5-1	#######	Alfe-H15	Floresta Nacional Tapajós	Brazil	03 30 00 S 55 04 00 W
	Allobates	femoralis	RCV2245	#######	#######	Alfe-H24	1-18	2-13	3-5	4-3	5-1	#######	Alfe-H14	Itapinima / Rio Madeira	Brazil	05 25 28 S 60 42 54 W
	Allobates	femoralis	237CM	#######	#######	Alfe-H02	1-1	2-1	3-1	4-1	5-1	#######	Alfe-H07	Piste St Elie	French Guiana	05 17 01 N 53 03 14 W
	Allobates	femoralis	451	#######	#######	Alfe-H03	1-1	2-1	3-1	4-1	5-1	#######	Alfe-H07	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
	Allobates	femoralis	19AF	#######	#######	Alfe-H04	1-1	2-1	3-1	4-1	5-1	#######	Alfe-H04	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Allobates	femoralis	72AF	#######	#######	Alfe-H05	1-2	2-1	3-1	4-1	5-1	#######	Alfe-H02	St Georges	French Guiana	03 52 00 N 51 48 00 W
	Allobates	femoralis	71AF	#######	#######	Alfe-H05	1-2	2-1	3-1	4-1	5-1	#######	Alfe-H10	St Georges	French Guiana	03 52 00 N 51 48 00 W
	Allobates	femoralis	383CM	#######	#######	Alfe-H06	1-3	2-2	3-1	4-1	5-1	#######	Alfe-H08	Régina	French Guiana	04 18 00 N 52 07 00 W

	Genus	species	Specimen	Acc1	Acc2	Hap	c1	c2	c3	c4	c5	Acc3	Hap2	Locality	Country	Coordinates
	Allobates	femoralis	15AF	#######	#######	Alfe-H08	1-5	2-4	3-3	4-1	5-1	#######	Alfe-H02	Kaw3	French Guiana	04 32 53 N 52 09 07 W
	Allobates	femoralis	427CM	#######	#######	Alfe-H09	1-5	2-4	3-3	4-1	5-1	#######	Alfe-H07	Cacao	French Guiana	04 34 00 N 52 28 00 W
	Allobates	femoralis	370CM	#######	#######	Alfe-H07	1-4	2-3	3-2	4-1	5-1	#######	Alfe-H05	Oyapoque	Brazil	03 49 01 N 51 50 50 W
	Allobates	femoralis	13936MTR	#######	#######	Alfe-H13	1-13	2-10	3-4	4-2	5-1	#######	Alfe-H13	Lourenço	Brazil	02 19 25 N 51 38 43 W
	Allobates	femoralis	13726MTR	#######	#######	Alfe-H14	1-14	2-11	3-4	4-2	5-1	#######	Alfe-H02	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Allobates	femoralis	13800MTR	#######	#######	Alfe-H14	1-14	2-11	3-4	4-2	5-1	#######	Alfe-H02	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Allobates	femoralis	12002SMNS	#######	#######	Alfe-H15	1-14	2-11	3-4	4-2	5-1	#######	Alfe-H02	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Allobates	femoralis	12003SMNS	#######	#######	Alfe-H15	1-14	2-11	3-4	4-2	5-1	#######	Alfe-H02	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Allobates	femoralis	12004SMNS	#######	#######	Alfe-H15	1-14	2-11	3-4	4-2	5-1	#######	Alfe-H02	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Allobates	femoralis	12006SMNS	#######	#######	Alfe-H15	1-14	2-11	3-4	4-2	5-1	#######	Alfe-H03	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Allobates	femoralis	12005SMNS	#######	#######	Alfe-H16	1-15	2-11	3-4	4-2	5-1	#######	Alfe-H02	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Allobates	femoralis	12008SMNS	#######	#######	Alfe-H17	1-15	2-11	3-4	4-2	5-1	#######	Alfe-H02	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Allobates	femoralis	13802MTR	#######	#######	Alfe-H18	1-16	2-11	3-4	4-2	5-1	#######	Alfe-H02	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Allobates	femoralis	13959MTR	#######	#######	Alfe-H10	1-6	2-5	3-3	4-1	5-1	#######	Alfe-H16	Laranjal do Jari	Brazil	00 43 00 S 52 23 00 W
	Allobates	femoralis	MRT6376	#######	#######	Alfe-H11	1-7	2-5	3-3	4-1	5-1	#######	Alfe-H16	Igarapé Camaipi	Brazil	00 01 27 S 51 53 50 W
	Allobates	femoralis	OMNH36070	DQ502092	DQ502092	Alfe-H32	1-23	2-17	3-10	4-5	5-2	#######	Alfe-H11	Porto Walter	Brazil	08 15 31 S 72 46 37 W
	Allobates	femoralis	230AF	#######	EU201064	Alfe-H01	1-1	2-1	3-1	4-1	5-1	#######	Alfe-H02	Angouleme	French Guiana	05 23 00 N 53 39 00 W
	Allobates	femoralis	226AF	#######	EU201064	Alfe-H01	1-1	2-1	3-1	4-1	5-1	#######	Alfe-H10	Angouleme	French Guiana	05 23 00 N 53 39 00 W
	Allobates	femoralis	231AF	#######	EU201064	Alfe-H01	1-1	2-1	3-1	4-1	5-1	#######	Alfe-H12	Angouleme	French Guiana	05 23 00 N 53 39 00 W
	Allobates	femoralis	T-4468	#######	EU201064	Alfe-H01	1-1	2-1	3-1	4-1	5-1	#######	Alfe-H10	Angoulème	French Guiana	05 23 00 N 53 39 00 W
	Allobates	femoralis	386CM	#######	EU201064	Alfe-H01	1-1	2-1	3-1	4-1	5-1	#######	Alfe-H10	Apatou	French Guiana	05 10 00 N 54 20 00 W
	Allobates	femoralis	179PG	#######	EU201064	Alfe-H01	1-1	2-1	3-1	4-1	5-1	#######	Alfe-H07	Aratai	French Guiana	03 59 41 N 52 35 45 W
	Allobates	femoralis	314CM	#######	EU201064	Alfe-H01	1-1	2-1	3-1	4-1	5-1	#######	Alfe-H10	crique Sparouine bassin du Maroni	French Guiana	05 16 00 N 54 16 00 W
	Allobates	femoralis	399CM	#######	EU201064	Alfe-H01	1-1	2-1	3-1	4-1	5-1	#######	Alfe-H07	Lucifer	French Guiana	04 46 00 N 53 55 00 W
	Allobates	femoralis	472PG	#######	EU201064	Alfe-H01	1-1	2-1	3-1	4-1	5-1	#######	Alfe-H10	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
	Allobates	femoralis	235AF	#######	EU201064	Alfe-H01	1-1	2-1	3-1	4-1	5-1	#######	Alfe-H01	Montagne des singes	French Guiana	05 04 00 N 52 43 00 W
	Allobates	femoralis	195AF	#######	EU201064	Alfe-H01	1-1	2-1	3-1	4-1	5-1	#######	Alfe-H09	Montagne des singes	French Guiana	05 04 00 N 52 43 00 W
	Allobates	femoralis	97BM	#######	EU201064	Alfe-H01	1-1	2-1	3-1	4-1	5-1	#######	Alfe-H07	Monts Bakra	French Guiana	03 18 08 N 52 56 73 W
	Allobates	femoralis	56AF	#######	EU201064	Alfe-H01	1-1	2-1	3-1	4-1	5-1	#######	Alfe-H01	Petit-saut	French Guiana	05 04 00 N 53 03 00 W
	Allobates	femoralis	57AF	#######	EU201064	Alfe-H01	1-1	2-1	3-1	4-1	5-1	#######	Alfe-H02	Petit-saut	French Guiana	05 04 00 N 53 03 00 W
	Allobates	femoralis	24AF	#######	EU201064	Alfe-H01	1-1	2-1	3-1	4-1	5-1	#######	Alfe-H06	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Allobates	femoralis	35AF	#######	EU201064	Alfe-H01	1-1	2-1	3-1	4-1	5-1	#######	Alfe-H07	Saül2	French Guiana	03 36 00 N 53 17 00 W
	Allobates	femoralis	32RB	#######	EU201064	Alfe-H01	1-1	2-1	3-1	4-1	5-1	#######	Alfe-H10	St Eugene	French Guiana	04 51 00 N 53 04 00 W
	Allobates	femoralis	106BM	#######	EU201064	Alfe-H01	1-1	2-1	3-1	4-1	5-1	#######	Alfe-H07	Trinité	French Guiana	04 35 00 N 53 21 00 W
	Allobates	femoralis	303CM	#######	EU201065	Alfe-H19	1-17	2-12	3-4	4-2	5-1	#######	Alfe-H02	Lac Toponowini	French Guiana	03 03 10 N 52 42 37 W
	Allobates	femoralis	246AF	#######	#######	Alfe-H08	1-5	2-4	3-3	4-1	5-1		Alfe-NA	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
	Allobates	femoralis	12007SMNS	#######	#######	Alfe-H16	1-15	2-11	3-4	4-2	5-2		Alfe-NA	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Allobates	femoralis	WED55470;KU205291	AY326026	AY326026	Alfe-H30	1-26	2-19	3-11	4-5	5-2		Alfe-NA	Cusco Amazonico	Peru	12 32 27 S 69 03 09 W
	Allobates	femoralis	WED55560;KU205292	AY326027	AY326027	Alfe-H29	1-25	2-19	3-11	4-5	5-2		Alfe-NA	Cusco Amazonico	Peru	12 32 27 S 69 03 09 W
	Allobates	femoralis	LSUMZ17552	DQ283045	DQ283045	Alfe-H23	1-8	2-7	3-5	4-3	5-1		Alfe-NA	Parque Estadual Guajira-Mirim	Brazil	10 19 17 S 64 33 48 W
	Allobates	femoralis	KU215179	DQ501990	DQ501990	Alfe-H27	1-24	2-18	3-11	4-5	5-2		Alfe-NA	Cusco Amazonico	Peru	12 32 27 S 69 03 09 W
	Allobates	femoralis	KU215177	DQ502014	DQ502014	Alfe-H28	1-24	2-18	3-11	4-5	5-2		Alfe-NA	Cusco Amazonico	Peru	12 32 27 S 69 03 09 W
	Allobates	femoralis	KU215180	DQ502015	DQ502015	Alfe-H28	1-24	2-18	3-11	4-5	5-2		Alfe-NA	Cusco Amazonico	Peru	12 32 27 S 69 03 09 W
	Allobates	femoralis	MPEG13415	DQ502088	DQ502088	Alfe-H23	1-8	2-7	3-5	4-3	5-1		Alfe-NA	Parque Estadual Guajira-Mirim	Brazil	10 19 17 S 64 33 48 W
	Allobates	femoralis	OMNH34568	DQ502089	DQ502089	Alfe-H21	1-10	2-9	3-6	4-2	5-1		Alfe-NA	Santarem	Brazil	03 09 00 S 54 50 00 W
	Allobates	femoralis	OMNH34572	DQ502090	DQ502090	Alfe-H21	1-10	2-9	3-6	4-2	5-1		Alfe-NA	Santarem	Brazil	03 09 00 S 54 50 00 W
	Allobates	femoralis	OMNH36066	DQ502091	DQ502091	Alfe-H31	1-22	2-17	3-10	4-5	5-2		Alfe-NA	Porto Walter	Brazil	08 15 31 S 72 46 37 W
	Allobates	femoralis	OMNH34102	DQ502093	DQ502093	Alfe-H35	1-21	2-16	3-9	4-4	5-1		Alfe-NA	Sucumbios	Ecuador	00 00 33 S 76 35 23 W
	Allobates	femoralis	OMNH34104	DQ502094	DQ502094	Alfe-H34	1-21	2-16	3-9	4-4	5-1		Alfe-NA	Sucumbios	Ecuador	00 00 33 S 76 35 23 W
	Allobates	femoralis	MJH3976	DQ502113	DQ502113	Alfe-H26	1-20	2-15	3-8	4-3	5-1		Alfe-NA	Reserva florestal A.ducke	Brazil	02 58 51 S 59 55 16 W
	Allobates	femoralis	MJH7354	DQ502117	DQ502117	Alfe-H25	1-19	2-14	3-7	4-3	5-1		Alfe-NA	Huanuco	Peru	09 23 02 S 75 52 57 W
	Allobates	femoralis	MPEG12021	DQ502220	DQ502220	Alfe-H22	1-11	2-9	3-6	4-2	5-1		Alfe-NA	Santarem	Brazil	03 09 00 S 54 50 00 W
	Allobates	femoralis	LSU12798	DQ502228	DQ502228	Alfe-H34	1-21	2-16	3-9	4-4	5-1		Alfe-NA	Sucumbios	Ecuador	00 00 33 S 76 35 23 W
	Allobates	femoralis	OMNH36073	DQ502231	DQ502231	Alfe-H33	1-23	2-17	3-10	4-5	5-2		Alfe-NA	Porto Walter	Brazil	08 15 31 S 72 46 37 W
	Allobates	femoralis	UTAA56478	DQ502246	DQ502246	Alfe-H14	1-14	2-11	3-4	4-2	5-1		Alfe-NA	Sipaliwini	Suriname	02 02 00 N 56 07 00 W
	Allobates	femoralis	6AF	#######	EU201064	Alfe-H01	1-1	2-1	3-1	4-1	5-1		Alfe-NA	Comté Terrain	French Guiana	04 41 30 N 52 24 00 W
	Allobates	femoralis	401CM	#######	EU201064	Alfe-H01	1-1	2-1	3-1	4-1	5-1		Alfe-NA	Lucifer	French Guiana	04 46 00 N 53 55 00 W
	Allobates	femoralis	18AF	#######	EU201064	Alfe-H01	1-1	2-1	3-1	4-1	5-1		Alfe-NA	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Allobates	femoralis	25AF	#######	EU201064	Alfe-H01	1-1	2-1	3-1	4-1	5-1		Alfe-NA	Saül1	French Guiana	03 37 32 N 53 12 26 W
CGsp	Allobates	gasconi	MPEG13003	DQ502052	DQ502052									Amazonas, Rio Ituxi, Scheffer Madeireira	Brazil	08 28 45 S 65 42 59 W
	Allobates	granti	231CM	#######	#######	Algr-H02	1-1	2-1	3-1			#######	Algr-H01	Saül1	French Guiana	03 37 32 N 53 12 26 W

	Genus	Species	Specimen	Seq1	Seq2	Hap1						Seq3	Hap2	Locality	Country	Coordinates
	Allobates	granti	302CM	#######	#######	Algr-H05	1-2	2-2	3-1			#######	Algr-H01	Lac Toponowini	French Guiana	03 03 10 N 52 42 37 W
	Allobates	granti	175PG	#######	#######	Algr-H03	1-2	2-2	3-1			#######	Algr-H01	Armontabo	French Guiana	03 48 16 N 52 17 17 W
	Allobates	granti	125PG	#######	#######	Algr-H05	1-2	2-2	3-1			#######	Algr-H01	Lac Toponowini	French Guiana	03 03 10 N 52 42 37 W
	Allobates	granti	301PG	#######	#######	Algr-H06	1-2	2-2	3-1			#######	Algr-H01	Haut Marwini	French Guiana	02 36 55 N 54 01 58 W
	Allobates	granti	233PG	#######	#######	Algr-H07	1-3	2-2	3-1			#######	Algr-H01	Haute Wanapi	French Guiana	02 30 57 N 53 49 56 W
	Allobates	granti	1054 BPN	#######	#######	Algr-H08	1-4	2-3	3-2			#######	Algr-H05	Lely Mountain	Suriname	04 16 00 N 54 44 00 W
	Allobates	granti	1055 BPN	#######	#######	Algr-H09	1-4	2-3	3-2			#######	Algr-H03	Lely Mountain	Suriname	04 16 00 N 54 44 00 W
	Allobates	granti	1056 BPN	#######	#######	Algr-H10	1-4	2-3	3-2			#######	Algr-H06	Lely Mountain	Suriname	04 16 00 N 54 44 00 W
	Allobates	granti	778 BPN	#######	#######	Algr-H11	1-5	2-3	3-2			#######	Algr-H02	Ralleighvallen	Suriname	04 43 00 N 56 13 00 W
	Allobates	granti	166 PG	#######	EU201066	Algr-H04	1-2	2-2	3-1			#######	Algr-H01	Armontabo	French Guiana	03 48 16 N 52 17 17 W
	Allobates	granti	591 PG	#######	EU201066	Algr-H04	1-2	2-2	3-1			#######	Algr-H01	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
	Allobates	granti	185 CM	#######	EU201066	Algr-H04	1-2	2-2	3-1			#######	Algr-H01	Trijonction	French Guiana	02 20 00 N 54 36 00 W
	Allobates	granti	299 PG	#######	EU201066	Algr-H04	1-2	2-2	3-1			#######	Algr-H01	Haut Marwini	French Guiana	02 36 55 N 54 01 58 W
	Allobates	granti	300 PG	#######	EU201066	Algr-H04	1-2	2-2	3-1			#######	Algr-H01	Haut Marwini	French Guiana	02 36 55 N 54 01 58 W
	Allobates	granti	T-3041 T	#######	EU201066	Algr-H04	1-2	2-2	3-1			#######	Algr-H01	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
	Allobates	granti	405 CM	#######	EU201067	Algr-H01	1-1	2-1	3-1			#######	Algr-H01	Lucifer	French Guiana	04 46 00 N 53 55 00 W
	Allobates	granti	406 CM	#######	EU201067	Algr-H01	1-1	2-1	3-1			#######	Algr-H01	Lucifer	French Guiana	04 46 00 N 53 55 00 W
	Allobates	granti	406 PG	#######	EU201067	Algr-H01	1-1	2-1	3-1			#######	Algr-H01	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
	Allobates	granti	467 PG	#######	EU201067	Algr-H01	1-1	2-1	3-1			#######	Algr-H01	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
	Allobates	granti	468 PG	#######	EU201067	Algr-H01	1-1	2-1	3-1			#######	Algr-H01	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
	Allobates	granti	275 AF	#######	EU201067	Algr-H01	1-1	2-1	3-1			#######	Algr-H01	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
	Allobates	granti	276 AF	#######	EU201067	Algr-H01	1-1	2-1	3-1			#######	Algr-H01	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
	Allobates	granti	206 CM	#######	EU201067	Algr-H01	1-1	2-1	3-1			#######	Algr-H01	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Allobates	granti	E49-5 RB	#######	EU201067	Algr-H01	1-1	2-1	3-1			#######	Algr-H01	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Allobates	granti	1612 BPN	#######	EU201067	Algr-H01	1-1	2-1	3-1			#######	Algr-H07	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Allobates	granti	38 RB	#######	EU201067	Algr-H01	1-1	2-1	3-1			#######	Algr-H01	St Eugene	French Guiana	04 51 00 N 53 04 00 W
	Allobates	granti	1687 BPN	#######	EU201067	Algr-H01	1-1	2-1	3-1			#######	Algr-H01	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Allobates	granti	1586 BPN	#######	EU201067	Algr-H01	1-1	2-1	3-1			#######	Algr-H01	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Allobates	granti	154 AF	#######	EU201068	Algr-H12	1-5	2-3	3-2			#######	Algr-H02	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Allobates	granti	148 AF	#######	EU201068	Algr-H12	1-5	2-3	3-2			#######	Algr-H04	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Allobates	granti	158 AF	#######	EU201068	Algr-H12	1-5	2-3	3-2			#######	Algr-H04	Brownsberg	Suriname	04 56 31 N 55 10 33 W
CGsp	Allobates	granti_2	E49-1 RB	#######	#######	Algr-H14						#######	Algr-H08	Saül1	French Guiana	03 37 32 N 53 12 26 W
CGsp	Allobates	granti_2	E49-2 RB	#######	EU201069	Algr-H13						#######	Algr-H08	Saül1	French Guiana	03 37 32 N 53 12 26 W
CGsp	Allobates	granti_2	E49-4 RB	#######	EU201069	Algr-H13						#######	Algr-H08	Saül1	French Guiana	03 37 32 N 53 12 26 W
CGsp	Allobates	granti_2	49 BM	#######	EU201069	Algr-H13						#######	Algr-H08	Saül1	French Guiana	03 34 00 N 53 13 00 W
CGsp	Allobates	granti_2	100 PG	#######	EU201069	Algr-H13							Algr-NA	Saül1	French Guiana	03 34 00 N 53 13 00 W
CGsp	Allobates	granti_2	101 PG	#######	EU201069	Algr-H13							Algr-NA	Saül1	French Guiana	03 34 00 N 53 13 00 W
CGsp	Allobates	insperatus	QCAZ16533	AY364557	AY364557										Ecuador	
CGsp	Allobates	juanii	ARA2394	DQ502271	DQ502271									Meta, Villavicencio, Pozo Azul, 560 m	Colombia	
CGsp	Allobates	kingsburyi	QCAZ16613	AY364550	AY364550										Ecuador	
CGsp	Allobates	nidicola	MPEG13819	DQ502210	DQ502210									Amazonas, Castanho, ca. 40 km S Manaus, at km 12 on road to Autazes	Brazil	03 37 10 S 59 86 00 W
CGsp	Allobates	sp.	MTR10.007	#######	#######							#######		Lago Cipotuba	Brazil	05 48 05 S 60 13 16 W
CGsp	Allobates	sp.	MTR10.054	#######	#######							#######		Santa Maria (Terra Preta)	Brazil	05 47 52 S 60 15 55 W
CGsp	Allobates	sp.	MTR10.084	#######	#######							#######		Santa Maria (Terra Preta)	Brazil	05 47 52 S 60 15 55 W
CGsp	Allobates	sp.	QCAZ16609	AY364561	AY364561										Ecuador	
CGsp	Allobates	sp.	QCAZ16601	AY364578	AY364578	Alfe-zaparo	1-27	2-20	3-14	4-7	5-3		Algr-NA		Ecuador	
CGsp	Allobates	sp. "Cuyabeno"	LSUMZ12948	DQ502239	DQ502239									Sucumbios, Estacion Cientifica de Universidad Catolica near Reserva Faunistica Cuyabeno	Ecuador	00 00 00 S 76 10 00 W
CGsp	Allobates	sp._"Magdalena"	MUJ3520	DQ502272	DQ502272									Caldas, La Dorada, San Roque, Reserva Natural Privada Riomanso, 280 m	Colombia	05 40 00 N 74 46 00 W
CGsp	Allobates	sp._"Manaus1"	MPEG12978	DQ502098	DQ502098									Amazonas, Rio Ituxi, Scheffer Madeireira		08 28 45 S 65 42 59 W
CGsp	Allobates	sp._"Nebulina"	AMCC106112	DQ502074	DQ502074									Amazonas, Rio Negro, Neblina Base, Camp on Rio Mawarinuma, 140 m	Venezuela	00 50 00 N 66 10 00 W
CGsp	Allobates	sp._"PEGM1"	LSUMZ17601	DQ502136	DQ502136									Rondonia, Parque Estadual Guajara-Mirim,	Brazil	10 19 17 S 64 33 48 W
CGsp	Allobates	sp._"PortoWalter2"	OMNH36026	DQ502198	DQ502198									Acre, Porto Walter	Brazil	08 15 31 S 72 46 37 W
CGsp	Allobates	sp._"ReservaDucke"	MJH3988	DQ502115	DQ502115									Amazonas, Reserva Florestal Adolfo Ducke		
CGsp	Allobates	sp._"RioItuxi"	MPEG13827	DQ502240	DQ502240									Amazonas, Castanho, ca. 40 km S Manaus, at km 12 on road to Autazes	Brazil	03 37 10 S 59 86 00 W
CGsp	Allobates	sp._"SaoFrancisco"	MJH3909	DQ502109	DQ502109									Amazonas, Facenda Sao Francisco, 2 km N km 49 on Manaus-Manacapuru road	Brazil	

Code	Genus	Species	Voucher	Gene1	Gene2	Hap1					Gene3	Hap2	Locality	Country	Coordinates
CGsp	*Allobates*	*sp.PEGM2*	OMNH36959	DQ502184	DQ502184								Rondonia, Parque Estadual Guajara-Mirim,	Brazil	10 19 17 S 64 33 48 W
CGsp	*Allobates*	*sp.PEGM3*	MPEG13386	DQ502139	DQ502139								Rondonia, Parque Estadual Guajara-Mirim,	Brazil	10 19 17 S 64 33 48 W
CGsp	*Allobates*	*sp.PEGM3*	MPEG13383	DQ502241	DQ502241								Rondonia, Parque Estadual Guajara-Mirim,	Brazil	10 19 17 S 64 33 48 W
CGsp	*Allobates*	*talamancae*	USNM-FS52055	AY843577	AY843577								Bocas del Toro	Panama	
CGsp	*Allobates*	*trilineatus*	MJH7477	DQ502118	DQ502118								Huanuco, Rio Llullapichis, Panguana	Peru	09 23 02 S 75 52 57 W
CGsp	*Allobates*	*undulatus*	AMNHA159139	DQ283044	DQ283044								Amazonas, Cerro Yutaje, 1700 m,	Venezuela	05 46 00 N 66 08 00 W
OGsp	*Ameerega*	*rivittata*	ICN50437								DQ503173		Amazonas, Leticia, Km 11(Leticia-Tarapaca)	Colombia	
OGsp	*Anaxyrus*	*boreas*	MVZ223292	DQ158436	DQ158436										
CGsp	*Anomaloglossus*	*sp. "Ayanganna"*	ROM39639	DQ502129	DQ502129						DQ503163		Mt Ayanganna northeast plateau1490-1550 m	Guyana	05 24 00 N 59 57 00 W
	Anomaloglossus	*baeobatrachus*	214 AF	#######	#######	Anba-H01	1-1	2-1	3-1	4-1	#######	Anba-H01	Angouleme	French Guiana	05 23 00 N 53 39 00 W
	Anomaloglossus	*baeobatrachus*	217 AF	#######	#######	Anba-H01	1-1	2-1	3-1	4-1	#######	Anba-H01	Angouleme	French Guiana	05 23 00 N 53 39 00 W
	Anomaloglossus	*baeobatrachus*	208 AF	#######	#######	Anba-H01	1-1	2-1	3-1	4-1	#######	Anba-H02	Angouleme	French Guiana	05 23 00 N 53 39 00 W
	Anomaloglossus	*baeobatrachus*	210 AF	#######	#######	Anba-H01	1-1	2-1	3-1	4-1	#######	Anba-H02	Angouleme	French Guiana	05 23 00 N 53 39 00 W
	Anomaloglossus	*baeobatrachus*	295 CM	#######	#######	Anba-H01	1-1	2-1	3-1	4-1	#######	Anba-H01	Camp Canopé	French Guiana	04 53 37 N 52 47 57 W
	Anomaloglossus	*baeobatrachus*	217 BM	#######	#######	Anba-H01	1-1	2-1	3-1	4-1	#######	Anba-H01	Kaw1	French Guiana	04 31 00 N 52 02 00 W
	Anomaloglossus	*baeobatrachus*	296 AF	#######	#######	Anba-H01	1-1	2-1	3-1	4-1	#######	Anba-H02	Kaw1	French Guiana	04 31 00 N 52 02 00 W
	Anomaloglossus	*baeobatrachus*	346 CM	#######	#######	Anba-H01	1-1	2-1	3-1	4-1	#######	Anba-H01	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Anomaloglossus	*baeobatrachus*	291 AF	#######	#######	Anba-H01	1-1	2-1	3-1	4-1	#######	Anba-H02	Kaw3	French Guiana	04 32 53 N 52 09 07 W
	Anomaloglossus	*baeobatrachus*	289 AF	#######	#######	Anba-H01	1-1	2-1	3-1	4-1	#######	Anba-H02	Montagne des singes	French Guiana	05 04 00 N 52 43 00 W
	Anomaloglossus	*baeobatrachus*	254 AF	#######	#######	Anba-H01	1-1	2-1	3-1	4-1	#######	Anba-H01	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
	Anomaloglossus	*baeobatrachus*	238 CM	#######	#######	Anba-H01	1-1	2-1	3-1	4-1	#######	Anba-H01	Piste St Elie	French Guiana	05 17 01 N 53 03 14 W
	Anomaloglossus	*baeobatrachus*	236 CM	#######	#######	Anba-H01	1-1	2-1	3-1	4-1	#######	Anba-H01	St Elie	French Guiana	04 50 00 N 53 15 00 W
	Anomaloglossus	*baeobatrachus*	36 RB	#######	#######	Anba-H01	1-1	2-1	3-1	4-1	#######	Anba-H01	St Eugene	French Guiana	04 51 00 N 53 04 00 W
	Anomaloglossus	*baeobatrachus*	37 RB	#######	#######	Anba-H01	1-1	2-1	3-1	4-1	#######	Anba-H01	St Eugene	French Guiana	04 51 00 N 53 04 00 W
	Anomaloglossus	*baeobatrachus*	300 AG	#######	#######	Anba-H01	1-1	2-1	3-1	4-1	#######	Anba-H01	Trinité	French Guiana	04 35 00 N 53 21 00 W
	Anomaloglossus	*baeobatrachus*	312 AG	#######	#######	Anba-H01	1-1	2-1	3-1	4-1	#######	Anba-H01	Trinité	French Guiana	04 35 00 N 53 21 00 W
	Anomaloglossus	*baeobatrachus*	304 AG	#######	#######	Anba-H01	1-1	2-1	3-1	4-1	#######	Anba-H10	Trinité	French Guiana	04 35 00 N 53 21 00 W
	Anomaloglossus	*baeobatrachus*	424 CM	#######	#######	Anba-H02	1-1	2-1	3-1	4-1	#######	Anba-H01	Cacao	French Guiana	04 34 00 N 52 28 00 W
	Anomaloglossus	*baeobatrachus*	243 AF	#######	#######	Anba-H02	1-1	2-1	3-1	4-1	#######	Anba-H01	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
	Anomaloglossus	*baeobatrachus*	271 AF	#######	#######	Anba-H02	1-1	2-1	3-1	4-1	#######	Anba-H02	Nouragues2	French Guiana	04 05 30 N 52 42 00 W
	Anomaloglossus	*baeobatrachus*	207 AF	#######	#######	Anba-H03	1-1	2-1	3-1	4-1	#######	Anba-H01	Angouleme	French Guiana	05 23 00 N 53 39 00 W
	Anomaloglossus	*baeobatrachus*	216 AF	#######	#######	Anba-H03	1-1	2-1	3-1	4-1	#######	Anba-H01	Angouleme	French Guiana	05 23 00 N 53 39 00 W
	Anomaloglossus	*baeobatrachus*	55 AF	#######	#######	Anba-H04	1-1	2-1	3-1	4-1	#######	Anba-H09	Petit-saut	French Guiana	05 04 00 N 53 03 00 W
	Anomaloglossus	*baeobatrachus*	23 RB	#######	#######	Anba-H05	1-1	2-1	3-1	4-1	#######	Anba-H01	St Eugene	French Guiana	04 51 00 N 53 04 00 W
	Anomaloglossus	*baeobatrachus*	382 CM	#######	#######	Anba-H07	1-2	2-1	3-1	4-1	#######	Anba-H02	Régina	French Guiana	04 18 00 N 52 07 00 W
	Anomaloglossus	*baeobatrachus*	59 CM	#######	#######	Anba-H09	1-3	2-2	3-1	4-1	#######	Anba-H01	Monts Bakra	French Guiana	03 18 08 N 52 56 73 W
	Anomaloglossus	*baeobatrachus*	60 CM	#######	#######	Anba-H09	1-3	2-2	3-1	4-1	#######	Anba-H01	Monts Bakra	French Guiana	03 18 08 N 52 56 73 W
	Anomaloglossus	*baeobatrachus*	266 CM	#######	#######	Anba-H11	1-4	2-1	3-1	4-1	#######	Anba-H01	DZ5	French Guiana	04 03 00 N 52 01 00 W
	Anomaloglossus	*baeobatrachus*	106 PG	#######	#######	Anba-H12	1-5	2-3	3-1	4-1	#######	Anba-H01	Mont Saint Marcel	French Guiana	02 23 09 N 53 00 58 W
	Anomaloglossus	*baeobatrachus*	107 PG	#######	#######	Anba-H12	1-5	2-3	3-1	4-1	#######	Anba-H03	Mont Saint Marcel	French Guiana	02 23 09 N 53 00 58 W
	Anomaloglossus	*baeobatrachus*	124 PG	#######	#######	Anba-H13	1-6	2-3	3-1	4-1	#######	Anba-H11	Lac Toponowini	French Guiana	03 03 10 N 52 42 37 W
	Anomaloglossus	*baeobatrachus*	92 PG	#######	#######	Anba-H14	1-6	2-3	3-1	4-1	#######	Anba-H01	Mont Saint Marcel	French Guiana	02 23 09 N 53 00 58 W
	Anomaloglossus	*baeobatrachus*	1699 BPN	#######	#######	Anba-H10	1-3	2-2	3-1	4-1	#######	Anba-H01	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Anomaloglossus	*baeobatrachus*	1480 BPN	#######	#######	Anba-H06	1-2	2-1	3-1	4-1	#######	Anba-H01	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Anomaloglossus	*baeobatrachus*	1629 BPN	#######	#######	Anba-H10	1-3	2-2	3-1	4-1	#######	Anba-H01	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Anomaloglossus	*baeobatrachus*	239 PG	#######	#######	Anba-H20	1-9	2-6	3-3	4-2	#######	Anba-H01	Haute Wanapi	French Guiana	02 30 57 N 53 49 56 W
	Anomaloglossus	*baeobatrachus*	246 PG	#######	#######	Anba-H20	1-9	2-6	3-3	4-2	#######	Anba-H01	Haute Wanapi	French Guiana	02 30 57 N 53 49 56 W
	Anomaloglossus	*baeobatrachus*	572 PG	#######	#######	Anba-H20	1-9	2-6	3-3	4-2	#######	Anba-H01	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
	Anomaloglossus	*baeobatrachus*	91 PG	#######	#######	Anba-H20	1-9	2-6	3-3	4-2	#######	Anba-H01	Mont Saint Marcel	French Guiana	02 23 09 N 53 00 58 W
	Anomaloglossus	*baeobatrachus*	T-3030 T	#######	#######	Anba-H21	1-9	2-6	3-3	4-2	#######	Anba-H01	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
	Anomaloglossus	*baeobatrachus*	414 CM	#######	#######	Anba-H22	1-10	2-6	3-3	4-2	#######	Anba-H01	Lucifer	French Guiana	04 46 00 N 53 55 00 W
	Anomaloglossus	*baeobatrachus*	465 PG	#######	#######	Anba-H22	1-10	2-6	3-3	4-2	#######	Anba-H01	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
	Anomaloglossus	*baeobatrachus*	466 PG	#######	#######	Anba-H22	1-10	2-6	3-3	4-2	#######	Anba-H01	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
	Anomaloglossus	*baeobatrachus*	13715 MTR	#######	#######	Anba-H22	1-10	2-6	3-3	4-2	#######	Anba-H01	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Anomaloglossus	*baeobatrachus*	13716 MTR	#######	#######	Anba-H22	1-10	2-6	3-3	4-2	#######	Anba-H01	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Anomaloglossus	*baeobatrachus*	13723 MTR	#######	#######	Anba-H22	1-10	2-6	3-3	4-2	#######	Anba-H01	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Anomaloglossus	*baeobatrachus*	13724 MTR	#######	#######	Anba-H22	1-10	2-6	3-3	4-2	#######	Anba-H01	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Anomaloglossus	*baeobatrachus*	13717 MTR	#######	#######	Anba-H22	1-10	2-6	3-3	4-2	#######	Anba-H04	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Anomaloglossus	*baeobatrachus*	13721 MTR	#######	#######	Anba-H22	1-10	2-6	3-3	4-2	#######	Anba-H08	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Anomaloglossus	*baeobatrachus*	305 CM	#######	#######	Anba-H23	1-10	2-6	3-3	4-2	#######	Anba-H01	Lac Toponowini	French Guiana	03 03 10 N 52 42 37 W
	Anomaloglossus	*baeobatrachus*	127 PG	#######	#######	Anba-H23	1-10	2-6	3-3	4-2	#######	Anba-H01	Lac Toponowini	French Guiana	03 03 10 N 52 42 37 W

	Genus	species	Voucher			Hap						Hap2	Locality	Country	Coordinates
	Anomaloglossus	*baeobatrachus*	128 PG	#######	#######	Anba-H23	1-10	2-6	3-3	4-2	#######	Anba-H01	Lac Toponowini	French Guiana	03 03 10 N 52 42 37 W
	Anomaloglossus	*baeobatrachus*	13833 MTR	#######	#######	Anba-H25	1-12	2-8	3-3	4-2	#######	Anba-H01	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Anomaloglossus	*baeobatrachus*	MRT6278	#######	#######	Anba-H24	1-11	2-7	3-3	4-2	#######	Anba-H01	Igarapé Camaipi	Brazil	00 01 27 S 51 53 50 W
	Anomaloglossus	*baeobatrachus*	13805 MTR	#######	#######	Anba-H19	1-9	2-6	3-3	4-2	#######	Anba-H05	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Anomaloglossus	*baeobatrachus*	13862 MTR	#######	#######	Anba-H16	1-8	2-5	3-2	4-2	#######	Anba-H01	Lourenço	Brazil	02 19 25 N 51 38 43 W
	Anomaloglossus	*baeobatrachus*	13856 MTR	#######	#######	Anba-H16	1-8	2-5	3-2	4-2	#######	Anba-H06	Lourenço	Brazil	02 19 25 N 51 38 43 W
	Anomaloglossus	*baeobatrachus*	13857 MTR	#######	#######	Anba-H16	1-8	2-5	3-2	4-2	#######	Anba-H12	Lourenço	Brazil	02 19 25 N 51 38 43 W
	Anomaloglossus	*baeobatrachus*	13863 MTR	#######	#######	Anba-H16	1-8	2-5	3-2	4-2	#######	Anba-H16	Lourenço	Brazil	02 19 25 N 51 38 43 W
	Anomaloglossus	*baeobatrachus*	13861 MTR	#######	#######	Anba-H17	1-8	2-5	3-2	4-2	#######	Anba-H12	Lourenço	Brazil	02 19 25 N 51 38 43 W
	Anomaloglossus	*baeobatrachus*	13929 MTR	#######	#######	Anba-H18	1-8	2-5	3-2	4-2	#######	Anba-H01	Lourenço	Brazil	02 19 25 N 51 38 43 W
	Anomaloglossus	*baeobatrachus*	13887 MTR	#######	#######	Anba-H15	1-7	2-4	3-2	4-2	#######	Anba-H01	Lourenço	Brazil	02 19 25 N 51 38 43 W
	Anomaloglossus	*baeobatrachus*	13877 MTR	#######	#######	Anba-H16	1-8	2-5	3-2	4-2	#######	Anba-H12	Lourenço	Brazil	02 19 25 N 51 38 43 W
	Anomaloglossus	*baeobatrachus*	13879 MTR	#######	#######	Anba-H16	1-8	2-5	3-2	4-2	#######	Anba-H12	Lourenço	Brazil	02 19 25 N 51 38 43 W
	Anomaloglossus	*baeobatrachus*	593 PG	#######	#######	Anba-H27	1-14	2-9	3-4	4-3	#######	Anba-H13	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
	Anomaloglossus	*baeobatrachus*	573 PG	#######	#######	Anba-H28	1-14	2-9	3-4	4-3	#######	Anba-H12	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
	Anomaloglossus	*baeobatrachus*	302 PG T	#######	#######	Anba-H29	1-15	2-9	3-4	4-3	#######	Anba-H13	Haut Marwini	French Guiana	02 36 55 N 54 01 58 W
	Anomaloglossus	*baeobatrachus*	T-3031 T	#######	#######	Anba-H26	1-13	2-9	3-4	4-3	#######	Anba-H14	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
	Anomaloglossus	*baeobatrachus*	590 PG	#######	#######	Anba-H26	1-13	2-9	3-4	4-3	#######	Anba-H15	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
	Anomaloglossus	*baeobatrachus*	149 AF	#######	#######	Anba-H30	1-16				#######	Anba-H17	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Anomaloglossus	*baeobatrachus*	151 AF	#######	#######	Anba-H30	1-16				#######	Anba-H17	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Anomaloglossus	*baeobatrachus*	156 AF	#######	#######	Anba-H30	1-16				#######	Anba-H17	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Anomaloglossus	*baeobatrachus*	188 AF	#######	#######	Anba-H30	1-16				#######	Anba-H17	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Anomaloglossus	*baeobatrachus*	122 AF	#######	#######	Anba-H30	1-16				#######	Anba-H18	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Anomaloglossus	*baeobatrachus*	849 BPN	#######	#######	Anba-H30	1-16				#######	Anba-H17	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Anomaloglossus	*baeobatrachus*	852 BPN	#######	#######	Anba-H30	1-16				#######	Anba-H17	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Anomaloglossus	*baeobatrachus*	853 BPN	#######	#######	Anba-H30	1-16				#######	Anba-H17	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Anomaloglossus	*baeobatrachus*	850 BPN	#######	#######	Anba-H30	1-16				#######	Anba-H18	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Anomaloglossus	*baeobatrachus*	851 BPN	#######	#######	Anba-H31	1-16				#######	Anba-H17	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Anomaloglossus	*baeobatrachus*	T-2532 T	#######	EU201070	Anba-H10	1-3	2-2	3-1	4-1	#######	Anba-H01	Pic Matecho	French Guiana	03 45 00 N 53 02 00 W
	Anomaloglossus	*baeobatrachus*	T-2533 T	#######	EU201070	Anba-H10	1-3	2-2	3-1	4-1	#######	Anba-H01	Pic Matecho	French Guiana	03 45 00 N 53 02 00 W
	Anomaloglossus	*baeobatrachus*	T-2565 T	#######	EU201070	Anba-H10	1-3	2-2	3-1	4-1	#######	Anba-H01	Pic Matecho	French Guiana	03 45 00 N 53 02 00 W
	Anomaloglossus	*baeobatrachus*	T-2566 T	#######	EU201070	Anba-H10	1-3	2-2	3-1	4-1	#######	Anba-H01	Pic Matecho	French Guiana	03 45 00 N 53 02 00 W
	Anomaloglossus	*baeobatrachus*	22 AF	#######	EU201070	Anba-H10	1-3	2-2	3-1	4-1	#######	Anba-H01	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Anomaloglossus	*baeobatrachus*	23 AF	#######	EU201070	Anba-H10	1-3	2-2	3-1	4-1	#######	Anba-H01	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Anomaloglossus	*baeobatrachus*	220 CM	#######	EU201070	Anba-H10	1-3	2-2	3-1	4-1	#######	Anba-H01	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Anomaloglossus	*baeobatrachus*	E49-3 RB	#######	EU201070	Anba-H10	1-3	2-2	3-1	4-1	#######	Anba-H01	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Anomaloglossus	*baeobatrachus*	592 PG	#######	EU201071	Anba-H26	1-13	2-9	3-4	4-3	#######	Anba-H12	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
	Anomaloglossus	*baeobatrachus*	T-3023 T	#######	EU201071	Anba-H26	1-13	2-9	3-4	4-3	#######	Anba-H13	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
	Anomaloglossus	*baeobatrachus*	T-3024 T	#######	EU201071	Anba-H26	1-13	2-9	3-4	4-3	#######	Anba-H14	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
	Anomaloglossus	*baeobatrachus*	T-3033 T	#######	EU201071	Anba-H26	1-13	2-9	3-4	4-3	#######	Anba-H14	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
	Anomaloglossus	*baeobatrachus*	182 CM	#######	EU201071	Anba-H26	1-13	2-9	3-4	4-3	#######	Anba-H14	Trijonction	French Guiana	02 20 00 N 54 36 00 W
	Anomaloglossus	*baeobatrachus*	303 PG	#######	EU201072	Anba-H19	1-9	2-6	3-3	4-2	#######	Anba-H01	Haut Marwini	French Guiana	02 36 55 N 54 01 58 W
	Anomaloglossus	*baeobatrachus*	T-3040 T	#######	EU201072	Anba-H19	1-9	2-6	3-3	4-2	#######	Anba-H01	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
	Anomaloglossus	*baeobatrachus*	148 CM	#######	EU201072	Anba-H19	1-9	2-6	3-3	4-2	#######	Anba-H07	Trijonction	French Guiana	02 20 00 N 54 36 00 W
	Anomaloglossus	*baeobatrachus*	252 AF	#######	#######	Anba-H01	1-1	2-1	3-1	4-1		Adan-NA	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
	Anomaloglossus	*baeobatrachus*	244 AF	#######	#######	Anba-H07	1-2	2-1	3-1	4-1		Adan-NA	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
	Anomaloglossus	*baeobatrachus*	134 BM	#######	#######	Anba-H08	1-2	2-1	3-1	4-1		Adan-NA	Mataroni	French Guiana	04 12 00 N 52 10 00 W
	Anomaloglossus	*baeobatrachus*	UTAA56469	DQ502249	DQ502249	Anba-H30	1-16					Adan-NA	Brownsberg Nature Park	Suriname	04 56 31 N 55 10 33 W
	Anomaloglossus	*baeobatrachus*	PK-437-1	DQ501980	DQ501980	Anba-H10	1-3	2-2	3-1	4-1		Adan-NA	Pic Matecho	French Guiana	03 37 32 N 53 12 26 W
	Anomaloglossus	*baeobatrachus*	PK-437-2	DQ501981	DQ501981	Anba-H10	1-3	2-2	3-1	4-1		Adan-NA	Pic Matecho	French Guiana	03 37 32 N 53 12 26 W
	Anomaloglossus	*baeobatrachus*	PK-437-3	DQ501982	DQ501982	Anba-H10	1-3	2-2	3-1	4-1		Adan-NA	Pic Matecho	French Guiana	03 37 32 N 53 12 26 W
	Anomaloglossus	*baeobatrachus*	PK-437-4	DQ501983	DQ501983	Anba-H10	1-3	2-2	3-1	4-1		Adan-NA	Pic Matecho	French Guiana	03 37 32 N 53 12 26 W
	Anomaloglossus	*baeobatrachus*	T-3038 T	#######	EU201071	Anba-H26	1-13	2-9	3-4	4-3		Anba-NA	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
CGsp	*Anomaloglossus*	*beebei*	933 PK	#######	#######	Anbe-H1					#######		Kaieteur NP	Guyana	05 16 07 N 59 46 7 W
CGsp	*Anomaloglossus*	*beebei*	ROM39631	DQ502127	DQ502127	Anbe-H1							Mt Ayanganna northeast plateau 1490-1550 m	Guyana	05 24 00 N 59 57 00 W
CGsp	*Anomaloglossus*	*beebei*	ROM39632	DQ502130	DQ502130	Anbe-H1							Mt Ayanganna northeast plateau 1490-1550 m	Guyana	05 24 00 N 59 57 00 W
	Anomaloglossus	*degranvillei*	285 AF	#######	#######	Ande-H01	1-1	2-1	3-1	4-1	#######	Ande-H01	Montagne des singes	French Guiana	05 04 00 N 52 43 00 W
	Anomaloglossus	*degranvillei*	286 AF	#######	#######	Ande-H01	1-1	2-1	3-1	4-1	#######	Ande-H01	Montagne des singes	French Guiana	05 04 00 N 52 43 00 W
	Anomaloglossus	*degranvillei*	287 AF	#######	#######	Ande-H01	1-1	2-1	3-1	4-1	#######	Ande-H01	Montagne des singes	French Guiana	05 04 00 N 52 43 00 W
	Anomaloglossus	*degranvillei*	288 AF	#######	#######	Ande-H01	1-1	2-1	3-1	4-1	#######	Ande-H01	Montagne des singes	French Guiana	05 04 00 N 52 43 00 W
	Anomaloglossus	*degranvillei*	298 AG	#######	#######	Ande-H01	1-1	2-1	3-1	4-1	#######	Ande-H04	Trinité	French Guiana	04 35 00 N 53 21 00 W

Anomaloglossus	degranvillei	34 RB	#######	#######	Ande-H02	1-2	2-1	3-1	4-1	#######	Ande-H01	St Eugene	French Guiana	04 51 00 N 53 04 00 W
Anomaloglossus	degranvillei	305 AG	#######	#######	Ande-H03	1-2	2-1	3-1	4-1	#######	Ande-H01	Trinité	French Guiana	04 35 00 N 53 21 00 W
Anomaloglossus	degranvillei	17 RB	#######	#######	Ande-H04	1-1	2-1	3-1	4-1	#######	Ande-H01	St Eugene	French Guiana	04 51 00 N 53 04 00 W
Anomaloglossus	degranvillei	245 AF	#######	#######	Ande-H05	1-3	2-1	3-1	4-1	#######	Ande-H01	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
Anomaloglossus	degranvillei	258 AF	#######	#######	Ande-H05	1-3	2-1	3-1	4-1	#######	Ande-H01	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
Anomaloglossus	degranvillei	259 AF	#######	#######	Ande-H05	1-3	2-1	3-1	4-1	#######	Ande-H01	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
Anomaloglossus	degranvillei	260 AF	#######	#######	Ande-H05	1-3	2-1	3-1	4-1	#######	Ande-H01	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
Anomaloglossus	degranvillei	250 AF	#######	#######	Ande-H06	1-4	2-1	3-1	4-1	#######	Ande-H01	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
Anomaloglossus	degranvillei	215 AF	#######	#######	Ande-H07	1-5	2-2	3-1	4-1	#######	Ande-H01	Angouleme	French Guiana	05 23 00 N 53 39 00 W
Anomaloglossus	degranvillei	218 AF	#######	#######	Ande-H07	1-5	2-2	3-1	4-1	#######	Ande-H01	Angouleme	French Guiana	05 23 00 N 53 39 00 W
Anomaloglossus	degranvillei	225 AF	#######	#######	Ande-H07	1-5	2-2	3-1	4-1	#######	Ande-H01	Angouleme	French Guiana	05 23 00 N 53 39 00 W
Anomaloglossus	degranvillei	213 AF	#######	#######	Ande-H08	1-5	2-2	3-1	4-1	#######	Ande-H01	Angouleme	French Guiana	05 23 00 N 53 39 00 W
Anomaloglossus	degranvillei	220 AF	#######	#######	Ande-H08	1-5	2-2	3-1	4-1	#######	Ande-H01	Angouleme	French Guiana	05 23 00 N 53 39 00 W
Anomaloglossus	degranvillei	355 CM	#######	#######	Ande-H09	1-6	2-3	3-2	4-1	#######	Ande-H02	Lucifer	French Guiana	04 46 00 N 53 55 00 W
Anomaloglossus	degranvillei	357 CM	#######	#######	Ande-H09	1-6	2-3	3-2	4-1	#######	Ande-H02	Lucifer	French Guiana	04 46 00 N 53 55 00 W
Anomaloglossus	degranvillei	337A PG	#######	#######	Ande-H10	1-7	2-4	3-2	4-1	#######	Ande-H01	Monts Bakra	French Guiana	03 18 08 N 52 56 73 W
Anomaloglossus	degranvillei	337H PG	#######	#######	Ande-H10	1-7	2-4	3-2	4-1	#######	Ande-H01	Monts Bakra	French Guiana	03 18 08 N 52 56 73 W
Anomaloglossus	degranvillei	337I PG	#######	#######	Ande-H10	1-7	2-4	3-2	4-1	#######	Ande-H01	Monts Bakra	French Guiana	03 18 08 N 52 56 73 W
Anomaloglossus	degranvillei	337C PG	#######	#######	Ande-H10	1-7	2-4	3-2	4-1	#######	Ande-H02	Monts Bakra	French Guiana	03 18 08 N 52 56 73 W
Anomaloglossus	degranvillei	337G PG	#######	#######	Ande-H10	1-7	2-4	3-2	4-1	#######	Ande-H02	Monts Bakra	French Guiana	03 18 08 N 52 56 73 W
Anomaloglossus	degranvillei	1 RB	#######	#######	Ande-H10	1-7	2-4	3-2	4-1	#######	Ande-H01	Pic Matecho	French Guiana	03 45 00 N 53 02 00 W
Anomaloglossus	degranvillei	337F PG	#######	#######	Ande-H11	1-7	2-4	3-2	4-1	#######	Ande-H01	Monts Bakra	French Guiana	03 18 08 N 52 56 73 W
Anomaloglossus	degranvillei	337B PG	#######	#######	Ande-H11	1-7	2-4	3-2	4-1	#######	Ande-H02	Monts Bakra	French Guiana	03 18 08 N 52 56 73 W
Anomaloglossus	degranvillei	337D PG	#######	#######	Ande-H11	1-7	2-4	3-2	4-1	#######	Ande-H02	Monts Bakra	French Guiana	03 18 08 N 52 56 73 W
Anomaloglossus	degranvillei	337E PG	#######	#######	Ande-H11	1-7	2-4	3-2	4-1	#######	Ande-H02	Monts Bakra	French Guiana	03 18 08 N 52 56 73 W
Anomaloglossus	degranvillei	2 RB	#######	#######	Ande-H11	1-7	2-4	3-2	4-1	#######	Ande-H01	Pic Matecho	French Guiana	03 45 00 N 53 02 00 W
Anomaloglossus	degranvillei	69 CM	#######	#######	Ande-H10	1-7	2-4	3-2	4-1	#######	Ande-H01	Monts Bakra	French Guiana	03 18 08 N 52 56 73 W
Anomaloglossus	degranvillei	68 CM	#######	#######	Ande-H10	1-7	2-4	3-2	4-1	#######	Ande-H02	Monts Bakra	French Guiana	03 18 08 N 52 56 73 W
Anomaloglossus	degranvillei	458 PG	#######	#######	Ande-H12	1-8	2-5	3-3	4-1	#######	Ande-H01	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
Anomaloglossus	degranvillei	394 PG	#######	#######	Ande-H13	1-9	2-5	3-3	4-1	#######	Ande-H01	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
Anomaloglossus	degranvillei	395 PG	#######	#######	Ande-H13	1-9	2-5	3-3	4-1	#######	Ande-H01	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
Anomaloglossus	degranvillei	407 PG	#######	#######	Ande-H13	1-9	2-5	3-3	4-1	#######	Ande-H01	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
Anomaloglossus	degranvillei	459 PG	#######	#######	Ande-H13	1-9	2-5	3-3	4-1	#######	Ande-H03	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
Anomaloglossus	degranvillei	457 PG	#######	#######	Ande-H13	1-9	2-5	3-3	4-1	#######	Ande-H06	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
Anomaloglossus	degranvillei	462 PG	#######	#######	Ande-H13	1-9	2-5	3-3	4-1	#######	Ande-H07	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
Anomaloglossus	degranvillei	464 PG	#######	#######	Ande-H13	1-9	2-5	3-3	4-1	#######	Ande-H08	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
Anomaloglossus	degranvillei	460 PG	#######	#######	Ande-H14	1-9	2-5	3-3	4-1	#######	Ande-H01	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
Anomaloglossus	degranvillei	463 PG	#######	#######	Ande-H15	1-10	2-5	3-3	4-1	#######	Ande-H05	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
Anomaloglossus	degranvillei	393 PG	#######	#######	Ande-H16	1-11	2-5	3-3	4-1	#######	Ande-H01	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
Anomaloglossus	degranvillei	461 PG	#######	#######	Ande-H17	1-12	2-6	3-3	4-1	#######	Ande-H01	Pic Matecho	French Guiana	03 45 00 N 53 02 00 W
Anomaloglossus	degranvillei	T-2535 T	#######	#######	Ande-H17	1-12	2-6	3-3	4-1	#######	Ande-H01	Pic Matecho	French Guiana	03 45 00 N 53 02 00 W
Anomaloglossus	degranvillei	T-2563 T	#######	#######	Ande-H17	1-12	2-6	3-3	4-1	#######	Ande-H01	Saül1	French Guiana	03 37 32 N 53 12 26 W
Anomaloglossus	degranvillei	26 AF	#######	#######	Ande-H18	1-12	2-6	3-3	4-1	#######	Ande-H01	Pic Matecho	French Guiana	03 45 00 N 53 02 00 W
Anomaloglossus	degranvillei	T-2564 T	#######	#######	Ande-H19	1-13	2-6	3-3	4-1	#######	Ande-H01	Saül1	French Guiana	03 37 32 N 53 12 26 W
Anomaloglossus	degranvillei	E49-6 RB	#######	#######	Ande-H23	1-16	2-9	3-4	4-2	#######	Ande-H12	Brownsberg	Suriname	04 56 31 N 55 10 33 W
Anomaloglossus	degranvillei	152 AF	#######	#######	Ande-H24	1-16	2-9	3-4	4-2	#######	Ande-H09	Brownsberg	Suriname	04 56 31 N 55 10 33 W
Anomaloglossus	degranvillei	147 AF	#######	#######	Ande-H24	1-16	2-9	3-4	4-2	#######	Ande-H10	Brownsberg	Suriname	04 56 31 N 55 10 33 W
Anomaloglossus	degranvillei	139 AF	#######	#######	Ande-H25	1-17	2-9	3-4	4-2	#######	Ande-H13	Brownsberg	Suriname	04 56 31 N 55 10 33 W
Anomaloglossus	degranvillei	138 AF	#######	#######	Ande-H22	1-15	2-8	3-4	4-2	#######	Ande-H11	Tafelberg	Suriname	03 47 00 N 56 09 00 W
Anomaloglossus	degranvillei	837 BPN	#######	#######	Ande-H26	1-18	2-10	3-5	4-3	#######	Ande-H01	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
Anomaloglossus	degranvillei	T-3026 T	#######	#######	Ande-H26	1-18	2-10	3-5	4-3	#######	Ande-H01	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
Anomaloglossus	degranvillei	T-3029 T	#######	#######	Ande-H27	1-18	2-10	3-5	4-3	#######	Ande-H01	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
Anomaloglossus	degranvillei	T-3025 T	#######	#######	Ande-H28	1-1	2-1	3-1		#######	Ande-H14	Armontabo	French Guiana	03 48 16 N 52 17 17 W
Anomaloglossus	degranvillei	163 PG	#######	#######	Ande-H28	1-1	2-1	3-1		#######	Ande-H14	Armontabo	French Guiana	03 48 16 N 52 17 17 W
Anomaloglossus	degranvillei	164 PG	#######	#######	Ande-H28	1-1	2-1	3-1		#######	Ande-H14	Kaw2	French Guiana	04 43 00 N 52 08 00 W
Anomaloglossus	degranvillei	292 AF	#######	#######	Ande-H28	1-1	2-1	3-1		#######	Ande-H14	Kaw2	French Guiana	04 43 00 N 52 08 00 W
Anomaloglossus	degranvillei	293 AF	#######	#######	Ande-H28	1-1	2-1	3-1		#######	Ande-H14	Kaw2	French Guiana	04 43 00 N 52 08 00 W
Anomaloglossus	degranvillei	294 AF	#######	#######	Ande-H28	1-1	2-1	3-1		#######	Ande-H14	Montagne Petite Tortue	French Guiana	05 10 46 N 52 55 53 W
Anomaloglossus	degranvillei	329 CM	#######	#######	Ande-H28	1-1	2-1	3-1		#######	Ande-H14	Tibourou	French Guiana	04 25 00 N 52 18 00 W
Anomaloglossus	degranvillei	110 CM	#######	#######	Ande-H28	1-1	2-1	3-1		#######	Ande-H14	Tibourou	French Guiana	04 25 00 N 52 18 00 W
Anomaloglossus	degranvillei	113 CM	#######	#######	Ande-H28	1-1	2-1	3-1		#######	Ande-H14	Tibourou	French Guiana	04 25 00 N 52 18 00 W

	Genus	species	voucher			haplo						code	locality	country	coordinates
	Anomaloglossus	*degranvillei*	1369 BPN	#######	#######	Ande-H28	1-1	2-1	3-1		#######	Ande-H14	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Anomaloglossus	*degranvillei*	230 CM	#######	#######	Ande-H29	1-2	2-2	3-2		#######	Ande-H14	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Anomaloglossus	*degranvillei*	39 AF	#######	#######	Ande-H30	1-3	2-3	3-2		#######	Ande-H14	Saül2	French Guiana	03 36 00 N 53 17 00 W
	Anomaloglossus	*degranvillei*	T-2536 T	#######	#######	Ande-H17	1-12	2-6	3-3	4-1		Adan-NA	Pic Matecho	French Guiana	03 45 00 N 53 02 00 W
	Anomaloglossus	*degranvillei*	120 BM	#######	#######	Ande-H20	1-14	2-7	3-3	4-1		Adan-NA	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Anomaloglossus	*degranvillei*	125 BM	#######	#######	Ande-H21	1-14	2-7	3-3	4-1		Adan-NA	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Anomaloglossus	*degranvillei*	143 AF	#######	#######	Ande-H23	1-16	2-9	3-4	4-2		Adan-NA	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Anomaloglossus	*degranvillei*	38 AF	#######	#######	Ande-H30	1-3	2-3	3-2			Adan-NA	Saül2	French Guiana	03 36 00 N 53 17 00 W
CGsp	*Anomaloglossus*	*kaiei*	1159 PK	#######	#######	Anka-H1					#######	holotype	Kaieteur NP	Guyana	05 16 07 N 59 46 7 W
CGsp	*Anomaloglossus*	*kaiei*	1287 PK	#######	#######	Anka-H2					#######		Kaieteur NP	Guyana	05 16 07 N 59 46 7 W
CGsp	*Anomaloglossus*	*kaiei*	1303 PK	#######	#######	Anka-H3					#######		Kaieteur NP	Guyana	05 16 07 N 59 46 7 W
CGsp	*Anomaloglossus*	*kaiei*	?	DQ502019	DQ502019	Anka-H5							Mereme Mountains	Guyana	
CGsp	*Anomaloglossus*	*kaiei*	?	DQ502020	DQ502020	Anka-H6							Mereme Mountains	Guyana	
CGsp	*Anomaloglossus*	*kaiei*	CPI10209	DQ502257	DQ502257	Anka-H4							Mt. Roraima 1075 m	Guyana	
CGsp	*Anomaloglossus*	*praderioi*	CPI10208	DQ502256	DQ502256								Mt. Roraima 1310 m	Guyana	
CGsp	*Anomaloglossus*	*roraima*	CPI10216	DQ502258	DQ502258								Mt. Roraima 1860-2350	Guyana	
CGsp	*Anomaloglossus*	*stepheni*	93 AF	#######	#######	Anst-H1					#######		Road to Apura	Suriname	05 11 00 N 55 37 00 W
CGsp	*Anomaloglossus*	*stepheni*	96 AF	#######	#######	Anst-H1					#######		Road to Apura	Suriname	05 11 00 N 55 37 00 W
CGsp	*Anomaloglossus*	*stepheni*	1063 BPN	#######	#######	Anst-H3					#######		Lely Mountain	Suriname	04 16 00 N 54 44 00 W
CGsp	*Anomaloglossus*	*stepheni*	836 BPN	#######	#######	Anst-H3					#######		Tafelberg	Suriname	03 47 00 N 56 09 00 W
CGsp	*Anomaloglossus*	*stepheni*	10269 MTR	#######	#######	Anst-H4					#######		Igarapé-Araras	Brazil	03 00 32 S 60 23 49 W
CGsp	*Anomaloglossus*	*stepheni*	10270 MTR	#######	#######	Anst-H4					#######		Igarapé-Araras	Brazil	03 00 32 S 60 23 49 W
CGsp	*Anomaloglossus*	*stepheni*	95 AF	#######	#######	Anst-H1							Road to Apura	Suriname	05 11 00 N 55 37 00 W
CGsp	*Anomaloglossus*	*stepheni*	94 AF	#######	#######	Anst-H2							Road to Apura	Suriname	05 11 00 N 55 37 00 W
CGsp	*Anomaloglossus*	*stepheni*	MJH3928	DQ502107	DQ502107	Anst-H6							Reserva florestal A.ducke	Brazil	02 58 51 S 59 55 16 W
CGsp	*Anomaloglossus*	*stepheni*	MJH3950	DQ502108	DQ502108	Anst-H5							Reserva florestal A.ducke	Brazil	02 58 51 S 59 55 16 W
CGsp	*Anomaloglossus*	*tepuyensis*	1299 BPN	#######	#######	Anth-H1					#######		Mount Thomasing	Guyana	
CGsp	*Anomaloglossus*	*tepuyensis*	1304 BPN	#######	#######	Anth-H1					#######		Mount Thomasing	Guyana	
CGsp	*Anomaloglossus*	*tepuyensis*	1305 BPN	#######	#######	Anth-H1					#######		Mount Thomasing	Guyana	
CGsp	*Anomaloglossus*	*tepuyensis*	ROM39637	DQ502128	DQ502128						DQ503162		Mt Ayanganna northeast plateau 1490-1550 m	Guyana	05 24 00 N 59 57 00 W
CGsp	*Anomaloglossus*	*tepuyensis*	UTAA56709	DQ502253	DQ502253	Anth-H1							Mount Thomasing (~2 km N Imbaimadai)	Guyana	05 44 23 N 60 17 51 W
CGsp	*Anomaloglossus*	*tepuyensis*	UTAA56710	DQ502254	DQ502254	Anth-H1							Mount Thomasing (~2 km N Imbaimadai)	Guyana	05 44 23 N 60 17 51 W
OGsp	*Aromobates*	*nocturnus*	AMNHA130042	DQ502156	DQ502156								Trujillo about 2km ESE Agua de Obispos	Venezuela	94 02 00 N 70 05 00 W
OGsp	*Bufo*	*bufo*	MVZ230209	DQ158438	DQ158438										
OGsp	*Chaunus*	*chavin*	MTD43789	DQ158441	DQ158441										
OGsp	*Chaunus*	*nesiotes*	UTA53310	DQ158478	DQ158478										
OGsp	*Cranopsis*	*coniferus*	KU217480	DQ158445	DQ158445										
OGsp	*Dendrobates*	*auratus*	USNM31318	AY843581	AY843581						DQ347160		Bocas del Toro	Panama	
CGsp	*Dendropsophus*	*anceps*	CFBH5797	AY843597	AY843597								Espirito Santo, Linhares (Povoacao)	Brazil	
CGsp	*Dendropsophus*	*berthalutzae*	CFBH5418	AY843607	AY843607						AY844052.		Rio de Janeiro, Duque de Caxias	Brazil	
CGsp	*Dendropsophus*	*bipunctatus*	MRT5946	AY843608	AY843608						AY844053		Bahia, Jussari,: Serra do Teimoso	Brazil	
CGsp	*Dendropsophus*	*brevifrons*	28 CM	EF376022	EF376058						#######		Kaw2	French Guiana	04 43 00 N 52 08 00 W
CGsp	*Dendropsophus*	*brevifrons*	MJH7101	AY843611	AY843611								Huanuco, Rio Llullapichis, Panguana	Peru	09 23 02 S 75 52 57 W
CGsp	*Dendropsophus*	*carnifex*	DFCH-USFQ899	AY843616	AY843616						AY844060		Pichincha, Tandayapa	Ecuador	
CGsp	*Dendropsophus*	*ebraccatus*	RdS790	AY843624	AY843624						AY844070		Stann Creek District, Cokscomb Basin Wildlife Santuary	Belize	
CGsp	*Dendropsophus*	*gaucheri*	1007 BPN	#######	#######						#######		Sipaliwini	Suriname	02 02 00 N 56 07 00 W
CGsp	*Dendropsophus*	*gaucheri*	1045 BPN	#######	#######						#######		Lely Mountain	Suriname	04 16 00 N 54 44 00 W
CGsp	*Dendropsophus*	*gaucheri*	62 BM	#######	#######								Savane Corossony	French Guiana	05 23 00 N 53 00 00 W
CGsp	*Dendropsophus*	*giesleri*	CFBHS/N	AY843629	AY843629						AY844075		Sao Paulo, Ubatuba (Picinguaba)	Brazil	
CGsp	*Dendropsophus*	*labialis*	QULC97005	AY843635	AY843635						AY844080		Parque Natural Nacional Chingaza	Colombia	
CGsp	*Dendropsophus*	*leali*	343 CM	#######	#######								Pidima	French Guiana	
CGsp	*Dendropsophus*	*leucophyllatus*	6315 MTR	#######	#######	Dele_H06	1-2				#######	Dele_H10	Serra do Kukoinhokren	Brazil	07 50 00 S 51 55 00 W
CGsp	*Dendropsophus*	*leucophyllatus*	Aukre-93045		AF308085	Dele_NA		2-2				Dele_NA	A,Ukre	Brazil	07 40 00 S 51 22 00 W
CGsp	*Dendropsophus*	*leucophyllatus*	AdC-95163		AF308089	Dele_NA		2-6				Dele_NA	Alter do Chão	Brazil	02 33 00 S 54 59 00 W
CGsp	*Dendropsophus*	*leucophyllatus*	Obd-95176		AF308090	Dele_NA		2-4				Dele_NA	Obidos	Brazil	01 55 00 S 55 31 00 W
CGsp	*Dendropsophus*	*leucophyllatus*	Tab-96018		AF308093	Dele_NA		2-4				Dele_NA	Tabatinga	Brazil	04 16 00 S 69 58 00 W
CGsp	*Dendropsophus*	*leucophyllatus*	Tab-96056		AF308094	Dele_NA		2-4				Dele_NA	Tabatinga	Brazil	04 16 00 S 69 58 00 W
CGsp	*Dendropsophus*	*leucophyllatus*	Jur-4273INPA4273		AF308095	Dele_NA		2-4				Dele_NA	Porongaba	Brazil	08 41 00 S 72 48 00 W
CGsp	*Dendropsophus*	*leucophyllatus*	R.Bran-95253		AF308097	Dele_NA		2-5				Dele_NA	Rio Branco	Brazil	09 58 00 S 67 48 00 W
CGsp	*Dendropsophus*	*leucophyllatus*	93042,93043		DQ393418	Dele_NA		2-2				Dele_NA	Redenção	Brazil	07 40 00 S 51 22 00 W

CGsp	*Dendropsophus*	*leucophyllatus*	93049			DQ393420	Dele_NA		2-3				Dele_NA	Redenção	Brazil	07 40 00 S 51 22 00 W
CGsp	*Dendropsophus*	*leucophyllatus*	93044			DQ393421	Dele_NA		2-5				Dele_NA	Redenção	Brazil	07 40 00 S 51 22 00 W
CGsp	*Dendropsophus*	*leucophyllatus*	95162			DQ393422	Dele_NA		2-7				Dele_NA	Alter do Chão	Brazil	02 32 00 S 54 58 00 W
CGsp	*Dendropsophus*	*leucophyllatus*	4483			DQ393430	Dele_NA		2-4				Dele_NA	Nova Vida	Brazil	08 22 00 S 72 49 00 W
CGsp	*Dendropsophus*	*leucophyllatus*	4273			DQ393431	Dele_NA		2-4				Dele_NA	Igarapé Porongaba	Brazil	08 40 00 S 72 47 00 W
	Dendropsophus	*leucophyllatus*	191 CM	#######	#######	Dele_H01	1-1				#######	Dele_H02	Apatou	French Guiana	05 10 00 N 54 20 00 W
	Dendropsophus	*leucophyllatus*	192 CM	#######	#######	Dele_H01	1-1				#######	Dele_H04	Apatou	French Guiana	05 10 00 N 54 20 00 W
	Dendropsophus	*leucophyllatus*	99 CM	#######	#######	Dele_H01	1-1				#######	Dele_H02	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Dendropsophus	*leucophyllatus*	123 CM	#######	#######	Dele_H01	1-1				#######	Dele_H02	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Dendropsophus	*leucophyllatus*	124 CM	#######	#######	Dele_H01	1-1				#######	Dele_H02	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Dendropsophus	*leucophyllatus*	125 CM	#######	#######	Dele_H01	1-1				#######	Dele_H02	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Dendropsophus	*leucophyllatus*	297 CM	#######	#######	Dele_H01	1-1				#######	Dele_H03	Lac Toponowini	French Guiana	03 03 10 N 52 42 37 W
	Dendropsophus	*leucophyllatus*	300 CM	#######	#######	Dele_H01	1-1				#######	Dele_H09	Lac Toponowini	French Guiana	03 03 10 N 52 42 37 W
	Dendropsophus	*leucophyllatus*	1033 BPN	#######	#######	Dele_H01	1-1				#######	Dele_H01	Lely Mountain	Suriname	04 16 00 N 54 44 00 W
	Dendropsophus	*leucophyllatus*	13911 MTR	#######	#######	Dele_H01	1-1				#######	Dele_H08	Lourenço	Brazil	02 19 25 N 51 38 43 W
	Dendropsophus	*leucophyllatus*	64 AF	#######	#######	Dele_H01	1-1				#######	Dele_H02	Petit-saut	French Guiana	05 04 00 N 53 03 00 W
	Dendropsophus	*leucophyllatus*	63 AF	#######	#######	Dele_H01	1-1				#######	Dele_H05	Petit-saut	French Guiana	05 04 00 N 53 03 00 W
	Dendropsophus	*leucophyllatus*	917 BPN	#######	#######	Dele_H01	1-1				#######	Dele_H04	Road to Apura	Suriname	05 11 00 N 55 39 00 W
	Dendropsophus	*leucophyllatus*	921 BPN	#######	#######	Dele_H01	1-1				#######	Dele_H04	Road to Apura	Suriname	05 11 00 N 55 39 00 W
	Dendropsophus	*leucophyllatus*	922 BPN	#######	#######	Dele_H01	1-1				#######	Dele_H07	Road to Apura	Suriname	05 11 00 N 55 39 00 W
	Dendropsophus	*leucophyllatus*	224 CM	#######	#######	Dele_H01	1-1				#######	Dele_H02	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Dendropsophus	*leucophyllatus*	13836 MTR	#######	#######	Dele_H01	1-1				#######	Dele_H03	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Dendropsophus	*leucophyllatus*	13834 MTR	#######	#######	Dele_H01	1-1				#######	Dele_H05	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Dendropsophus	*leucophyllatus*	13835 MTR	#######	#######	Dele_H01	1-1				#######	Dele_H06	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Dendropsophus	*leucophyllatus*	923 BPN	#######	#######	Dele_H04	1-1				#######	Dele_H02	Road to Apura	Suriname	05 11 00 N 55 39 00 W
	Dendropsophus	*leucophyllatus*	919 BPN	#######	#######	Dele_H04	1-1				#######	Dele_H04	Road to Apura	Suriname	05 11 00 N 55 39 00 W
	Dendropsophus	*leucophyllatus*	918 BPN	#######	#######	Dele_H05	1-1				#######	Dele_H03	Road to Apura	Suriname	05 11 00 N 55 39 00 W
	Dendropsophus	*leucophyllatus*	36 CM	EF376023	EF376059	Dele_H02	1-1				EF376129	Dele_H05	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Dendropsophus	*leucophyllatus*	1034 BPN	#######	#######	Dele_H01	1-1					Dele_NA	Lely Mountain	Suriname	04 16 00 N 54 44 00 W
	Dendropsophus	*leucophyllatus*	920 BPN	#######	#######	Dele_H01	1-1					Dele_NA	Road to Apura	Suriname	05 11 00 N 55 39 00 W
	Dendropsophus	*leucophyllatus*	13837 MTR	#######	#######	Dele_H01	1-1					Dele_NA	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Dendropsophus	*leucophyllatus*	404 CM	#######	#######	Dele_H01	1-1					Dele_NA	Lucifer	French Guiana	04 46 00 N 53 55 00 W
	Dendropsophus	*leucophyllatus*	373 CM	#######	#######	Dele_H03	1-1					Dele_NA	Apatou	French Guiana	05 10 00 N 54 20 00 W
	Dendropsophus	*leucophyllatus*	SdN-95143		AF308087	Dele_NA						Dele_NA	Serra do Navio, Amapà	Brazil	00 55 05 N 52 00 10 W
	Dendropsophus	*leucophyllatus*	SdN-95156		AF308088	Dele_NA						Dele_NA	Serra do Navio, Amapà	Brazil	00 55 05 N 52 00 10 W
	Dendropsophus	*leucophyllatus*	Man-95231		AF308091	Dele_NA						Dele_NA	Manaus, Amazonas	Brazil	02 28 00 S 60 00 57 W
	Dendropsophus	*leucophyllatus*	Man-95232		AF308092	Dele_NA						Dele_NA	Manaus, Amazonas	Brazil	02 28 00 S 60 00 57 W
	Dendropsophus	*leucophyllatus*	95161		DQ393416	Dele_NA						Dele_NA	Alter do Chão	Brazil	02 32 00 S 54 58 00 W
CGsp	*Dendropsophus*	*marmoratus*	MJH7116	AY843640	AY843640								Huanuco, Rio Llullapichis, Panguana	Peru	09 23 02 S 75 52 57 W
CGsp	*Dendropsophus*	*melanargyreus*	47 PG	#######	#######								Kaw2	French Guiana	04 43 00 N 52 08 00 W
CGsp	*Dendropsophus*	*microcephalus*	UTAA-50632	AY843643	AY843643								Atlantida, Cordillera Nombre de Dios, Aldea Rio Viejo	Honduras	
	Dendropsophus	*minusculus*	13 PG	#######	#######	Desp_H01	1-1	2-1	3-1	4-1	#######	Desp_H05	Pic Matecho	French Guiana	03 45 00 N 53 02 00 W
	Dendropsophus	*minusculus*	84 AF	#######	#######	Desp_H01	1-1	2-1	3-1	4-1	#######	Desp_H02	St Georges	French Guiana	03 52 00 N 51 48 00 W
	Dendropsophus	*minusculus*	39 BM	#######	#######	Desp_H01	1-1	2-1	3-1	4-1	#######	Desp_H02	Trinité	French Guiana	04 35 00 N 53 21 00 W
	Dendropsophus	*minusculus*	202 BM	#######	#######	Desp_H01	1-1	2-1	3-1	4-1	#######	Desp_H12	Trinité	French Guiana	04 35 00 N 53 21 00 W
	Dendropsophus	*minusculus*	13 BM	#######	#######	Desp_H02	1-1	2-1	3-1	4-1	#######	Desp_H03	Trinité	French Guiana	04 35 00 N 53 21 00 W
	Dendropsophus	*minusculus*	207 CM	#######	#######	Desp_H03	1-1	2-1	3-1	4-1	#######	Desp_H05	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Dendropsophus	*minusculus*	66 AF	#######	#######	Desp_H04	1-1	2-1	3-1	4-1	#######	Desp_H07	Petit-saut	French Guiana	05 04 00 N 53 03 00 W
	Dendropsophus	*minusculus*	280 CM	#######	#######	Desp_H05	1-2	2-2	3-1	4-1	#######	Desp_H05	St Elie	French Guiana	04 50 00 N 53 15 00 W
	Dendropsophus	*minusculus*	201 BM	#######	#######	Desp_H06	1-3	2-1	3-1	4-1	#######	Desp_H03	Trinité	French Guiana	04 35 00 N 53 21 00 W
	Dendropsophus	*minusculus*	98 CM	#######	#######	Desp_H07	1-4	2-1	3-1	4-1	#######	Desp_H02	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Dendropsophus	*minusculus*	131 PG	#######	#######	Desp_H09	1-4	2-1	3-1	4-1	#######	Desp_H03	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Dendropsophus	*minusculus*	215 BM	#######	#######	Desp_H10	1-5	2-1	3-1	4-1	#######	Desp_H02	crique wapou	French Guiana	04 26 00 N 52 09 00 W
	Dendropsophus	*minusculus*	9 AF	#######	#######	Desp_H10	1-5	2-1	3-1	4-1	#######	Desp_H01	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Dendropsophus	*minusculus*	132 PG	#######	#######	Desp_H10	1-5	2-1	3-1	4-1	#######	Desp_H02	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Dendropsophus	*minusculus*	214 BM	#######	#######	Desp_H11	1-5	2-1	3-1	4-1	#######	Desp_H08	crique wapou	French Guiana	04 26 00 N 52 09 00 W
	Dendropsophus	*minusculus*	13910 MTR	#######	#######	Desp_H12	1-6	2-3	3-2	4-1	#######	Desp_H02	Lourenço	Brazil	02 19 25 N 51 38 43 W
	Dendropsophus	*minusculus*	13795 MTR	#######	#######	Desp_H12	1-6	2-3	3-2	4-1	#######	Desp_H10	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Dendropsophus	*minusculus*	202 CM	#######	#######	Desp_H14	1-8	2-1	3-1	4-1	#######	Desp_H03	Apatou	French Guiana	05 10 00 N 54 20 00 W
	Dendropsophus	*minusculus*	234 CM	#######	#######	Desp_H14	1-8	2-1	3-1	4-1	#######	Desp_H03	Grand Santi	French Guiana	04 20 00 N 54 15 00 W

	Genus	Species	Specimen			Hap1							Hap2	Locality	Country	Coordinates
	Dendropsophus	*minusculus*	401 PG	#######	#######	Desp_H14	1-8	2-1	3-1	4-1		#######	Desp_H02	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
	Dendropsophus	*minusculus*	399 PG	#######	#######	Desp_H14	1-8	2-1	3-1	4-1		#######	Desp_H03	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
	Dendropsophus	*minusculus*	397 PG	#######	#######	Desp_H14	1-8	2-1	3-1	4-1		#######	Desp_H05	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
	Dendropsophus	*minusculus*	400 PG	#######	#######	Desp_H14	1-8	2-1	3-1	4-1		#######	Desp_H11	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
	Dendropsophus	*minusculus*	130 PG	#######	#######	Desp_H14	1-8	2-1	3-1	4-1		#######	Desp_H05	Papaichton	French Guiana	03 48 51 N 54 08 75 W
	Dendropsophus	*minusculus*	281 CM	#######	#######	Desp_H15	1-8	2-1	3-1	4-1		#######	Desp_H03	St Elie	French Guiana	04 50 00 N 53 15 00 W
	Dendropsophus	*minusculus*	65 AF	#######	#######	Desp_H16	1-8	2-1	3-1	4-1		#######	Desp_H08	Petit-saut	French Guiana	05 04 00 N 53 03 00 W
	Dendropsophus	*minusculus*	298 PG	#######	#######	Desp_H17	1-9	2-5	3-1	4-1		#######	Desp_H04	Haut Marwini	French Guiana	02 36 55 N 54 01 58 W
	Dendropsophus	*minusculus*	145 AF	#######	#######	Desp_H18	1-10	2-6	3-3	4-1		#######	Desp_H02	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Dendropsophus	*minusculus*	142 AF	#######	#######	Desp_H18	1-10	2-6	3-3	4-1		#######	Desp_H09	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Dendropsophus	*minusculus*	171 AF	#######	#######	Desp_H18	1-10	2-6	3-3	4-1		#######	Desp_H02	Road to Apura	Suriname	05 11 00 N 55 37 00 W
	Dendropsophus	*minusculus*	172 AF	#######	#######	Desp_H18	1-10	2-6	3-3	4-1		#######	Desp_H09	Road to Apura	Suriname	05 11 00 N 55 37 00 W
	Dendropsophus	*minusculus*	173 AF	#######	#######	Desp_H18	1-10	2-6	3-3	4-1		#######	Desp_H09	Road to Apura	Suriname	05 11 00 N 55 37 00 W
	Dendropsophus	*minusculus*	791 BPN	#######	#######	Desp_H18	1-10	2-6	3-3	4-1		#######	Desp_H09	Sipaliwini	Suriname	02 02 00 N 56 07 00 W
	Dendropsophus	*minusculus*	124 AF	#######	#######	Desp_H19	1-11	2-6	3-3	4-1		#######	Desp_H02	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Dendropsophus	*minusculus*	125 AF	#######	#######	Desp_H19	1-11	2-6	3-3	4-1		#######	Desp_H09	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Dendropsophus	*minusculus*	134 AF	#######	#######	Desp_H20	1-11	2-6	3-3	4-1		#######	Desp_H09	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Dendropsophus	*minusculus*	13943 MTR	#######	#######	Desp_H21	1-12	2-7	3-3	4-1		#######	Desp_H02	Laranjal do Jari	Brazil	00 43 00 S 52 23 00 W
	Dendropsophus	*minusculus*	13973 MTR	#######	#######	Desp_H21	1-12	2-7	3-3	4-1		#######	Desp_H02	Laranjal do Jari	Brazil	00 43 00 S 52 23 00 W
	Dendropsophus	*minusculus*	13974 MTR	#######	#######	Desp_H21	1-12	2-7	3-3	4-1		#######	Desp_H02	Laranjal do Jari	Brazil	00 43 00 S 52 23 00 W
	Dendropsophus	*minusculus*	13942 MTR	#######	#######	Desp_H21	1-12	2-7	3-3	4-1		#######	Desp_H06	Laranjal do Jari	Brazil	00 43 00 S 52 23 00 W
	Dendropsophus	*minusculus*	13972 MTR	#######	#######	Desp_H21	1-12	2-7	3-3	4-1		#######	Desp_H06	Laranjal do Jari	Brazil	00 43 00 S 52 23 00 W
	Dendropsophus	*minusculus*	46 CM	#######	#######	Desp_H08	1-4	2-1	3-1	4-1		#######	Desp_H03	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Dendropsophus	*minusculus*	USNM-FS196772	DQ380362										St. Patrick: 6.7km E of Bonasse, on S Main Rd, 3km W ofGranville Beach Rd junction and 9.2km W of Chatham Rd junction	Trinidad	
	Dendropsophus	*minusculus*	48 CM	EF376025	EF376061	Desp_H22	1-13	2-8	3-4	4-2		EF376131	Desp_H13	Mana	French Guiana	05 39 00 N 53 47 00 W
	Dendropsophus	*minusculus*	396 PG	#######	#######	Desp_H01	1-1	2-1	3-1	4-1			Desp_NA	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
	Dendropsophus	*minusculus*	12027 SMNS	#######	#######	Desp_H13	1-7	2-4	3-2	4-1			Desp_NA	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Dendropsophus	*minusculus*	12028 SMNS	#######	#######	Desp_H13	1-7	2-4	3-2	4-1			Desp_NA	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Dendropsophus	*minusculus*	12029 SMNS	#######	#######	Desp_H13	1-7	2-4	3-2	4-1			Desp_NA	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Dendropsophus	*minusculus*	12030 SMNS	#######	#######	Desp_H13	1-7	2-4	3-2	4-1			Desp_NA	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Dendropsophus	*minusculus*	12031 SMNS	#######	#######	Desp_H13	1-7	2-4	3-2	4-1			Desp_NA	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Dendropsophus	*minusculus*	12032 SMNS	#######	#######	Desp_H13	1-7	2-4	3-2	4-1			Desp_NA	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
CGsp	*Dendropsophus*	*minutus*	114 CM	EF376027	EF376063									Kaw2	French Guiana	04 43 00 N 52 08 00 W
CGsp	*Dendropsophus*	*minutus*	MACN33799	AY549345	AY549345							AY844089		Misiones: Depto. Guarany: San Vicente	Argentina	
CGsp	*Dendropsophus*	*miyatai*	JPC10772;LSUMZH-12939	AY843647	AY843647							AY844092		Sucumbios	Ecuador	
CGsp	*Dendropsophus*	*nanus*	47 BM	#######	#######									Savane Corossony	French Guiana	05 23 00 N 53 00 00 W
CGsp	*Dendropsophus*	*nanus*	MACN37785	AY549346	AY549346									Entre Rios: Dto. Islas del Ibicuy	Argentina	
CGsp	*Dendropsophus*	*parviceps*	AMNHA-139315	AY843652	AY843652							AY844097		Acre, Centro Experimental da Universidade do Acre 23km on Rio Branco-Porto Velho Road	Brazil	
CGsp	*Dendropsophus*	*rhodopeplus*	MHZ462	AY843658	AY843658									Loreto, Jenaro Herrera	Peru	
CGsp	*Dendropsophus*	*rubicundulus*	IT-H0653	AY843661	AY843661									Sao Paulo, Buri	Brazil	
CGsp	*Dendropsophus*	*sanborni*	MACN38638	AY843663	AY843663							AY844106		ntre Rios, Dto. Islas del Ibicuy, Ruta 12 vieja, entre Brazo Largo y Arroyo Luciano		
CGsp	*Dendropsophus*	*sarayacuensis*	MJH7143	AY843664	AY843664									Huanuco, Rio Llullapichis, Panguana	Peru	09 23 02 S 75 52 57 W
CGsp	*Dendropsophus*	*seniculus*	CFBH5761	AY843666	AY843666									Rio de Janeiro, Angra dos Reis	Brazil	
CGsp	*Dendropsophus*	*triangulum*	MJH3844	AY843680	AY843680							AY844122		Acre, Lago Catalao, Ilha Xiborena	Brazil	
CGsp	*Dendropsophus*	*walfordi*	MJH129	AY843683	AY843683									?	Brazil	
OGsp	*Eleutherodactylus*	*dolops*		EF493394	EF493394											
OGsp	*Eleutherodactylus*	*martinicensis*	USNM5650	EF493343	EF493343							EF493456		Basse-Terre, 1 km E St. Claude	Guadeloupe	
OGsp	*Epipedobates*	*tricolor*	QCAZ16596	AY364577	AY364577										Ecuador	
OGsp	*Hyla*	*arborea*		AY843601	AY843601							AY844046		Petrade	Germany	
OGsp	*Hyla*	*arenicolor*	UMMZ7755	AY843603	AY843603							DQ347187		Arizona, Gila Co., Houston creek just N HWY 260, approx. 4 MI E of Payson	USA	
OGsp	*Hypsiboas*	*boans*	RWM17746	AY843610	AY843610							AY844055		Amazonas, Cano Agua Blanca, 3.5 Km SE Neblina Base Camp on Rio Mawarinuma	Venezuela	
OGsp	*Ischnocnema*	*parva*		EF493532	EF493532									Sao Paulo, Estacao Biologica de Borgceia	Brazil	
CGsp	*Leptodactylus*	*didymus*	USNM268970	AY948957	AY948957	Lemy_H37	1-22	2-11	3-7	4-4	5-2			Tambopata	Peru	14 13 25 S 69 10 36 w
CGsp	*Leptodactylus*	*elenae*	USNM319643	AY948955	AY948955											
CGsp	*Leptodactylus*	*fuscus*	152 CM	#######	#######							#######		Montsinery	French Guiana	04 53 00 N 52 29 00 W

CGsp	Genus	species	Voucher	GenBank1	GenBank2	Hap1	c1	c2	c3	c4	c5	GenBank3	Hap2	Locality	Country	Coordinates
CGsp	*Leptodactylus*	*knudseni*	QCAZ13077	AY947863	AY947863									Francisco de Orellana, PN Yasuní, Napo	Ecuador	00 26 56 S 77 00 55 W
CGsp	*Leptodactylus*	*labyrinthicus*	UC233	AY947875	AY947875											
CGsp	*Leptodactylus*	*leptodactyloides*	MZUSP70969	AY943236	AY943236	LewaG_H01							LewaC_NA	Serra do Kukoinhokren	Brazil	07 50 00 S 51 55 00 W
CGsp	*Leptodactylus*	*longirostris*	76 BM	#######	EU201119							#######		Mont Arawa	French Guiana	02 48 59 N 53 21 59 W
CGsp	*Leptodactylus*	*melanonotus*										DQ347193				
CGsp	*Leptodactylus*	*myersi*	T-1890 T	#######	#######							#######		Trinité	French Guiana	04 35 00 N 53 21 00 W
	Leptodactylus	*mystaceus*	201 AF	#######	#######	Lemy_H05	1-1	2-1	3-1	4-1	5-1	#######	Lemy_H01	Angouleme	French Guiana	05 23 00 N 53 39 00 W
	Leptodactylus	*mystaceus*	205 AF	#######	#######	Lemy_H05	1-1	2-1	3-1	4-1	5-1	#######	Lemy_H01	Angouleme	French Guiana	05 23 00 N 53 39 00 W
	Leptodactylus	*mystaceus*	12037 SMNS	#######	#######	Lemy_H15	1-8	2-3	3-2	4-2	5-1	#######	Lemy_H02	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Leptodactylus	*mystaceus*	12038 SMNS	#######	#######	Lemy_H15	1-8	2-3	3-2	4-2	5-1	#######	Lemy_H02	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Leptodactylus	*mystaceus*	MSH10352	#######	#######	Lemy_H16	1-11	2-4	3-2	4-2	5-1	#######	Lemy_H01	E.E. Anavilhanas- Base 2	Brazil	02 32 04 S 60 50 12 W
	Leptodactylus	*mystaceus*	MSH10356	#######	#######	Lemy_H16	1-11	2-4	3-2	4-2	5-1	#######	Lemy_H01	E.E. Anavilhanas- Base 2	Brazil	02 32 04 S 60 50 12 W
	Leptodactylus	*mystaceus*	12039 SMNS	#######	#######	Lemy_H19	1-10	2-3	3-2	4-2	5-1	#######	Lemy_H02	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Leptodactylus	*mystaceus*	12036 SMNS	#######	#######	Lemy_H20	1-12	2-5	3-2	4-2	5-1	#######	Lemy_H03	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Leptodactylus	*mystaceus*	13764 MTR	#######	#######	Lemy_H22	1-14	2-7	3-4	4-2	5-1	#######	Lemy_H01	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Leptodactylus	*mystaceus*	13786 MTR	#######	#######	Lemy_H22	1-14	2-7	3-4	4-2	5-1	#######	Lemy_H01	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Leptodactylus	*mystaceus*	13787 MTR	#######	#######	Lemy_H22	1-14	2-7	3-4	4-2	5-1	#######	Lemy_H01	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Leptodactylus	*mystaceus*	13788 MTR	#######	#######	Lemy_H22	1-14	2-7	3-4	4-2	5-1	#######	Lemy_H01	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Leptodactylus	*mystaceus*	MTR10.120	#######	#######	Lemy_H34	1-21	2-10	3-6	4-3	5-1	#######	Lemy_H01	Lago Cipotuba	Brazil	05 48 05 S 60 13 16 W
	Leptodactylus	*mystaceus*	MTR10.103	#######	#######	Lemy_H34	1-21	2-10	3-6	4-3	5-1	#######	Lemy_H09	Lago Cipotuba	Brazil	05 48 05 S 60 13 16 W
	Leptodactylus	*mystaceus*	298AF MTR	#######	#######	Lemy_H35	1-23	2-12	3-8	4-5	5-1	#######	Lemy_H11	Vila Rica	Brazil	09 55 27 S 51 14 18 W
	Leptodactylus	*mystaceus*	299AF MTR	#######	#######	Lemy_H36	1-24	2-12	3-8	4-5	5-3	#######	Lemy_H10	Vila Rica	Brazil	09 55 27 S 51 14 18 W
	Leptodactylus	*mystaceus*	351 CM	#######	#######	Lemy_H02	1-1	2-1	3-1	4-1	5-1	#######	Lemy_H01	Lucifer	French Guiana	04 46 00 N 53 55 00 W
	Leptodactylus	*mystaceus*	417 CM	#######	#######	Lemy_H03	1-1	2-1	3-1	4-1	5-1	#######	Lemy_H01	Lucifer	French Guiana	04 46 00 N 53 55 00 W
	Leptodactylus	*mystaceus*	254 BM	#######	#######	Lemy_H04	1-1	2-1	3-1	4-1	5-1	#######	Lemy_H01	Lucifer	French Guiana	04 46 00 N 53 55 00 W
	Leptodactylus	*mystaceus*	237 BM	#######	#######	Lemy_H06	1-2	2-1	3-1	4-1	5-1	#######	Lemy_H01	Lucifer	French Guiana	04 46 00 N 53 55 00 W
	Leptodactylus	*mystaceus*	194 BM	#######	#######	Lemy_H07	1-3	2-1	3-1	4-1	5-1	#######	Lemy_H01	Trinité	French Guiana	04 35 00 N 53 21 00 W
	Leptodactylus	*mystaceus*	117 BM	#######	#######	Lemy_H08	1-3	2-1	3-1	4-1	5-1	#######	Lemy_H08	Kourou	French Guiana	05 09 00 N 52 38 00 W
	Leptodactylus	*mystaceus*	91 CM	#######	#######	Lemy_H09	1-4	2-2	3-1	4-1	5-1	#######	Lemy_H01	Trois Sauts	French Guiana	02 14 00 N 52 52 00 W
	Leptodactylus	*mystaceus*	90 AF	#######	#######	Lemy_H10	1-4	2-2	3-1	4-1	5-1	#######	Lemy_H01	St Georges	French Guiana	03 52 00 N 51 48 00 W
	Leptodactylus	*mystaceus*	1683 BPN	#######	#######	Lemy_H11	1-5	2-2	3-1	4-1	5-1	#######	Lemy_H01	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Leptodactylus	*mystaceus*	7 AF	#######	#######	Lemy_H12	1-6	2-2	3-1	4-1	5-1	#######	Lemy_H01	Kaw3	French Guiana	04 32 53 N 52 09 07 W
	Leptodactylus	*mystaceus*	133 CM	#######	#######	Lemy_H13	1-6	2-2	3-1	4-1	5-1	#######	Lemy_H01	crique Margot	French Guiana	05 28 00 N 53 57 00 W
	Leptodactylus	*mystaceus*	116 AF	#######	#######	Lemy_H31	1-19	2-9	3-5	4-3	5-1	#######	Lemy_H01	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Leptodactylus	*mystaceus*	113 AF	#######	#######	Lemy_H32	1-20	2-9	3-5	4-3	5-1	#######	Lemy_H04	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Leptodactylus	*mystaceus*	112 AF	#######	#######	Lemy_H33	1-20	2-9	3-5	4-3	5-1	#######	Lemy_H01	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Leptodactylus	*mystaceus*	1367 BPN	#######	#######	Lemy_H14	1-7	2-2	3-1	4-1	5-1	#######	Lemy_H01	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Leptodactylus	*mystaceus*	337 CM	#######	#######	Lemy_H23	1-14	2-7	3-4	4-2	5-1	#######	Lemy_H01	Régina	French Guiana	04 18 00 N 52 07 00 W
	Leptodactylus	*mystaceus*	1388 BPN	#######	#######	Lemy_H24	1-15	2-8	3-4	4-2	5-1	#######	Lemy_H07	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Leptodactylus	*mystaceus*	14 AF	#######	#######	Lemy_H24	1-15	2-8	3-4	4-2	5-1	#######	Lemy_H06	Kaw3	French Guiana	04 32 53 N 52 09 07 W
	Leptodactylus	*mystaceus*	13 AF	#######	#######	Lemy_H25	1-15	2-8	3-4	4-2	5-1	#######	Lemy_H08	Montjoly	French Guiana	04 55 00 N 52 16 00 W
	Leptodactylus	*mystaceus*	1538 BPN	#######	#######	Lemy_H26	1-16	2-8	3-4	4-2	5-1	#######	Lemy_H01	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Leptodactylus	*mystaceus*	1565 BPN	#######	#######	Lemy_H26	1-16	2-8	3-4	4-2	5-1	#######	Lemy_H01	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Leptodactylus	*mystaceus*	1383 BPN	#######	#######	Lemy_H27	1-17	2-8	3-4	4-2	5-1	#######	Lemy_H06	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Leptodactylus	*mystaceus*	1537 BPN	#######	#######	Lemy_H28	1-18	2-8	3-4	4-2	5-1	#######	Lemy_H01	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Leptodactylus	*mystaceus*	1529 BPN	#######	#######	Lemy_H29	1-18	2-8	3-4	4-2	5-1	#######	Lemy_H01	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Leptodactylus	*mystaceus*	1162 BPN	#######	#######	Lemy_H18	1-9	2-3	3-2	4-2	5-1	#######	Lemy_H05	Imbaimadai	Guyana	05 44 23 N 60 17 51 W
	Leptodactylus	*mystaceus*	1126 BPN	#######	EU201114	Lemy_H17	1-9	2-3	3-2	4-2	5-1	#######	Lemy_H01	Imbaimadai	Guyana	05 44 23 N 60 17 51 W
	Leptodactylus	*mystaceus*	1164 BPN	#######	EU201114	Lemy_H17	1-9	2-3	3-2	4-2	5-1	#######	Lemy_H01	Imbaimadai	Guyana	05 44 23 N 60 17 51 W
	Leptodactylus	*mystaceus*	167 CM	#######	EU201115	Lemy_H21	1-13	2-6	3-3	4-2	5-1	#######	Lemy_H01	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Leptodactylus	*mystaceus*	115 AF	#######	EU201116	Lemy_H30	1-19	2-9	3-5	4-3	5-1	#######	Lemy_H01	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Leptodactylus	*mystaceus*	289 CM	#######	EU201117	Lemy_H01	1-1	2-1	3-1	4-1	5-1	#######	Lemy_H01	Camp Canopé	French Guiana	04 53 37 N 52 47 57 W
	Leptodactylus	*mystaceus*	134 CM	#######	EU201117	Lemy_H01	1-1	2-1	3-1	4-1	5-1	#######	Lemy_H01	crique Margot	French Guiana	05 28 00 N 53 57 00 W
	Leptodactylus	*mystaceus*	135 CM	#######	EU201117	Lemy_H01	1-1	2-1	3-1	4-1	5-1	#######	Lemy_H01	crique Margot	French Guiana	05 28 00 N 53 57 00 W
	Leptodactylus	*mystaceus*	B CM	#######	EU201117	Lemy_H01	1-1	2-1	3-1	4-1	5-1	#######	Lemy_H01	Grand Santi	French Guiana	04 20 00 N 54 15 00 W
	Leptodactylus	*mystaceus*	367 CM	#######	EU201117	Lemy_H01	1-1	2-1	3-1	4-1	5-1	#######	Lemy_H01	Lucifer	French Guiana	04 46 00 N 53 55 00 W
	Leptodactylus	*mystaceus*	474 PG	#######	EU201117	Lemy_H01	1-1	2-1	3-1	4-1	5-1	#######	Lemy_H01	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
	Leptodactylus	*mystaceus*	73 AF	#######	EU201118	Lemy_H23	1-14	2-7	3-4	4-2	5-1	#######	Lemy_H01	St georges PK160	French Guiana	03 52 00 N 51 48 00 W
	Leptodactylus	*mystaceus*	195 BM	#######	#######	Lemy_H11	1-5	2-2	3-1	4-1	5-1		Lemy_NA	Trinité	French Guiana	04 35 00 N 53 21 00 W
CGsp	*Leptodactylus*	*notoaktites*	USNM303191	AY948954	AY948954											
CGsp	*Leptodactylus*	*ocellatus*	MACN38648	AY843688	AY843688									BuenosAires,Escobar,LomaVerde,Ea.LosCipreses	Argentina	35 16 56 S 58 25 18 W

CGsp		species	voucher		accession	haplotype	1-	2-	3-	4-		haplotype2	locality	country	coordinates
CGsp	*Leptodactylus*	*pentadactylus*	181 CM	######	EU201134						######		Tibourou	French Guiana	04 25 00 N 52 18 00 W
CGsp	*Leptodactylus*	*rhodomystax*	213 CM	######	EU201122						######		Montagne des singes	French Guiana	05 04 00 N 52 43 00 W
CGsp	*Leptodactylus*	*spixi*	USNM534008	AY948952	AY948952										
CGsp	*Leptodactylus*	*stenodema*	187 CM	######	######						######		Tibourou	French Guiana	04 25 00 N 52 18 00 W
CGsp	*Leptodactylus*	*wagneriA*	11 AF	######	######	LewaA_H02	1-1				######	LewaA_H01	Montjoly	French Guiana	04 55 00 N 52 16 00 W
CGsp	*Leptodactylus*	*wagneriA*	12525 SMNS	######	######	LewaA_H03	1-2				######	LewaA_H03	Bamboo landing	Guyana	05 19 30 N 58 02 44 W
CGsp	*Leptodactylus*	*wagneriA*	12526 SMNS	######	######	LewaA_H04	1-3				######	LewaA_H01	Bamboo landing	Guyana	05 19 30 N 58 02 44 W
CGsp	*Leptodactylus*	*wagneriA*	194 AF	######	EU201128	LewaA_H01	1-1				######	LewaA_H02	CD8 entre mana et couachimana	French Guiana	05 37 00 N 53 42 00 W
CGsp	*Leptodactylus*	*wagneriA*	150 CM	######	EU201128	LewaA_H01	1-1				######	LewaA_H01	Guatemala	French Guiana	05 09 00 N 52 38 00 W
CGsp	*Leptodactylus*	*wagneriA*	173 CM	######	EU201128	LewaA_H01	1-1				######	LewaA_H01	Guatemala	French Guiana	05 09 00 N 52 38 00 W
CGsp	*Leptodactylus*	*wagneriA*	247 BM	######	EU201128	LewaA_H01	1-1				######	LewaA_H01	Comté Terrain	French Guiana	04 41 30 N 52 24 00 W
CGsp	*Leptodactylus*	*wagneriA*	81 CM	######	EU201128	LewaA_H01	1-1				######	LewaA_H01	Montjoly	French Guiana	04 55 00 N 52 16 00 W
CGsp	*Leptodactylus*	*wagneriA*	237 AF	######	EU201128	LewaA_H01	1-1				######	LewaA_H01	Montagne des singes	French Guiana	05 04 00 N 52 43 00 W
CGsp	*Leptodactylus*	*wagneriA*	3 AF	######	EU201128	LewaA_H01	1-1				######	LewaA_H01	Montjoly	French Guiana	04 55 00 N 52 16 00 W
CGsp	*Leptodactylus*	*wagneriA*	41 BM	######	EU201128	LewaA_H01	1-1				######	LewaA_H01	Montjoly	French Guiana	04 55 00 N 52 16 00 W
CGsp	*Leptodactylus*	*wagneriA*	261 CM	######	EU201128	LewaA_H01	1-1				######	LewaA_H01	Montsinery	French Guiana	04 53 00 N 52 29 00 W
CGsp	*Leptodactylus*	*wagneriA*	147 BM	######	EU201128	LewaA_H01	1-1				######	LewaA_H01	Comté Terrain	French Guiana	04 41 30 N 52 24 00 W
CGsp	*Leptodactylus*	*wagneriA*	119 BM	######	EU201128	LewaA_H01	1-1				######	LewaA_H02	Mana	French Guiana	05 39 00 N 53 47 00 W
	Leptodactylus	*wagneriB*	MSH10374	######	######	LewaB_H17	1-13	2-8	3-5	4-3	######	LewaB_H02	E.E. Anavilhanas- Base 2	Brazil	02 32 04 S 60 50 12 W
	Leptodactylus	*wagneriB*	199 AF	######	######	LewaB_H05	1-2	2-1	3-1	4-1	######	LewaB_H01	Montagne des singes	French Guiana	05 04 00 N 52 43 00 W
	Leptodactylus	*wagneriB*	13775 MTR	######	######	LewaB_H15	1-10	2-6	3-1		######	LewaB_H03	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Leptodactylus	*wagneriB*	12079 SMNS	######	######	LewaB_H19	1-12	2-7	3-4	4-2	######	LewaB_H10	Iwokrama forest	Guyana	04 40 17 N 58 41 06 W
	Leptodactylus	*wagneriB*	AMNH-A166312	######	######	LewaB_H18	1-12	2-7	3-4	4-2	######	LewaB_H08	Berebice River camp	Guyana	05 03 30 N 58 14 21 W
	Leptodactylus	*wagneriB*	1506 PK	######	######	LewaB_H18	1-12	2-7	3-4	4-2	######	LewaB_H10	Kaieteur NP	Guyana	05 16 07 N 59 46 7 W
	Leptodactylus	*wagneriB*	1664 PK	######	######	LewaB_H18	1-12	2-7	3-4	4-2	######	LewaB_H10	Kaieteur NP	Guyana	05 16 07 N 59 46 7 W
	Leptodactylus	*wagneriB*	12043 SMNS	######	######	LewaB_H18	1-12	2-7	3-4	4-2	######	LewaB_H08	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Leptodactylus	*wagneriB*	12044 SMNS	######	######	LewaB_H18	1-12	2-7	3-4	4-2	######	LewaB_H08	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Leptodactylus	*wagneriB*	12045 SMNS	######	######	LewaB_H18	1-12	2-7	3-4	4-2	######	LewaB_H08	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Leptodactylus	*wagneriB*	12042 SMNS	######	######	LewaB_H18	1-12	2-7	3-4	4-2	######	LewaB_H09	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Leptodactylus	*wagneriB*	12040 SMNS	######	######	LewaB_H18	1-12	2-7	3-4	4-2	######	LewaB_H10	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Leptodactylus	*wagneriB*	12041 SMNS	######	######	LewaB_H18	1-12	2-7	3-4	4-2	######	LewaB_H10	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Leptodactylus	*wagneriB*	226 BM	######	######	LewaB_H01	1-1	2-1	3-1	4-1	######	LewaB_H01	Kaw1	French Guiana	04 31 00 N 52 02 00 W
	Leptodactylus	*wagneriB*	293 CM	######	######	LewaB_H02	1-1	2-1	3-1	4-1	######	LewaB_H02	Pont Nancibo	French Guiana	04 40 00 N 52 30 00 W
	Leptodactylus	*wagneriB*	10 AF	######	######	LewaB_H07	1-4	2-2	3-1	4-1	######	LewaB_H02	Kaw3	French Guiana	04 32 53 N 52 09 07 W
	Leptodactylus	*wagneriB*	8 AF	######	######	LewaB_H08	1-4	2-2	3-1	4-1	######	LewaB_H06	Kaw3	French Guiana	04 32 53 N 52 09 07 W
	Leptodactylus	*wagneriB*	17 BM	######	######	LewaB_H07	1-4	2-2	3-1	4-1	######	LewaB_H02	Lac des Américains	French Guiana	04 51 00 N 52 21 00 W
	Leptodactylus	*wagneriB*	408 CM	######	######	LewaB_H06	1-3	2-1	3-1	4-1	######	LewaB_H07	Lucifer	French Guiana	04 46 00 N 53 55 00 W
	Leptodactylus	*wagneriB*	44 BM	######	######	LewaB_H07	1-4	2-2	3-1	4-1	######	LewaB_H02	Kaw3	French Guiana	04 32 53 N 52 09 07 W
	Leptodactylus	*wagneriB*	67 BM	######	######	LewaB_H07	1-4	2-2	3-1	4-1	######	LewaB_H02	Kaw3	French Guiana	04 32 53 N 52 09 07 W
	Leptodactylus	*wagneriB*	90 BM	######	######	LewaB_H07	1-4	2-2	3-1	4-1	######	LewaB_H02	Kaw3	French Guiana	04 32 53 N 52 09 07 W
	Leptodactylus	*wagneriB*	184 BM	######	######	LewaB_H03	1-2	2-1	3-1	4-1	######	LewaB_H07	Trinité	French Guiana	04 35 00 N 53 21 00 W
	Leptodactylus	*wagneriB*	182 BM	######	######	LewaB_H04	1-2	2-1	3-1	4-1	######	LewaB_H01	Trinité	French Guiana	04 35 00 N 53 21 00 W
	Leptodactylus	*wagneriB*	132 CM	######	######	LewaB_H09	1-5	2-3	3-2	4-1	######	LewaB_H01	crique Margot	French Guiana	05 28 00 N 53 57 00 W
	Leptodactylus	*wagneriB*	197 CM	######	######	LewaB_H11	1-7	2-3	3-2	4-1	######	LewaB_H02	Apatou	French Guiana	05 10 00 N 54 20 00 W
	Leptodactylus	*wagneriB*	1684 BPN	######	######	LewaB_H13	1-8	2-4	3-3	4-1	######	LewaB_H02	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Leptodactylus	*wagneriB*	890 BPN	######	######	LewaB_H14	1-9	2-5	3-3	4-1	######	LewaB_H04	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Leptodactylus	*wagneriB*	0938 MTR	######	######	LewaB_H16	1-11	2-6	3-3	4-1	######	LewaB_H06	Igarapé Camaipi	Brazil	00 01 27 S 51 53 50 W
	Leptodactylus	*wagneriB*	1385 BPN	######	EU201125	LewaB_H02	1-1	2-1	3-1	4-1	######	LewaB_H02	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Leptodactylus	*wagneriB*	8 BM	######	EU201125	LewaB_H02	1-1	2-1	3-1	4-1	######	LewaB_H02	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Leptodactylus	*wagneriB*	81 BM	######	EU201125	LewaB_H02	1-1	2-1	3-1	4-1	######	LewaB_H01	Kaw3	French Guiana	04 32 53 N 52 09 07 W
	Leptodactylus	*wagneriB*	51 BM	######	EU201125	LewaB_H02	1-1	2-1	3-1	4-1	######	LewaB_H02	Kaw3	French Guiana	04 32 53 N 52 09 07 W
	Leptodactylus	*wagneriB*	170 CM	######	EU201126	LewaB_H10	1-6	2-3	3-2	4-1	######	LewaB_H01	St Laurent	French Guiana	05 32 00 N 54 01 00 W
	Leptodactylus	*wagneriB*	66 BM	######	EU201127	LewaB_H12	1-8	2-4	3-3	4-1	######	LewaB_H02	Mont Arawa	French Guiana	02 48 59 N 53 21 59 W
	Leptodactylus	*wagneriB*	13812 MTR			LewaB_NA			3-3		######	LewaB_H01	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Leptodactylus	*wagneriB*	13810 MTR			LewaB_NA			3-3		######	LewaB_H05	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Leptodactylus	*wagneriB*	13811 MTR			LewaB_NA			3-3		######	LewaB_H05	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Leptodactylus	*wagneriB*	12046 SMNS	######	######	LewaB_H18	1-12	2-7	3-4	4-2		LewaB_NA	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Leptodactylus	*wagneriB*	12047 SMNS	######	######	LewaB_H18	1-12	2-7	3-4	4-2		LewaB_NA	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Leptodactylus	*wagneriC*	91 AF	######	######	LewaC_H07	1-5	2-2	3-1		######	LewaC_H01	St Georges	French Guiana	03 52 00 N 51 48 00 W
	Leptodactylus	*wagneriC*	36 BM	######	######	LewaC_H05	1-4	2-2	3-1		######	LewaC_H05	Trinité	French Guiana	04 35 00 N 53 21 00 W
	Leptodactylus	*wagneriC*	183 BM	######	######	LewaC_H06	1-4	2-2	3-1		######	LewaC_H01	Trinité	French Guiana	04 35 00 N 53 21 00 W

	Genus	Species	Voucher	Acc1	Acc2	Hap1					Acc3	Hap2	Locality	Country	Coordinates
	Leptodactylus	*wagneriC*	40 AF	#######	#######	LewaC_H03	1-2	2-1	3-1		#######	LewaC_H03	Saül2	French Guiana	03 36 00 N 53 17 00 W
	Leptodactylus	*wagneriC*	243 BM	#######	#######	LewaC_H02	1-1	2-1	3-1		#######	LewaC_H03	Lucifer	French Guiana	04 46 00 N 53 55 00 W
	Leptodactylus	*wagneriC*	13809 MTR	#######	#######	LewaC_NA					#######	LewaC_H02	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Leptodactylus	*wagneriC*	179 AF	#######	#######	LewaC_H08	1-6	2-3	3-2		#######	LewaC_H01	Road to Apura	Suriname	05 11 00 N 55 37 00 W
	Leptodactylus	*wagneriC*	215 CM	#######	EU201129	LewaC_H04	1-3	2-2	3-1		#######	LewaC_H04	Apatou	French Guiana	05 10 00 N 54 20 00 W
	Leptodactylus	*wagneriC*	415 CM	#######	EU201130	LewaC_H01	1-1	2-1	3-1		#######	LewaC_H01	Lucifer	French Guiana	04 46 00 N 53 55 00 W
	Leptodactylus	*wagneriC*	78 BM	#######	EU201130	LewaC_H01	1-1	2-1	3-1		#######	LewaC_H04	Trinité	French Guiana	04 35 00 N 53 21 00 W
	Leptodactylus	*wagneriC*	181 BM	#######	EU201130	LewaC_H01	1-1	2-1	3-1		#######	LewaC_H05	Trinité	French Guiana	04 35 00 N 53 21 00 W
	Leptodactylus	*wagneriC*	183 AF	#######	EU201131	LewaC_H09	1-6	2-3	3-2			LewaC_NA	Road to Apura	Suriname	05 11 00 N 55 37 00 W
CGsp	*Leptodactylus*	*wagneriD*	1092 BPN	#######	#######	LewaD_H02					#######	LewaD_H02	Kartabo	Guyana	06 23 00 N 58 42 00 W
CGsp	*Leptodactylus*	*wagneriD*	129 AF	#######	EU201133	LewaD_H01					#######	LewaD_H01	Brownsberg	Suriname	04 56 31 N 55 10 33 W
CGsp	*Leptodactylus*	*wagneriD*	131 AF	#######	EU201133	LewaD_H01					#######	LewaD_H01	Brownsberg	Suriname	04 56 31 N 55 10 33 W
CGsp	*Leptodactylus*	*wagneriE*	C CM	#######	#######	LewaE_H01	1-1				#######	LewaE_H01	Kaw1	French Guiana	04 31 00 N 52 02 00 W
CGsp	*Leptodactylus*	*wagneriE*	D CM	#######	#######	LewaE_H01	1-1				#######	LewaE_H01	Kaw1	French Guiana	04 31 00 N 52 02 00 W
CGsp	*Leptodactylus*	*wagneriE*	E CM	#######	#######	LewaE_H01	1-1				#######	LewaE_H01	Kaw1	French Guiana	04 31 00 N 52 02 00 W
CGsp	*Leptodactylus*	*wagneriE*	13986 MTR	#######	#######	LewaE_H03	1-2				#######	LewaE_H01	Macapa	Brazil	00 02 45 N 51 03 00 W
CGsp	*Leptodactylus*	*wagneriE*	13985 MTR	#######	#######	LewaE_H03	1-2				#######	LewaE_H02	Macapa	Brazil	00 02 45 N 51 03 00 W
CGsp	*Leptodactylus*	*wagneriE*	155 CM	#######	EU201132	LewaE_H02	1-1				#######	LewaE_H01	Kaw1	French Guiana	04 31 00 N 52 02 00 W
CGsp	*Leptodactylus*	*wagneriF*	5426 MTR	#######	#######	LewaF_H01					#######	LewaF_H01	APM Manso	Brazil	15 09 00 S 55 04 00 W
CGsp	*Leptodactylus*	*wagneriF*	5492 MTR	#######	#######	LewaF_H02					#######	LewaF_H01	APM Manso	Brazil	15 09 00 S 55 04 00 W
CGsp	*Leptodactylus*	*wagneriH*	VOGT2172	#######	#######	LewaH_H01					#######	LewaH_H01	Cachoeirinha ME Rio Madeira	Brazil	05 29 40 S 60 49 23 W
CGsp	*Leptodactylus*	*wagneriI*	978129 MTR	#######	#######	LewaI_H01					#######	LewaI_H01	Vila Rica	Brazil	09 55 27 S 51 14 18 W
CGsp	*Leptodactylus*	*wagneriJ*	978163 MTR	#######	#######	LewaI_H02					#######	LewaI_H01	Vila Rica	Brazil	09 55 27 S 51 14 18 W
CGsp	*Leptodactylus.*	*albilabris*		EF091411	EF091411										
OGsp	*Lithodytes*	*lineatus*	USP968438	AY326012	AY326012								Mato grosso, Apiacas	Brazil	09 39 09 S 57 23 36 W
OGsp	*Lithodytes*	*lineatus*	AMNH-A166426	AY843690	AY843690								Berebice River camp at ca 18mi SW Kwakwani	Guyana	05 05 06 N 58 14 14 W
OGsp	*Lithodytes*	*lineatus*	55 CM	#######	EU201136								Grand-Santi	French Guiana	04 20 00 N 54 15 00 W
OGsp	*Litoria*	*caerulea*	DMH	AY326038	AY326038						AY844131			Australia	
OGsp	*Myersiohyla*	*kanaima*	ROM39582	AY843634	AY843634						AY844079		Mt Ayangana	Guyana	
OGsp	*Nephelobates*	sp.	WES626	DQ502242	DQ502242								Estado Trujillo, Carretera Humocaro Bajo-Agua de Obispos, 2400 m	Venezuela	
OGsp	*Osteocephalus*	*taurinus*	WED55452;KU205406	AY326041	AY326041						AY844140		Madre de Dios: Cusco Amazonico	Peru	
OGsp	*Phrynopus*	*bracki*	USNM286919	EF493709	EF493709						EF493507		Pasco, 2.9 km N, 5.5 km E Oxapampa	Peru	
OGsp	*Phrynopus*	*brunneus*	KU178258	EF493357	EF493357								Carchi, 14.6 km NW Carchi	Ecuador	
OGsp	*Phrynopus*	*peraccai*	KU178266	EF493710	EF493710								Napo, 2 km W Papallacta	Ecuador	
OGsp	*Phyllobates*	*vittatus*		DQ502152	DQ502152						DQ503166		captive bred		
OGsp	*Phyllomedusa*	*vaillanti*	AMNH-A1662888	AY549363	AY549363						AY844158		Berebice River camp at ca 18mi SW Kwakwani	Guyana	
CGsp	*Pristimantis*	*acerus*	KU217786	EF493678	EF493678								Napo, 6.8 km E Papallacta	Ecuador	
CGsp	*Pristimantis*	*achatinus*	KU217809	EF493827	EF493660								Manabi, Rio Cuaque E Pedernales	Ecuador	
CGsp	*Pristimantis*	*actites*	KU217830	EF493696	EF493696						EF493494		Cotopasi, Pilalo	Ecuador	
CGsp	*Pristimantis*	*altamazonicus*	KU215460	EF493670	EF493670								Cuzco Amazonico, 15 km E Puerto Maldonado	Peru	
CGsp	*Pristimantis*	*aniptopalmatus*	KU291627	EF493390	EF493390								Pasco, 2.9 km N, 5.5 km E Oxapampa	Peru	
CGsp	*Pristimantis*	*appendiculatus*	KU17763	EF493524	EF493524								Pichincha, Quebradas Zapadores	Ecuador	
CGsp	*Pristimantis*	*bipunctatus*	KU291638	EF493702	EF493702						EF493492		Pasco, 2.9 km N, 5.5 km E Oxapampa	Peru	
CGsp	*Pristimantis*	*bromeliaceus*	KU291702	EF493351	EF493351								Pasco, 2.9 km N, 5.5 km E Oxapampa	Peru	
CGsp	*Pristimantis*	*buckleyi*	KU217836	EF493350	EF493350								Carchi, 9.0 km E El Angel	Ecuador	
CGsp	*Pristimantis*	*cajamarcensis*	KU217845	EF493823	EF493663								Loja, 13 km S Yangana	Ecuador	
CGsp	*Pristimantis*	*calcarulatus*	KU177658	EF493523	EF493523								Pichincha, Tandapi	Ecuador	
CGsp	*Pristimantis*	*caprifer*	KU177680	EF493391	EF493391								Pichincha, La Palma	Ecuador	
CGsp	*Pristimantis*	*celator*	KU177684	EF493685	EF493685								Carchi, Maldonado	Ecuador	
CGsp	*Pristimantis*	*ceuthospilus*	KU212216	EF493520	EF493520								Cajamarca, Chota, 12 km W Llama	Peru	
CGsp	*Pristimantis*	*chalceus*	KU177638	EF493675	EF493675								Carchi, Maldonado	Ecuador	
	Pristimantis	*chiastonotus*	428 CM	#######	#######	Prch_H04	1-2	2-1	3-1		#######	Prch_H03	Cacao	French Guiana	04 34 00 N 52 28 00 W
	Pristimantis	*chiastonotus*	283 AF	#######	#######	Prch_H04	1-2	2-1	3-1		#######	Prch_H01	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Pristimantis	*chiastonotus*	1362 BPN	#######	#######	Prch_H04	1-2	2-1	3-1		#######	Prch_H01	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Pristimantis	*chiastonotus*	247 AF	#######	#######	Prch_H04	1-2	2-1	3-1		#######	Prch_H03	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
	Pristimantis	*chiastonotus*	255 AF	#######	#######	Prch_H04	1-2	2-1	3-1		#######	Prch_H03	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
	Pristimantis	*chiastonotus*	256 AF	#######	#######	Prch_H04	1-2	2-1	3-1		#######	Prch_H04	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
	Pristimantis	*chiastonotus*	1387 BPN	#######	#######	Prch_H05	1-2	2-1	3-1		#######	Prch_H01	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Pristimantis	*chiastonotus*	1611 BPN	#######	#######	Prch_H10	1-3	2-2	3-1		#######	Prch_H01	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Pristimantis	*chiastonotus*	1653 BPN	#######	#######	Prch_H10	1-3	2-2	3-1		#######	Prch_H01	Saül1	French Guiana	03 37 32 N 53 12 26 W

	Genus	species	voucher										locality	country	coordinates
	Pristimantis	*chiastonotus*	1654 BPN	#######	#######	Prch_H10	1-3	2-2	3-1		#######	Prch_H01	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Pristimantis	*chiastonotus*	1677 BPN	#######	#######	Prch_H10	1-3	2-2	3-1		#######	Prch_H01	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Pristimantis	*chiastonotus*	1678 BPN	#######	#######	Prch_H10	1-3	2-2	3-1		#######	Prch_H01	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Pristimantis	*chiastonotus*	1679 BPN	#######	#######	Prch_H10	1-3	2-2	3-1		#######	Prch_H01	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Pristimantis	*chiastonotus*	13848 MTR	#######	#######	Prch_H11	1-5	2-3	3-2		#######	Prch_H01	Lourenço	Brazil	02 19 25 N 51 38 43 W
	Pristimantis	*chiastonotus*	13849 MTR	#######	#######	Prch_H11	1-5	2-3	3-2		#######	Prch_H01	Lourenço	Brazil	02 19 25 N 51 38 43 W
	Pristimantis	*chiastonotus*	13855 MTR	#######	#######	Prch_H11	1-5	2-3	3-2		#######	Prch_H08	Lourenço	Brazil	02 19 25 N 51 38 43 W
	Pristimantis	*chiastonotus*	13847 MTR	#######	#######	Prch_H12	1-5	2-3	3-2		#######	Prch_H01	Lourenço	Brazil	02 19 25 N 51 38 43 W
	Pristimantis	*chiastonotus*	13740 MTR	#######	#######	Prch_H12	1-5	2-3	3-2		#######	Prch_H01	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Pristimantis	*chiastonotus*	13765 MTR	#######	#######	Prch_H12	1-5	2-3	3-2		#######	Prch_H01	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Pristimantis	*chiastonotus*	13792 MTR	#######	#######	Prch_H12	1-5	2-3	3-2		#######	Prch_H01	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Pristimantis	*chiastonotus*	13722 MTR	#######	#######	Prch_H13	1-6	2-4	3-2		#######	Prch_H01	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Pristimantis	*chiastonotus*	13965 MTR	#######	#######	Prch_H14	1-7	2-4	3-2		#######	Prch_H01	Laranjal do Jari	Brazil	00 43 00 S 52 23 00 W
	Pristimantis	*chiastonotus*	13966 MTR	#######	#######	Prch_H14	1-7	2-4	3-2		#######	Prch_H01	Laranjal do Jari	Brazil	00 43 00 S 52 23 00 W
	Pristimantis	*chiastonotus*	13967 MTR	#######	#######	Prch_H14	1-7	2-4	3-2		#######	Prch_H01	Laranjal do Jari	Brazil	00 43 00 S 52 23 00 W
	Pristimantis	*chiastonotus*	0937 MTR	#######	#######	Prch_H15	1-8	2-5	3-2		#######	Prch_H01	Igarapé Camaipi	Brazil	00 01 27 S 51 53 50 W
	Pristimantis	*chiastonotus*	13960 MTR	#######	#######	Prch_H15	1-8	2-5	3-2		#######	Prch_H06	Laranjal do Jari	Brazil	00 43 00 S 52 23 00 W
	Pristimantis	*chiastonotus*	13983 MTR	#######	#######	Prch_H16	1-9	2-5	3-2		#######	Prch_H07	maraca	Brazil	00 12 00 S 51 54 00 W
	Pristimantis	*chiastonotus*	372 CM	#######	#######	Prch_H02	1-1	2-1	3-1		#######	Prch_H03	Régina	French Guiana	04 18 00 N 52 07 00 W
	Pristimantis	*chiastonotus*	366 CM	#######	#######	Prch_H03	1-1	2-1	3-1		#######	Prch_H04	Lucifer	French Guiana	04 46 00 N 53 55 00 W
	Pristimantis	*chiastonotus*	103 CM	#######	#######	Prch_H04	1-2	2-1	3-1		#######	Prch_H01	Tibourou	French Guiana	04 25 00 N 52 18 00 W
	Pristimantis	*chiastonotus*	177 BM	#######	#######	Prch_H04	1-2	2-1	3-1		#######	Prch_H01	Trinité	French Guiana	04 35 00 N 53 21 00 W
	Pristimantis	*chiastonotus*	180 BM	#######	#######	Prch_H04	1-2	2-1	3-1		#######	Prch_H01	Trinité	French Guiana	04 35 00 N 53 21 00 W
	Pristimantis	*chiastonotus*	185 BM	#######	#######	Prch_H04	1-2	2-1	3-1		#######	Prch_H01	Trinité	French Guiana	04 35 00 N 53 21 00 W
	Pristimantis	*chiastonotus*	111 CM	#######	#######	Prch_H06	1-2	2-1	3-1		#######	Prch_H01	Tibourou	French Guiana	04 25 00 N 52 18 00 W
	Pristimantis	*chiastonotus*	112 PG	#######	#######	Prch_H07	1-3	2-2	3-1		#######	Prch_H01	Mont Saint Marcel	French Guiana	02 23 09 N 53 00 58 W
	Pristimantis	*chiastonotus*	183 CM	#######	#######	Prch_H07	1-3	2-2	3-1		#######	Prch_H01	Trijonction	French Guiana	02 20 00 N 54 36 00 W
	Pristimantis	*chiastonotus*	22 2001.0800MNHN	#######	#######	Prch_H08	1-4	2-2	3-1		#######	Prch_H01	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
	Pristimantis	*chiastonotus*	30 AF	#######	#######	Prch_H10	1-3	2-2	3-1		#######	Prch_H01	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Pristimantis	*chiastonotus*	123 BM	#######	#######	Prch_H10	1-3	2-2	3-1		#######	Prch_H01	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Pristimantis	*chiastonotus*	32 AF	#######	#######	Prch_H10	1-3	2-2	3-1		#######	Prch_H01	Saül2	French Guiana	03 36 00 N 53 17 00 W
	Pristimantis	*chiastonotus*	34 AF	#######	#######	Prch_H10	1-3	2-2	3-1		#######	Prch_H01	Saül2	French Guiana	03 36 00 N 53 17 00 W
	Pristimantis	*chiastonotus*	33 AF	#######	#######	Prch_H10	1-3	2-2	3-1		#######	Prch_H03	Saül2	French Guiana	03 36 00 N 53 17 00 W
	Pristimantis	*chiastonotus*	351 PG	#######	#######	Prch_H10	1-4	2-2	3-1		#######	Prch_H01	Haute Wanapi	French Guiana	02 30 00 N 53 49 00 W
	Pristimantis	*chiastonotus*	1620 BPN	#######	#######	Prch_H10	1-3	2-2	3-1		#######	Prch_H01	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Pristimantis	*chiastonotus*	202 AF	#######	EU201060	Prch_H01	1-1	2-1	3-1		#######	Prch_H01	Angouleme	French Guiana	05 23 00 N 53 39 00 W
	Pristimantis	*chiastonotus*	204 AF	#######	EU201060	Prch_H01	1-1	2-1	3-1		#######	Prch_H01	Angouleme	French Guiana	05 23 00 N 53 39 00 W
	Pristimantis	*chiastonotus*	227 AF	#######	EU201060	Prch_H01	1-1	2-1	3-1		#######	Prch_H01	Angouleme	French Guiana	05 23 00 N 53 39 00 W
	Pristimantis	*chiastonotus*	265 CM	#######	EU201060	Prch_H01	1-1	2-1	3-1		#######	Prch_H01	DZ5	French Guiana	04 03 00 N 52 01 00 W
	Pristimantis	*chiastonotus*	350 CM	#######	EU201060	Prch_H01	1-1	2-1	3-1		#######	Prch_H01	Lucifer	French Guiana	04 46 00 N 52 07 00 W
	Pristimantis	*chiastonotus*	371 CM	#######	EU201060	Prch_H01	1-1	2-1	3-1		#######	Prch_H01	Régina	French Guiana	04 18 00 N 52 07 00 W
	Pristimantis	*chiastonotus*	82 AF	#######	EU201060	Prch_H01	1-1	2-1	3-1		#######	Prch_H05	St Georges	French Guiana	03 52 00 N 51 48 00 W
	Pristimantis	*chiastonotus*	83 AF	#######	EU201060	Prch_H01	1-1	2-1	3-1		#######	Prch_H05	St Georges	French Guiana	03 52 00 N 51 48 00 W
	Pristimantis	*chiastonotus*	101 CM	#######	EU201060	Prch_H01	1-1	2-1	3-1		#######	Prch_H01	Tibourou	French Guiana	04 25 00 N 52 18 00 W
	Pristimantis	*chiastonotus*	167 AF	#######	EU201061	Prch_H17	1-10	2-6	3-3		#######	Prch_H02	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Pristimantis	*chiastonotus*	166 AF	#######	EU201061	Prch_H17	1-10	2-6	3-3		#######	Prch_H02	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Pristimantis	*chiastonotus*	162 AF	#######	EU201061	Prch_H17	1-10	2-6	3-3		#######	Prch_H02	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Pristimantis	*chiastonotus*	163 AF	#######	EU201061	Prch_H17	1-10	2-6	3-3		#######	Prch_H02	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Pristimantis	*chiastonotus*	13846 MTR			Prch_NA					#######	Prch_H01	Lourenço	Brazil	02 19 25 N 51 38 43 W
	Pristimantis	*chiastonotus*	112 CM	#######	#######	Prch_H05	1-2	2-1	3-1			Prch_NA	Tibourou	French Guiana	04 25 00 N 52 18 00 W
	Pristimantis	*chiastonotus*	120 PG	#######	#######	Prch_H07	1-3	2-2	3-1			Prch_NA	Mont Saint Marcel	French Guiana	02 23 09 N 53 00 58 W
	Pristimantis	*chiastonotus*	196 AF	#######	EU201060	Prch_H01	1-1	2-1	3-1			Prch_NA	Montagne des singes	French Guiana	05 04 00 N 52 43 00 W
	Pristimantis	*chiastonotus*	197 AF	#######	EU201060	Prch_H01	1-1	2-1	3-1			Prch_NA	Montagne des singes	French Guiana	05 04 00 N 52 43 00 W
CGsp	*Pristimantis*	*chloronotus*	KU202325	AY326007	AY326007								Napo; 3.5 km E Santa Barbara	Ecuador	
CGsp	*Pristimantis*	*citriogaster*	KU212278	EF493700	EF493700								San Martin, San Martin, Cataratas Ahnashiyacu, 14 km NE Tarapoto	Peru	
CGsp	*Pristimantis*	*colomai*	QCAZ17101	EF493354	EF493354					EF493502			Esmeraldes, Alto Tambo	Ecuador	
CGsp	*Pristimantis*	*condor*	KU217857	EF493701	EF493701					EF493504			Morona-Santaigo, 4.6 km N Gualaquiza	Ecuador	
CGsp	*Pristimantis*	*conspicillatus*	QCAZ28448	EF493529	EF493529					EF493499			Sucumbios, Monte Tour	Ecuador	
CGsp	*Pristimantis*	*cremnobates*	KU177252	EF493528	EF493528					EF493486			Napo, Rio Salado	Ecuador	
CGsp	*Pristimantis*	*crenunguis*	KU1	EF493693	EF493666								Pichincha, Tandapi	Ecuador	

CGsp	Genus	Species	Voucher					Locality	Country	Coordinates
CGsp	Pristimantis	croceoinguinis		EF493669	EF493669			Morona-Santiago, 53.8 km E Bella Union via Santiago	Ecuador	
CGsp	Pristimantis	cruentus	AMNHA12444-8	EF493697	EF493697			Ratibor, Finca Ojo de Agua	Panama	
CGsp	Pristimantis	cryophilius	KU217863	EF493672	EF493672			Azuay, 4 km W Laguna Torcadorn	Ecuador	
CGsp	Pristimantis	curtipes	KU217871	EF493513	EF493513		EF493497	Pichircha, Bosque de Pasocha	Ecuador	
CGsp	Pristimantis	devillei	KU217991	EF493688	EF493688			Napo, 6.1 km E Papallacta	Ecuador	
CGsp	Pristimantis	dissimulatus	KU1790	EF493522	EF493522			Pichincha, Quebrada Zapadores	Ecuador	
CGsp	Pristimantis	duellmani	KU202404;KU217998	AY326003	AY326003		EF493500	Carchi; ~5 km W La Gruel; 2340 m	Ecuador	
CGsp	Pristimantis	euphronides	BWMC6918	EF493527	EF493527		EF493489	Grand Etang	Grenada	
CGsp	Pristimantis	fenestratus	?	EF493703	EF493703			?	Peru	
CGsp	Pristimantis	gentryi	KU218109	EF493511	EF493511			Cotopaxi, 27.6 km E Pilabo	Ecuador	
CGsp	Pristimantis	glandulosus	KU218002	EF493676	EF493676			Napo, 2.7 km W Cuyuja	Ecuador	
CGsp	Pristimantis	gutturalis	557 PG				#######	Armontabo	French Guiana	03 48 16 N 52 17 17 W
CGsp	Pristimantis	gutturalis	577 PG	#######	#######			Mitaraka	French Guiana	02 16 00 N 54 31 00 W
CGsp	Pristimantis	imitatrix	KU21	EF493824	EF493667			Cuzco Amazonico, 15 km E Puerto Maldonado	Peru	
CGsp	Pristimantis	inguinalis	1685 BPN				#######	Saül1		
CGsp	Pristimantis	inguinalis	204 BM	#######	#######			Trinité	French Guiana	04 35 00 N 53 21 00 W
CGsp	Pristimantis	inusitatus	KU218015	EF493677	EF493677			Napo, 31 km N Jondachi	Ecuador	
CGsp	Pristimantis	labiosus	QCAZ19771	EF493694	EF493694			Pichincha, 4 km NW La Florida. Finca Gloria	Ecuador	
CGsp	Pristimantis	lanthanites	KU222001	EF493695	EF493695			Loreto, San Jacinto	Peru	
CGsp	Pristimantis	latidiscus	KU218016	EF493698	EF493698			Pichincha, 5 km W La Florida	Ecuador	
CGsp	Pristimantis	leoni	KU218227	EF493684	EF493684		EF493495	Carchi, 51.3 km W Tulcan	Ecuador	
CGsp	Pristimantis	lirellus	KU212226	EF493521	EF493521			San Martin Rioja Rio Cerranayaca76kmNW Rioja	Peru	
CGsp	Pristimantis	luteolateralis	KU17780	EF493517	EF493517			Pichincha, Tandapi	Ecuador	
CGsp	Pristimantis	lymani	KU218019	EF493392	EF493392			Loja, 3.9 km E Loja	Ecuador	
CGsp	Pristimantis	marmoratus	21 AF	#######	#######		#######	Saül1	French Guiana	03 37 32 N 53 12 26 W
CGsp	Pristimantis	marmoratus	110 BM	#######	EU201063			Kaw3	French Guiana	04 32 53 N 52 09 07 W
CGsp	Pristimantis	melanogaster		EF493826	EF493826			Amazonas, N. Slobe Abra Barro Negro, 28 kmSSW Leimebambe	Peru	
CGsp	Pristimantis	nyctophylax	KU177812	EF493526	EF493526		EF493487	Pichincha, Tandapi	Ecuador	
CGsp	Pristimantis	ockendeni	KU222023	EF493519	EF493519		EF493496	Loreto, 1.5 km N Teniente Lopez	Peru	
CGsp	Pristimantis	ocreatus	KU208508	EF493682	EF493682			Carchi, 26.6 km W Tulcan	Ecuador	
CGsp	Pristimantis	orcesi	KU218021	EF493679	EF493679			Pichincha, Bosque de Pasochoa	Ecuador	
CGsp	Pristimantis	orestes	KU218257	EF493388	EF493388			Azuay, 7 km E Sigsig	Ecuador	
CGsp	Pristimantis	parvillus	KU177821	EF493352	EF493352			Pichincha	Ecuador	
CGsp	Pristimantis	peruvianus		EF493707	EF493707		EF493498	?	Peru	
CGsp	Pristimantis	petrobardus		EF493825	EF493367			Cajamarca, Chota, ca 2 km W Huambos	Peru	
CGsp	Pristimantis	pluvicanorus	AMNH16	AY843586	AY843586		AY844035	Santa Cruz, Caballero, Canton San Juan, Amboro National Park	Bolivia	
CGsp	Pristimantis	pycnodermis	KU218028	EF493680	EF493680			Morona Santiago, Ca Gualaceo-Limon Rd.,2.4 km E Azuay border	Ecuador	
CGsp	Pristimantis	pyrrhomerus	KU218030	EF493683	EF493683			Bolivar, Bosque Protector Cashca Totoras	Ecuador	
CGsp	Pristimantis	quinquagesimus	KU17937	EF493690	EF493690			Pichincha, Quebrada Zapadores	Ecuador	
CGsp	Pristimantis	rhabdolaemus	KU1734	EF493706	EF493706			Cuzco, Buenos Aires	Peru	
CGsp	Pristimantis	rhodoplichus	KU2197	EF493674	EF493674			Piura, Le Tambo	Peru	
CGsp	Pristimantis	ridens	AMNHA124551	EF493355	EF493355			Cocle, El Valle	Panama	
CGsp	Pristimantis	riveti	KU218035	EF493348	EF493348			Azuay, 8.1 km W Morona-Santiago border on Gualaceo-Limon Rd.	Ecuador	
CGsp	Pristimantis	rozei		EF493691	EF493691		EF493491	Road to King's Bay Reservoir	Trini and Tobago	
CGsp	Pristimantis	sagittulus	KU291635	EF493705	EF493705		EF493501	Pasco, 0.9 km N, 2.1 km E Oxapampa	Peru	
CGsp	Pristimantis	schultei	KU212220	EF493681	EF493681			Amazonas, Chachapoyas, 5 km N Levan	Peru	
CGsp	Pristimantis	shrevei		EF493692	EF493692			St. Andrew Parish, 1.6 mi. NE Vermont	St Vincent	
CGsp	Pristimantis	simonbolivari	KU218	EF493671	EF493671			Bosque Protector, Cashca Tororas	Peru	
CGsp	Pristimantis	skydmainos		EF493393	EF493393			?	Peru	
CGsp	Pristimantis	sp.	SBH2007	EF493356	EF493356			?	Peru	
CGsp	Pristimantis	sp.2	395 CM	#######	#######		#######	Lucifer	French Guiana	04 46 00 N 53 55 00 W
CGsp	Pristimantis	sp.3_"nourages"	264 AF	#######	#######		#######	Nouragues2	French Guiana	04 05 30 N 52 42 00 W
CGsp	Pristimantis	sp.4	257 AF				#######	Nouragues1	French Guiana	
CGsp	Pristimantis	sp.4	317 CM	#######	#######			Cisame	French Guiana	04 11 00 N 52 22 00 W
CGsp	Pristimantis	spinosus	KU218052	EF493673	EF493673			Morona-Santiago, 10.6 km W Plan de Miglio	Ecuador	
CGsp	Pristimantis	stictogaster	KU291659	EF493704	EF493704		EF493506	Pasco, 2.9 km N, 5.5 km E Oxapampa	Peru	

	Genus	Species	ID			Prze_Ha						Prze_Hb	Locality	Country	Coordinates
CGsp	*Pristimantis*	subsigillatus	KU218147	EF493525	EF493525								Azuay, 11.2 km W Luz Maria	Ecuador	
CGsp	*Pristimantis*	supernatis	KU202432	AY326005	AY326005								Napo; 3.5 km E Santa Barbara	Ecuador	
CGsp	*Pristimantis*	thymalopsoides	KU17786	EF493514	EF493514								Cotopaxi, Pilalo	Ecuador	
CGsp	*Pristimantis*	thymelensis	QCAZ16428	EF493516	EF493516						EF493503		Napo, Paramo de Guamani"	Ecuador	
CGsp	*Pristimantis*	thymelensis	KU20251	AY326009	AY326009								Carchi; 12 km W Tufino; 3520 m	Ecuador	
CGsp	*Pristimantis*	toftae	KU215493	EF493353	EF493353								Cuzco Amazonico, 15 km E Puerto Maldonado	Peru	
CGsp	*Pristimantis*	trepidotus	KU218234	EF493515	EF493515								Imbabara, 13.8 km W Tabacundo	Ecuador	
CGsp	*Pristimantis*	truebae	KU218013	EF493512	EF493512								Cotopaxi, 24.6 km E Pilabo	Ecuador	
CGsp	*Pristimantis*	unistrigatus	KU218057	EF493387	EF493387						EF493505		Imbabura, 35 km E Pquela	Ecuador	
CGsp	*Pristimantis*	urichi	USNM336098	EF493699	EF493699						EF493488		Arima Valley	Trinidad	
CGsp	*Pristimantis*	verecundus	QCAZ12410	EF493686	EF493686								Cotopaxi, Otonga	Ecuador	
CGsp	*Pristimantis*	versicolor	KU218096	EF493389	EF493389						EF493493		Zamora-Chinchipe, 1.7 km E Loja border	Ecuador	
CGsp	*Pristimantis*	vertebralis	KU177972	EF493689	EF493689								Imbabara, La Delicia	Ecuador	
CGsp	*Pristimantis*	walkeri	KU218116	EF493518	EF493518						EF493490		Pichincha, 5 km W La Florida	Ecuador	
CGsp	*Pristimantis*	wiensi	KU21979	EF493377	EF493668								Piura, 12.7 km E Canchaque	Peru	
CGsp	*Pristimantis*	wnigrum	KU205076	AY326004	AY326004								Carchi; ~5 km W La Gruel; 2340 m	Ecuador	
	Pristimantis	zeuctotylus	425 CM	#######	#######	Prze_H01	1-1	2-1	3-1	4-1	#######	Prze_H02	Cacao	French Guiana	04 34 00 N 52 28 00 W
	Pristimantis	zeuctotylus	248 AF	#######	#######	Prze_H01	1-1	2-1	3-1	4-1	#######	Prze_H02	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
	Pristimantis	zeuctotylus	253 AF	#######	#######	Prze_H01	1-1	2-1	3-1	4-1	#######	Prze_H02	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
	Pristimantis	zeuctotylus	281 AF	#######	#######	Prze_H01	1-1	2-1	3-1	4-1	#######	Prze_H02	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
	Pristimantis	zeuctotylus	280 AF	#######	#######	Prze_H02	1-1	2-1	3-1	4-1	#######	Prze_H02	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
	Pristimantis	zeuctotylus	13827 MTR	#######	#######	Prze_H04	1-2	2-1	3-1	4-1	#######	Prze_H02	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Pristimantis	zeuctotylus	13976 MTR	#######	#######	Prze_H05	1-3	2-1	3-1	4-1	#######	Prze_H10	Laranjal do Jari	Brazil	00 43 00 S 52 23 00 W
	Pristimantis	zeuctotylus	11997 SMNS	#######	#######	Prze_H06	1-4	2-2	3-2	4-1	#######	Prze_H02	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Pristimantis	zeuctotylus	11998 SMNS	#######	#######	Prze_H06	1-4	2-2	3-2	4-1	#######	Prze_H02	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Pristimantis	zeuctotylus	11999 SMNS	#######	#######	Prze_H06	1-4	2-2	3-2	4-1	#######	Prze_H02	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Pristimantis	zeuctotylus	12000 SMNS	#######	#######	Prze_H06	1-4	2-2	3-2	4-1	#######	Prze_H02	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W
	Pristimantis	zeuctotylus	Z-66 PG	#######	#######	Prze_H09	1-7	2-4	3-4	4-1	#######	Prze_H01	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
	Pristimantis	zeuctotylus	Z-60 PG	#######	#######	Prze_H09	1-7	2-4	3-4	4-1	#######	Prze_H02	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
	Pristimantis	zeuctotylus	Z-62 PG	#######	#######	Prze_H09	1-7	2-4	3-4	4-1	#######	Prze_H02	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
	Pristimantis	zeuctotylus	Z-63 PG	#######	#######	Prze_H09	1-7	2-4	3-4	4-1	#######	Prze_H02	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
	Pristimantis	zeuctotylus	Z-65 PG	#######	#######	Prze_H09	1-7	2-4	3-4	4-1	#######	Prze_H02	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
	Pristimantis	zeuctotylus	Z-61 PG	#######	#######	Prze_H10	1-8	2-5	3-4	4-1	#######	Prze_H02	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
	Pristimantis	zeuctotylus	Z-64 PG	#######	#######	Prze_H10	1-8	2-5	3-4	4-1	#######	Prze_H02	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
	Pristimantis	zeuctotylus	209 AF	#######	#######	Prze_H17	1-11	2-7	3-6	4-2	#######	Prze_H01	Angouleme	French Guiana	05 23 00 N 53 39 00 W
	Pristimantis	zeuctotylus	17 CM	#######	#######	Prze_H14	1-10	2-7	3-6	4-2	#######	Prze_H05	Kaw	French Guiana	04 43 00 N 52 08 00 W
	Pristimantis	zeuctotylus	97 CM	#######	#######	Prze_H14	1-10	2-7	3-6	4-2	#######	Prze_H01	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Pristimantis	zeuctotylus	80 AF	#######	#######	Prze_H15	1-12	2-8	3-6	4-2	#######	Prze_H01	St Georges	French Guiana	03 52 00 N 51 48 00 W
	Pristimantis	zeuctotylus	81 AF	#######	#######	Prze_H16	1-13	2-8	3-6	4-2	#######	Prze_H07	St Georges	French Guiana	03 52 00 N 51 48 00 W
	Pristimantis	zeuctotylus	33 RB	#######	#######	Prze_H18	1-11	2-7	3-6	4-2	#######	Prze_H01	St Eugene	French Guiana	04 51 00 N 53 04 00 W
	Pristimantis	zeuctotylus	84 PG	#######	#######	Prze_H01	1-1	2-1	3-1	4-1	#######	Prze_H02	Mont Saint Marcel	French Guiana	02 23 09 N 53 00 58 W
	Pristimantis	zeuctotylus	70 AF	#######	#######	Prze_H01	1-1	2-1	3-1	4-1	#######	Prze_H06	Petit-saut	French Guiana	05 04 00 N 53 03 00 W
	Pristimantis	zeuctotylus	43 AF	#######	#######	Prze_H01	1-1	2-1	3-1	4-1	#######	Prze_H09	Petit-saut	French Guiana	05 04 00 N 53 03 00 W
	Pristimantis	zeuctotylus	227 CM	#######	#######	Prze_H01	1-1	2-1	3-1	4-1	#######	Prze_H01	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Pristimantis	zeuctotylus	347 CM	#######	#######	Prze_H03	1-2	2-1	3-1	4-1	#######	Prze_H08	Lucifer	French Guiana	04 46 00 N 53 55 00 W
	Pristimantis	zeuctotylus	356 CM	#######	#######	Prze_H03	1-2	2-1	3-1	4-1	#######	Prze_H08	Lucifer	French Guiana	04 46 00 N 53 55 00 W
	Pristimantis	zeuctotylus	785 BPN	#######	#######	Prze_H06	1-4	2-2	3-2	4-1	#######	Prze_H02	Ralleighvallen	Suriname	04 43 00 N 56 13 00 W
	Pristimantis	zeuctotylus	321 CM	#######	#######	Prze_H12	1-9	2-6	3-5	4-2	#######	Prze_H02	Langatabiki	Suriname	05 14 01 N 54 35 51 W
	Pristimantis	zeuctotylus	1593 BPN	#######	#######	Prze_H01	1-1	2-1	3-1	4-1	#######	Prze_H02	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Pristimantis	zeuctotylus	1594 BPN	#######	#######	Prze_H01	1-1	2-1	3-1	4-1	#######	Prze_H02	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Pristimantis	zeuctotylus	1681 BPN	#######	#######	Prze_H01	1-1	2-1	3-1	4-1	#######	Prze_H02	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Pristimantis	zeuctotylus	987 BPN	#######	#######	Prze_H08	1-6	2-3	3-3	4-1	#######	Prze_H02	Sipaliwini	Suriname	02 02 00 N 56 07 00 W
	Pristimantis	zeuctotylus	985 BPN	#######	#######	Prze_H08	1-6	2-3	3-3	4-1	#######	Prze_H03	Sipaliwini	Suriname	02 02 00 N 56 07 00 W
	Pristimantis	zeuctotylus	986 BPN	#######	#######	Prze_H08	1-6	2-3	3-5	4-1	#######	Prze_H03	Sipaliwini	Suriname	02 02 00 N 56 07 00 W
	Pristimantis	zeuctotylus	1069 BPN	#######	#######	Prze_H11	1-9	2-6	3-5	4-2	#######	Prze_H01	Lely Mountain	Suriname	04 16 00 N 54 44 00 W
	Pristimantis	zeuctotylus	1559 BPN	#######	#######	Prze_H14	1-10	2-7	3-6	4-2	#######	Prze_H01	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Pristimantis	zeuctotylus	1560 BPN	#######	#######	Prze_H14	1-10	2-7	3-6	4-2	#######	Prze_H01	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Pristimantis	zeuctotylus	95 CM	#######	EF376083	Prze_H13	1-10	2-7	3-6	4-2	#######	Prze_H01	Tibourou	French Guiana	04 25 00 N 52 18 00 W
	Pristimantis	zeuctotylus	129 CM	#######	EF376083	Prze_H13	1-10	2-7	3-6	4-2	#######	Prze_H01	Tibourou	French Guiana	04 25 00 N 52 18 00 W
	Pristimantis	zeuctotylus	117 AF	#######	EU201059	Prze_H07	1-5	2-2	3-2	4-1	#######	Prze_H01	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Pristimantis	zeuctotylus	128 AF	#######	EU201059	Prze_H07	1-5	2-2	3-2	4-1	#######	Prze_H01	Brownsberg	Suriname	04 56 31 N 55 10 33 W

	Genus	species	specimen	GB1	GB2	Hap1	c1	c2	c3	c4	GB3	Hap2	Locality	Country	Coordinates
	Pristimantis	zeuctotylus	136 AF	#######	EU201059	Prze_H07	1-5	2-2	3-2	4-1	#######	Prze_H01	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Pristimantis	zeuctotylus	137 AF	#######	EU201059	Prze_H07	1-5	2-2	3-2	4-1	#######	Prze_H01	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Pristimantis	zeuctotylus	133 AF	#######	EU201059	Prze_H07	1-5	2-2	3-2	4-1	#######	Prze_H04	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Pristimantis	zeuctotylus	100 AF	#######	EU201059	Prze_H07	1-5	2-2	3-2	4-1	#######	Prze_H01	Road to Apura	Suriname	05 11 00 N 55 37 00 W
	Pristimantis	zeuctotylus	101 AF	#######	EU201059	Prze_H07	1-5	2-2	3-2	4-1	#######	Prze_H01	Road to Apura	Suriname	05 11 00 N 55 37 00 W
	Pristimantis	zeuctotylus	102 AF	#######	EU201059	Prze_H07	1-5	2-2	3-2	4-1	#######	Prze_H01	Road to Apura	Suriname	05 11 00 N 55 37 00 W
	Pristimantis	zeuctotylus	118 PG	#######	#######	Prze_H01	1-1	2-1	3-1	4-1		Prze_NA	Mont Saint Marcel	French Guiana	02 23 09 N 53 00 58 W
	Pristimantis	zeuctotylus	119 PG	#######	#######	Prze_H01	1-1	2-1	3-1	4-1		Prze_NA	Mont Saint Marcel	French Guiana	02 23 09 N 53 00 58 W
	Pristimantis	zeuctotylus	43 BM	#######	EF376083	Prze_H13	1-10	2-7	3-6	4-2		Prze_NA	Cisame	French Guiana	04 11 00 N 52 22 00 W
OGsp	Pseudis	paradoxa	MACN38642	AY843740	AY843740						AY844167		Corrientes Dto. Bellavista Camino San Roque-Bellavista		
OGsp	Pseudis	paradoxa	394 MC	#######	#######								Kourou	French Guiana	05 09 00 N 52 38 00 W
OGsp	Pseudis	paradoxa	DCC3284	AY326032	AY326032								Sao Paulo Santa Helena ~18km S.LuizAntonio"		
OGsp	Pseudis	paradoxa	MACN38584	AY549364	AY549364								Formosa: Laguna Yema		
OGsp	Rhaebo	guttatus									EF364361				
OGsp	Rhamphophryne	festae	KU217501	DQ158423	DQ158423										
OGsp	Rheobates	palmatus		DQ502262	DQ502262								Cundimamarca, La Mesa, finca Tacarcuna, km 3 via Chachipay, 1300 m	Colombia	
CGsp	Rhinella	castaenotica		DQ158440	DQ158440	Rhca_H20	1-10	2-6	3-4	4-3		Rhca_NA	Santarem	Brazil	03 09 00 S 54 50 00 W
	Rhinella	castaenotica	206 AF	#######	#######	Rhca_H01	1-1	2-1	3-1	4-1	#######	Rhca_H02	Angouleme	French Guiana	05 23 00 N 53 39 00 W
	Rhinella	castaenotica	249 AF	#######	#######	Rhca_H01	1-1	2-1	3-1	4-1	#######	Rhca_H03	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
	Rhinella	castaenotica	563 PG	#######	#######	Rhca_H01	1-1	2-1	3-1	4-1	#######	Rhca_H02	Pic Coudreau de l'Est	French Guiana	03 18 02 N 52 56 77 W
	Rhinella	castaenotica	562 PG	#######	#######	Rhca_H01	1-1	2-1	3-1	4-2	#######	Rhca_H03	Pic Coudreau de l'Est	French Guiana	03 18 02 N 52 56 77 W
	Rhinella	castaenotica	263 AF	#######	#######	Rhca_H03	1-1	2-1	3-1	4-1	#######	Rhca_H02	Nouragues2	French Guiana	04 05 30 N 52 42 00 W
	Rhinella	castaenotica	560 PG	#######	#######	Rhca_H07	1-2	2-1	3-1	4-1	#######	Rhca_H02	Pic Coudreau de l'Est	French Guiana	03 18 02 N 52 56 77 W
	Rhinella	castaenotica	561 PG	#######	#######	Rhca_H08	1-2	2-1	3-1	4-1	#######	Rhca_H05	Pic Coudreau de l'Est	French Guiana	03 18 02 N 52 56 77 W
	Rhinella	castaenotica	409 CM	#######	#######	Rhca_H07	1-2	2-1	3-1	4-1	#######	Rhca_H05	Lucifer	French Guiana	04 46 00 N 53 55 00 W
	Rhinella	castaenotica	376 CM	#######	#######	Rhca_H10	1-3	2-1	3-1	4-1	#######	Rhca_H02	Régina	French Guiana	04 18 00 N 52 07 00 W
	Rhinella	castaenotica	13791 MTR	#######	#######	Rhca_H11	1-4	2-2	3-1	4-1	#######	Rhca_H01	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Rhinella	castaenotica	13780 MTR	#######	#######	Rhca_H11	1-4	2-2	3-1	4-1	#######	Rhca_H01	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Rhinella	castaenotica	13978 MTR	#######	#######	Rhca_H12	1-5	2-2	3-1	4-1	#######	Rhca_H02	Laranjal do Jari	Brazil	00 43 00 S 52 23 00 W
	Rhinella	castaenotica	13984 MTR	#######	#######	Rhca_H12	1-5	2-2	3-1	4-1	#######	Rhca_H06	maraca	Brazil	00 12 00 S 51 54 00 W
	Rhinella	castaenotica	13766 MTR	#######	#######	Rhca_H13	1-5	2-2	3-1	4-1	#######	Rhca_H01	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Rhinella	castaenotica	13772 MTR	#######	#######	Rhca_H13	1-5	2-2	3-1	4-1	#######	Rhca_H01	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Rhinella	castaenotica	13982 MTR	#######	#######	Rhca_H14	1-5	2-2	3-1	4-1	#######	Rhca_H02	PK42 apres laranjal	Brazil	00 27 59 S 51 58 20 W
	Rhinella	castaenotica	13756 MTR	#######	#######	Rhca_H15	1-5	2-2	3-1	4-1	#######	Rhca_H01	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Rhinella	castaenotica	13781 MTR	#######	#######	Rhca_H15	1-5	2-2	3-1	4-1	#######	Rhca_H01	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Rhinella	castaenotica	13771 MTR	#######	#######	Rhca_H15	1-5	2-2	3-1	4-1	#######	Rhca_H02	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Rhinella	castaenotica	13732 MTR	#######	#######	Rhca_H16	1-6	2-3	3-2	4-1	#######	Rhca_H05	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Rhinella	castaenotica	13757 MTR	#######	#######	Rhca_H16	1-6	2-3	3-2	4-1	#######	Rhca_H05	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Rhinella	castaenotica	13897 MTR	#######	#######	Rhca_H17	1-8	2-4	3-2	4-1	#######	Rhca_H01	Lourenço	Brazil	02 19 25 N 51 38 43 W
	Rhinella	castaenotica	13937 MTR	#######	#######	Rhca_H17	1-8	2-4	3-2	4-1	#######	Rhca_H01	Lourenço	Brazil	02 19 25 N 51 38 43 W
	Rhinella	castaenotica	13938 MTR	#######	#######	Rhca_H17	1-8	2-4	3-2	4-1	#######	Rhca_H02	Lourenço	Brazil	02 19 25 N 51 38 43 W
	Rhinella	castaenotica	13958 MTR	#######	#######	Rhca_H18	1-7	2-3	3-2	4-1	#######	Rhca_H07	Laranjal do Jari	Brazil	00 43 00 S 52 23 00 W
	Rhinella	castaenotica	60 AF	#######	#######	Rhca_H06	1-1	2-1	3-1	4-2	#######	Rhca_H03	Petit-saut	French Guiana	05 04 00 N 53 03 00 W
	Rhinella	castaenotica	363 CM	#######	#######	Rhca_H09	1-2	2-1	3-1	4-2	#######	Rhca_H11	Lucifer	French Guiana	04 46 00 N 53 55 00 W
	Rhinella	castaenotica	MTR10.003	#######	#######	Rhca_H19	1-9	2-5	3-3	4-2	#######	Rhca_H09	Lago Cipotuba	Brazil	05 48 05 S 60 13 16 W
	Rhinella	castaenotica	MTR10.006	#######	#######	Rhca_H19	1-9	2-5	3-3	4-2	#######	Rhca_H09	Lago Cipotuba	Brazil	05 48 05 S 60 13 16 W
	Rhinella	castaenotica	299 AF	EF364263	EF364289	Rhca_H01	1-1	2-1	3-1	4-1	#######	Rhca_H02	Kaw1	French Guiana	04 31 00 N 52 02 00 W
	Rhinella	castaenotica	298 AF	EF364263	EF364289	Rhca_H01	1-1	2-1	3-1	4-1	#######	Rhca_H03	Kaw1	French Guiana	04 31 00 N 52 02 00 W
	Rhinella	castaenotica	T-4460 T	EF364263	EF364289	Rhca_H01	1-1	2-1	3-1	4-1	#######	Rhca_H03	Angoulème	French Guiana	05 23 00 N 53 39 00 W
	Rhinella	castaenotica	206 BM	EF364263	EF364289	Rhca_H01	1-1	2-1	3-1	4-1	#######	Rhca_H04	DZ5	French Guiana	04 06 00 N 52 03 45 W
	Rhinella	castaenotica	332 CM	EF364263	EF364289	Rhca_H01	1-1	2-1	3-1	4-1	#######	Rhca_H03	Montagne Petite Tortue	French Guiana	05 10 46 N 52 55 53 W
	Rhinella	castaenotica	490 PG	EF364263	EF364289	Rhca_H01	1-1	2-1	3-1	4-1	#######	Rhca_H03	Montagne Tortue	French Guiana	04 18 00 N 52 22 00 W
	Rhinella	castaenotica	244 BM	EF364263	EF364289	Rhca_H01	1-1	2-1	3-1	4-1	#######	Rhca_H11	piton remarquable	French Guiana	03 41 00 N 52 14 00 W
	Rhinella	castaenotica	28 AF	EF364263	EF364289	Rhca_H01	1-1	2-1	3-1	4-1	#######	Rhca_H02	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Rhinella	castaenotica	36 AF	EF364263	EF364289	Rhca_H01	1-1	2-1	3-1	4-1	#######	Rhca_H02	Saül2	French Guiana	03 36 00 N 53 17 00 W
	Rhinella	castaenotica	75 AF	EF364263	EF364289	Rhca_H01	1-1	2-1	3-1	4-1	#######	Rhca_H01	St Georges	French Guiana	03 52 00 N 51 48 00 W
	Rhinella	castaenotica	76 AF	EF364263	EF364289	Rhca_H01	1-1	2-1	3-1	4-1	#######	Rhca_H01	St Georges	French Guiana	03 52 00 N 51 48 00 W
	Rhinella	castaenotica	286 AG	EF364263	EF364289	Rhca_H01	1-1	2-1	3-1	4-1	#######	Rhca_H02	St Georges	French Guiana	03 52 00 N 51 48 00 W
	Rhinella	castaenotica	287 AG	EF364263	EF364289	Rhca_H01	1-1	2-1	3-1	4-1	#######	Rhca_H05	St Georges	French Guiana	03 52 00 N 51 48 00 W

	Rhinella	*castaenotica*	131 BM	EF364261	EF364287	Rhca_H07	1-2	2-1	3-1	4-1	EF364344	Rhca_H02	Mataroni	French Guiana	04 12 00 N 52 10 00 W
	Rhinella	*castaenotica*	133 BM	EF364263	EF364289	Rhca_H01	1-1	2-1	3-1	4-1	EF364345	Rhca_H01	Mataroni	French Guiana	04 12 00 N 52 10 00 W
	Rhinella	*castaenotica*	135 BM	EF364263	EF364289	Rhca_H01	1-1	2-1	3-1	4-1	EF364346	Rhca_H05	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Rhinella	*castaenotica*	169 CM	EF364263	EF364289	Rhca_H01	1-1	2-1	3-1	4-1	EF364347	Rhca_H03	Tibourou	French Guiana	04 25 00 N 52 18 00 W
	Rhinella	*castaenotica*	186 BM	EF364263	EF364289	Rhca_H01	1-1	2-1	3-1	4-1	EF364348	Rhca_H01	Trinité	French Guiana	04 35 00 N 53 21 00 W
	Rhinella	*castaenotica*	198 BM	EF364263	EF364289	Rhca_H01	1-1	2-1	3-1	4-1	EF364349	Rhca_H02	Trinité	French Guiana	04 35 00 N 53 21 00 W
	Rhinella	*castaenotica*	211 CM	EF364264	EF364290	Rhca_H02	1-1	2-1	3-1	4-1	EF364350	Rhca_H02	Montagne des singes	French Guiana	05 04 00 N 52 43 00 W
	Rhinella	*castaenotica*	212 CM	EF364264	EF364290	Rhca_H02	1-1	2-1	3-1	4-1	EF364351	Rhca_H02	Montagne des singes	French Guiana	05 04 00 N 52 43 00 W
	Rhinella	*castaenotica*	254 CM	EF364260	EF364286	Rhca_H04	1-4	2-2	3-1	4-1	EF364352	Rhca_H02	Camopi	French Guiana	03 20 00 N 52 17 00 W
	Rhinella	*castaenotica*	110 PG	EF364259	EF364285	Rhca_H05	1-4	2-2	3-1	4-1	EF364353	Rhca_H08	Mont Saint Marcel	French Guiana	02 23 09 N 53 00 58 W
	Rhinella	*castaenotica*	65 CM	EF364263	EF364289	Rhca_H01	1-1	2-1	3-1	4-1	EF364354	Rhca_H10	Monts Bakra	French Guiana	03 18 08 N 52 56 73 W
	Rhinella	*castaenotica*	104 CM	EF364263	EF364289	Rhca_H01	1-1	2-1	3-1	4-1	EF364355	Rhca_H03	Tibourou	French Guiana	04 25 00 N 52 18 00 W
	Rhinella	*castaenotica*	145 CM	EF364263	EF364289	Rhca_H01	1-1	2-1	3-1	4-1	EF364356	Rhca_H02	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Rhinella	*castaenotica*	161 CM	EF364262	EF364288	Rhca_H01	1-1	2-1	3-1	4-1	EF364357	Rhca_H02	Ouanary	French Guiana	04 15 00 N 51 40 00 W
	Rhinella	*castaenotica*	248 CM	EF364263	EF364289	Rhca_H01	1-1	2-1	3-1	4-1	EF364358	Rhca_H11	Kaw1	French Guiana	04 31 00 N 52 02 00 W
	Rhinella	*castaenotica*	293 AG	#######	#######	Rhca_H01	1-1	2-1	3-1	4-1		Rhca_NA	Trinité	French Guiana	04 35 00 N 53 21 00 W
	Rhinella	*castaenotica*	308 AG	#######	#######	Rhca_H01	1-1	2-1	3-1	4-1		Rhca_NA	Trinité	French Guiana	04 35 00 N 53 21 00 W
	Rhinella	*castaenotica*	132 BM	EF364261	EF364287	Rhca_H07	1-2	2-1	3-1	4-1		Rhca_NA	Mataroni	French Guiana	04 12 00 N 52 10 00 W
	Rhinella	*castaenotica*	128 BM	EF364263	EF364289	Rhca_H01	1-1	2-1	3-1	4-1		Rhca_NA	Mataroni	French Guiana	04 12 00 N 52 10 00 W
	Rhinella	*castaenotica*	129 BM	EF364263	EF364289	Rhca_H01	1-1	2-1	3-1	4-1		Rhca_NA	Mataroni	French Guiana	04 12 00 N 52 10 00 W
	Rhinella	*castaenotica*	27 AF	EF364263	EF364289	Rhca_H01	1-1	2-1	3-1	4-1		Rhca_NA	Saül1	French Guiana	03 37 32 N 53 12 26 W
CGsp	*Rhinella*	*dapsilis*	QCAZ3509	DQ158448	DQ158448	Rhma_H22	1-10	2-3	3-2			Rhma_NA	Pichincha	Ecuador	00 00 01 S 79 22 59 W
CGsp	*Rhinella*	*lescurei*	574 PG	#######	#######	Rhle_H02	1-2	2-1			#######	Rhle_H01	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
CGsp	*Rhinella*	*lescurei*	579 PG	#######	#######	Rhle_H02	1-2	2-1			#######	Rhle_H01	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
CGsp	*Rhinella*	*lescurei*	588 PG	#######	#######	Rhle_H02	1-2	2-1			#######	Rhle_H01	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
CGsp	*Rhinella*	*lescurei*	569 PG	#######	#######	Rhle_H03	1-3	2-2			#######	Rhle_H01	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
CGsp	*Rhinella*	*lescurei*	571 PG	#######	#######	Rhle_H03	1-3	2-2			#######	Rhle_H01	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
CGsp	*Rhinella*	*lescurei*	580 PG	#######	#######	Rhle_H03	1-3	2-2			#######	Rhle_H01	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
CGsp	*Rhinella*	*lescurei*	587 PG	#######	#######	Rhle_H03	1-3	2-2			#######	Rhle_H01	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
CGsp	*Rhinella*	*lescurei*	570 PG	#######	#######	Rhle_H03	1-3	2-2			#######	Rhle_H01	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
CGsp	*Rhinella*	*lescurei*	224 2006.2609MNHN	#######	#######	Rhle_H05	1-4	2-2			#######	Rhle_H01	Haute Wanapi	French Guiana	02 30 59 N 53 49 15 W
CGsp	*Rhinella*	*lescurei*	225 2006.2610MNHN	#######	#######	Rhle_H05	1-4	2-2			#######	Rhle_H01	Haute Wanapi	French Guiana	02 30 59 N 53 49 15 W
CGsp	*Rhinella*	*lescurei*	230 2006.2611MNHN	#######	#######	Rhle_H05	1-4	2-2			#######	Rhle_H01	Haute Wanapi	French Guiana	02 30 59 N 53 49 15 W
CGsp	*Rhinella*	*lescurei*	231 2006.2612MNHN	#######	#######	Rhle_H05	1-4	2-2			#######	Rhle_H01	Haute Wanapi	French Guiana	02 30 59 N 53 49 15 W
CGsp	*Rhinella*	*lescurei*	232 2006.2613MNHN	#######	#######	Rhle_H05	1-4	2-2			#######	Rhle_H01	Haute Wanapi	French Guiana	02 30 59 N 53 49 15 W
CGsp	*Rhinella*	*lescurei*	223 2006.2608MNHN	#######	#######	Rhle_H05	1-4	2-2			#######	Rhle_H03	Haute Wanapi	French Guiana	02 30 59 N 53 49 15 W
CGsp	*Rhinella*	*lescurei*	5' CM	EF364278	EF364304	Rhle_H01	1-1	2-1			#######	Rhle_H01	Cisame	French Guiana	04 11 00 N 52 22 00 W
CGsp	*Rhinella*	*lescurei*	T-3027 T	EF364279	EF364305	Rhle_H03	1-3	2-2			#######	Rhle_H01	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
CGsp	*Rhinella*	*lescurei*	589 PG			Rhle_NA					#######	Rhle_H03	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
CGsp	*Rhinella*	*lescurei*	103 PG	EF364278	EF364304	Rhle_H01	1-1	2-1			EF364339	Rhle_H02	Saül1	French Guiana	03 37 32 N 53 12 26 W
CGsp	*Rhinella*	*lescurei*	104 PG	EF364278	EF364304	Rhle_H01	1-1	2-1			EF364340	Rhle_H02	Saül1	French Guiana	03 37 32 N 53 12 26 W
CGsp	*Rhinella*	*lescurei*	121 BM	EF364278	EF364304	Rhle_H01	1-1	2-1			EF364341	Rhle_H02	Saül1	French Guiana	03 37 32 N 53 12 26 W
CGsp	*Rhinella*	*lescurei*	5 CM	EF364278	EF364304	Rhle_H01	1-1	2-1			EF364342	Rhle_H01	Cisame	French Guiana	04 11 00 N 52 22 00 W
CGsp	*Rhinella*	*lescurei*	112 BM	EF364279	EF364305	Rhle_H03	1-3	2-2			EF364343	Rhle_H01	Litany	French Guiana	02 26 19 N 54 25 18 W
CGsp	*Rhinella*	*lescurei*	284 AF	#######	#######	Rhle_H04	1-3	2-2				Rhle_NA	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
	Rhinella	*margaritifera*	MSH10226	#######	#######	Rhma_H32					#######	Rhma_H01	E.E. Anavilhanas- Base 2	Brazil	02 32 04 S 60 50 12 W
	Rhinella	*margaritifera*	MSH10339	#######	#######	Rhma_H33					#######	Rhma_H01	E.E. Anavilhanas- Terra firme 1	Brazil	02 32 04 S 60 50 12 W
	Rhinella	*margaritifera*	6317 MTR	#######	#######	Rhma_H23	1-11	2-4	3-2		#######	Rhma_H10	Serra do Kukoinhokren	Brazil	07 50 00 S 51 55 00 W
	Rhinella	*margaritifera*	6313 MTR	#######	#######	Rhma_H24	1-12	2-4	3-2		#######	Rhma_H10	Serra do Kukoinhokren	Brazil	07 50 00 S 51 55 00 W
	Rhinella	*margaritifera*	473 PG	#######	#######	Rhma_H02	1-2	2-1	3-1		#######	Rhma_H01	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
	Rhinella	*margaritifera*	420 PG	#######	#######	Rhma_H03	1-2	2-1	3-1		#######	Rhma_H01	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
	Rhinella	*margaritifera*	390 CM	#######	#######	Rhma_H11	1-4	2-1	3-1		#######	Rhma_H02	St Georges	French Guiana	03 52 00 N 51 48 00 W
	Rhinella	*margaritifera*	T-2559 T	#######	#######	Rhma_H12	1-5	2-1	3-1		#######	Rhma_H01	Pic Matecho	French Guiana	03 45 00 N 53 02 00 W
	Rhinella	*margaritifera*	T-2539 T	#######	#######	Rhma_H12	1-5	2-1	3-1		#######	Rhma_H02	Pic Matecho	French Guiana	03 45 00 N 53 02 00 W
	Rhinella	*margaritifera*	421 CM	#######	#######	Rhma_H14	1-6	2-1	3-1		#######	Rhma_H01	Lucifer	French Guiana	04 46 00 N 53 55 00 W
	Rhinella	*margaritifera*	288 AG	#######	#######	Rhma_H18	1-1	2-1	3-1		#######	Rhma_H01	St Georges	French Guiana	03 52 00 N 51 48 00 W
	Rhinella	*margaritifera*	374 CM	#######	#######	Rhma_H10	1-4	2-1	3-1		#######	Rhma_H02	Régina	French Guiana	04 18 00 N 52 07 00 W
	Rhinella	*margaritifera*	479 PG	#######	#######	Rhma_H06	1-5	2-1	3-1		#######	Rhma_H06	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
	Rhinella	*margaritifera*	T-4482 T	#######	#######	Rhma_H01	1-1	2-1	3-1		#######	Rhma_H02	Angoulème	French Guiana	05 23 00 N 53 39 00 W
	Rhinella	*margaritifera*	T-2033 T	#######	#######	Rhma_H01	1-1	2-1	3-1		#######	Rhma_H01	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
	Rhinella	*margaritifera*	13873 MTR	#######	#######	Rhma_H20	1-8	2-2	3-1		#######	Rhma_H01	Lourenço	Brazil	02 19 25 N 51 38 43 W

Rhinella	margaritifera	13872 MTR	#######	#######	Rhma_H20	1-8	2-2	3-1		#######	Rhma_H01	Lourenço	Brazil	02 19 25 N 51 38 43 W
Rhinella	margaritifera	13878 MTR	#######	#######	Rhma_H20	1-8	2-2	3-1		#######	Rhma_H01	Lourenço	Brazil	02 19 25 N 51 38 43 W
Rhinella	margaritifera	13874 MTR	#######	#######	Rhma_H21	1-9	2-2	3-1		#######	Rhma_H01	Lourenço	Brazil	02 19 25 N 51 38 43 W
Rhinella	margaritifera	PHAN1 PG	EF364266	EF364292	Rhma_H01	1-1	2-1	3-1		#######	Rhma_H01	Armontabo	French Guiana	03 48 16 N 52 17 17 W
Rhinella	margaritifera	290 CM	EF364266	EF364292	Rhma_H01	1-1	2-1	3-1		#######	Rhma_H02	Camp Canopé	French Guiana	04 53 37 N 52 47 57 W
Rhinella	margaritifera	307 PG	EF364266	EF364292	Rhma_H01	1-1	2-1	3-1		#######	Rhma_H01	Lac Toponowini	French Guiana	03 02 93 N 52 42 15 W
Rhinella	margaritifera	361 CM	EF364266	EF364292	Rhma_H01	1-1	2-1	3-1		#######	Rhma_H05	Lucifer	French Guiana	04 46 00 N 53 55 00 W
Rhinella	margaritifera	408 PG	EF364266	EF364292	Rhma_H01	1-1	2-1	3-1		#######	Rhma_H02	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
Rhinella	margaritifera	409 PG	EF364266	EF364292	Rhma_H01	1-1	2-1	3-1		#######	Rhma_H02	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
Rhinella	margaritifera	421 PG	EF364266	EF364292	Rhma_H01	1-1	2-1	3-1		#######	Rhma_H02	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
Rhinella	margaritifera	74 AF	EF364266	EF364292	Rhma_H01	1-1	2-1	3-1		#######	Rhma_H02	St Georges	French Guiana	03 52 00 N 51 48 00 W
Rhinella	margaritifera	T-2034 T	EF364266	EF364292	Rhma_H01	1-1	2-1	3-1		#######	Rhma_H02	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
Rhinella	margaritifera	T-2035 T	EF364266	EF364292	Rhma_H01	1-1	2-1	3-1		#######	Rhma_H09	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
Rhinella	margaritifera	294 CM	EF364266	EF364292	Rhma_H01	1-1	2-1	3-1		#######	Rhma_H02	Camp Canopé	French Guiana	04 53 37 N 52 47 57 W
Rhinella	margaritifera	389 CM			Rhma_NA					#######	Rhma_H02	Apatou	French Guiana	05 10 00 N 54 20 00 W
Rhinella	margaritifera	144 PG	EF364276	EF364302	Rhma_H19	1-7	2-2	3-1		EF364311	Rhma_H01	Kaw2	French Guiana	04 43 00 N 52 08 00 W
Rhinella	margaritifera	143 PG	EF364276	EF364302	Rhma_H19	1-7	2-2	3-1		EF364312	Rhma_H02	Kaw2	French Guiana	04 43 00 N 52 08 00 W
Rhinella	margaritifera	2 BM	EF364267	EF364293	Rhma_H04	1-1	2-1	3-1		EF364313	Rhma_H02	Cisame	French Guiana	04 11 00 N 52 22 00 W
Rhinella	margaritifera	92 BM	EF364275	EF364301	Rhma_H09	1-1	2-1	3-1		EF364314	Rhma_H07	Cisame	French Guiana	04 11 00 N 52 22 00 W
Rhinella	margaritifera	158 BM	EF364266	EF364292	Rhma_H01	1-1	2-1	3-1		EF364315	Rhma_H01	Guatemala	French Guiana	05 09 00 N 52 38 00 W
Rhinella	margaritifera	159 BM	EF364266	EF364292	Rhma_H01	1-1	2-1	3-1		EF364316	Rhma_H02	Guatemala	French Guiana	05 09 00 N 52 38 00 W
Rhinella	margaritifera	160 BM	EF364266	EF364292	Rhma_H01	1-1	2-1	3-1		EF364317	Rhma_H02	Guatemala	French Guiana	05 09 00 N 52 38 00 W
Rhinella	margaritifera	161 BM	EF364266	EF364292	Rhma_H01	1-1	2-1	3-1		EF364318	Rhma_H02	Guatemala	French Guiana	05 09 00 N 52 38 00 W
Rhinella	margaritifera	162 BM	EF364266	EF364292	Rhma_H01	1-1	2-1	3-1		EF364319	Rhma_H02	Guatemala	French Guiana	05 09 00 N 52 38 00 W
Rhinella	margaritifera	163 BM	EF364266	EF364292	Rhma_H01	1-1	2-1	3-1		EF364320	Rhma_H03	Guatemala	French Guiana	05 09 00 N 52 38 00 W
Rhinella	margaritifera	164 BM	EF364266	EF364292	Rhma_H01	1-1	2-1	3-1		EF364321	Rhma_H02	Montagne des Singes	French Guiana	05 04 00 N 52 43 00 W
Rhinella	margaritifera	165 BM	EF364266	EF364292	Rhma_H01	1-1	2-1	3-1		EF364322	Rhma_H01	Montagne des Singes	French Guiana	05 04 00 N 52 43 00 W
Rhinella	margaritifera	176 BM	EF364266	EF364292	Rhma_H01	1-1	2-1	3-1		EF364323	Rhma_H02	Trinité	French Guiana	04 35 00 N 53 21 00 W
Rhinella	margaritifera	178 BM	EF364271	EF364297	Rhma_H15	1-6	2-1	3-1		EF364324	Rhma_H02	Trinité	French Guiana	04 35 00 N 53 21 00 W
Rhinella	margaritifera	195 CM	EF364266	EF364292	Rhma_H01	1-1	2-1	3-1		EF364325	Rhma_H02	Kaw2	French Guiana	04 43 00 N 52 08 00 W
Rhinella	margaritifera	196 CM	EF364272	EF364298	Rhma_H07	1-1	2-1	3-1		EF364326	Rhma_H09	Kaw2	French Guiana	04 43 00 N 52 08 00 W
Rhinella	margaritifera	203 CM	EF364269	EF364295	Rhma_H16	1-1	2-1	3-1		EF364327	Rhma_H01	Saül1	French Guiana	03 37 32 N 53 12 26 W
Rhinella	margaritifera	204 CM	EF364269	EF364295	Rhma_H16	1-1	2-1	3-1		EF364328	Rhma_H02	Saül1	French Guiana	03 37 32 N 53 12 26 W
Rhinella	margaritifera	217 CM	EF364273	EF364299	Rhma_H13	1-1	2-1	3-1		EF364329	Rhma_H02	Grand Santi	French Guiana	04 20 00 N 54 15 00 W
Rhinella	margaritifera	225 CM	EF364266	EF364292	Rhma_H08	1-3	2-1	3-1		EF364330	Rhma_H02	Piste St Elie	French Guiana	05 17 01 N 53 03 14 W
Rhinella	margaritifera	285 CM	EF364274	EF364300	Rhma_H17	1-1	2-1	3-1		EF364331	Rhma_H01	St Elie	French Guiana	04 50 00 N 53 15 00 W
Rhinella	margaritifera	286 CM	EF364270	EF364296	Rhma_H06	1-1	2-1	3-1		EF364332	Rhma_H02	St Elie	French Guiana	04 50 00 N 53 15 00 W
Rhinella	margaritifera	108 CM	EF364266	EF364292	Rhma_H01	1-1	2-1	3-1		EF364333	Rhma_H02	Kaw2	French Guiana	04 43 00 N 52 08 00 W
Rhinella	margaritifera	66 CM	EF364272	EF364298	Rhma_H07	1-1	2-1	3-1		EF364334	Rhma_H09	Monts Bakra	French Guiana	03 18 08 N 52 56 73 W
Rhinella	margaritifera	136 CM	EF364266	EF364292	Rhma_H01	1-1	2-1	3-1		EF364335	Rhma_H01	crique Margot	French Guiana	05 28 00 N 53 57 00 W
Rhinella	margaritifera	284 CM	EF364266	EF364292	Rhma_H01	1-1	2-1	3-1		EF364336	Rhma_H01	St Elie	French Guiana	04 50 00 N 53 15 00 W
Rhinella	margaritifera	ZUEC,DCC3393	AY980262	AY980262	Rhma_H34						Rhma_NA	Santo Aleixo	Brazil	22 33 54 S 43 04 09 W
Rhinella	margaritifera	KU215145	DQ158491	DQ158491	Rhma_H31						Rhma_NA	Madre de dios	Peru	11 39 00 S 70 33 35 W
Rhinella	margaritifera	137 CM	EF364268	EF364294	Rhma_H05	1-1	2-1	3-1			Rhma_NA	crique Margot	French Guiana	05 28 00 N 53 57 00 W
Rhinella	martyi	229 PG	#######	#######	Rhma_H27	1-14	2-5	3-3		#######	Rhma_H01	Haute Wanapi	French Guiana	02 30 59 N 53 49 15 W
Rhinella	martyi	135AF 2006.2604MNHN	#######	#######	Rhma_H28	1-15	2-5	3-3		#######	Rhma_H01	Brownsberg	Suriname	04 56 31 N 55 10 33 W
Rhinella	martyi	130AF 2006.2602MNHN	#######	#######	Rhma_H28	1-15	2-5	3-3		#######	Rhma_H01	Brownsberg	Suriname	04 56 31 N 55 10 33 W
Rhinella	martyi	165AF AF	#######	#######	Rhma_H28	1-15	2-5	3-3		#######	Rhma_H04	Brownsberg	Suriname	04 56 31 N 55 10 33 W
Rhinella	martyi	150AF 2006.2605MNHN	#######	#######	Rhma_H28	1-15	2-5	3-3		#######	Rhma_H08	Brownsberg	Suriname	04 56 31 N 55 10 33 W
Rhinella	martyi	98AF 2006.2606MNHN	#######	#######	Rhma_H28	1-15	2-5	3-3		#######	Rhma_H01	Road to Apura	Suriname	05 11 00 N 55 37 00 W
Rhinella	martyi	111AF 2006.2601MNHN	#######	#######	Rhma_H29	1-15	2-5	3-3		#######	Rhma_H01	Brownsberg	Suriname	04 56 31 N 55 10 33 W
Rhinella	martyi	132AF 2006.2603MNHN	#######	#######	Rhma_H29	1-15	2-5	3-3		#######	Rhma_H08	Brownsberg	Suriname	04 56 31 N 55 10 33 W
Rhinella	martyi	99AF 2006.2607MNHN	#######	#######	Rhma_H30	1-15	2-5	3-3		#######	Rhma_H04	Road to Apura	Suriname	05 11 00 N 55 37 00 W
Rhinella	martyi	MRT6213	#######	#######	Rhma_H25	1-13	2-5	3-3		#######	Rhma_H01	Igarapé Camaipi	Brazil	00 01 27 S 51 53 50 W
Rhinella	martyi	MRT6227	#######	#######	Rhma_H25	1-13	2-5	3-3		#######	Rhma_H01	Igarapé Camaipi	Brazil	00 01 27 S 51 53 50 W
Rhinella	martyi	MRT6228R	#######	#######	Rhma_H26	1-13	2-5	3-3		#######	Rhma_H01	Igarapé Camaipi	Brazil	00 01 27 S 51 53 50 W
Rhinella	martyi	T-3022 T	EF364277	EF364303	Rhma_H28	1-15	2-5	3-3		#######	Rhma_H01	Mitaraka	French Guiana	02 16 00 N 54 31 00 W
Rhinella	martyi	156 CM	EF364277	EF364303	Rhma_H28	1-15	2-5	3-3		EF364337	Rhma_H01	Trijonction	French Guiana	02 20 00 N 54 36 00 W
Rhinella	martyi	157 CM	EF364277	EF364303	Rhma_H28	1-15	2-5	3-3		EF364337	Rhma_H01	Trijonction	French Guiana	02 20 00 N 54 36 00 W
Rhinella	martyi	MRT6229	#######	#######	Rhma_H26	1-13	2-5	3-3			Rhma_NA	Igarapé Camaipi	Brazil	00 01 27 S 51 53 50 W
Rhinella	martyi	157' CM	EF364277	EF364303	Rhma_H28	1-15	2-5	3-3			Rhma_NA	Trijonction	French Guiana	02 20 00 N 54 36 00 W

	Rhinella	martyi	ROM22813,22833			Rhma_NA						Rhma_NA	Baramita	Guyana	07 22 00 N 60 29 00 W
	Rhinella	martyi	BPN42,59			Rhma_NA						Rhma_NA	Bartica	Guyana	06 22 00 N 58 39 00 W
	Rhinella	martyi	UTACV55742-3			Rhma_NA						Rhma_NA	Ellerts de Haan airstrip	Suriname	03 06 00 N 56 28 00 W
	Rhinella	martyi	ROM20652-20654			Rhma_NA						Rhma_NA	Kurupukari	Guyana	04 40 00 N 58 39 00 W
	Rhinella	martyi	BPN1053,1062			Rhma_NA						Rhma_NA	Lely Mountains	Suriname	04 16 00 N 54 44 00 W
	Rhinella	martyi	UTACV55740-1			Rhma_NA						Rhma_NA	Ralleighvallen	Suriname	04 41 00 N 56 08 00 W
	Rhinella	martyi	BPN984,990-91			Rhma_NA						Rhma_NA	Sipaliwini	Suriname	02 02 00 N 56 07 00 W
CGsp	Rhinella	sp.	QCAZ10601	DQ158470	DQ158470							Rhma_NA	Francisco de Orellana, P Nacional Yasuní,Napo	Ecuador	00 26 56 S 77 00 55 W
CGsp	Rhinella	sp.	QCAZ13896	DQ158471	DQ158471							Rhma_NA	Cañar, Manta Real	Ecuador	02 30 44 S 79 04 56 W
CGsp	Rhinella	sp.	QCAZ11597	DQ158472	DQ158472							Rhma_NA	Provincia Esmeraldas, Bosque Protector, 30 km from San Lorenzo by way of Ibarra	Ecuador	01 16 47 N 78 42 29 W
CGsp	Rhinella	sp.	USNM268828	DQ158490	DQ158490							Rhma_NA	Madre de Dios	Peru	11 39 00 S 70 33 35 W
	Rhinella	sp.	MTR10.019	#######	#######	Rhca_H21					#######	Rhca_H09	Santa Maria (Terra Preta)	Brazil	05 47 52 S 60 15 55 W
CGsp	Rhinella_(Bufo)	ocellatus	MZUSP103261	DQ158479	DQ158479								Peixe Tocantins	Brazil	
OGsp	Scarthyla	goinorum		AY843752	AY843752										
CGsp	Scinax	acuminatus	MACN38649	AY843753	AY843753					AY844176			Corientes, Paso de la patria	Argentina	
CGsp	Scinax	berthae	MLPA2137	AY843754	AY843754								Buenso Aires, Atalaya	Argentina	
	Scinax	boesemani	231 BM	#######	#######	Scbo_H15	1-9	2-5	3-3	4-2	#######	Scbo_H04	St georges RN2/PK 165	French Guiana	03 52 00 N 51 48 00 W
	Scinax	boesemani	44 AF	#######	#######	Scbo_H16	1-8	2-5	3-3	4-2	#######	Scbo_H12	Petit-saut	French Guiana	05 04 00 N 53 03 00 W
	Scinax	boesemani	233 BM	#######	#######	Scbo_H13	1-8	2-5	3-3	4-2	#######	Scbo_H01	St georges RN2/PK 165	French Guiana	03 52 00 N 51 48 00 W
	Scinax	boesemani	1020 BPN	#######	#######	Scbo_H22	1-12	2-7	3-4	4-2	#######	Scbo_H04	Sipaliwini	Suriname	02 02 00 N 56 07 00 W
	Scinax	boesemani	1000 BPN	#######	#######	Scbo_H22	1-12	2-7	3-4	4-2	#######	Scbo_H07	Sipaliwini	Suriname	02 02 00 N 56 07 00 W
	Scinax	boesemani	1002 BPN	#######	#######	Scbo_H22	1-12	2-7	3-4	4-2	#######	Scbo_H18	Sipaliwini	Suriname	02 02 00 N 56 07 00 W
	Scinax	boesemani	1001 BPN	#######	#######	Scbo_H22	1-12	2-7	3-4	4-2	#######	Scbo_H04	Sipaliwini	Suriname	02 02 00 N 56 07 00 W
	Scinax	boesemani	1021 BPN	#######	#######	Scbo_H22	1-12	2-7	3-4	4-2	#######	Scbo_H04	Sipaliwini	Suriname	02 02 00 N 56 07 00 W
	Scinax	boesemani	931 BPN	#######	#######	Scbo_H21	1-11	2-6	3-3	4-2	#######	Scbo_H01	Road to Apura	Suriname	05 11 00 N 55 39 00 W
	Scinax	boesemani	928 BPN	#######	#######	Scbo_H20	1-11	2-6	3-3	4-2	#######	Scbo_H01	Road to Apura	Suriname	05 11 00 N 55 39 00 W
	Scinax	boesemani	933 BPN	#######	#######	Scbo_H20	1-11	2-6	3-3	4-2	#######	Scbo_H01	Road to Apura	Suriname	05 11 00 N 55 39 00 W
	Scinax	boesemani	929 BPN	#######	#######	Scbo_H21	1-11	2-6	3-3	4-2	#######	Scbo_H01	Road to Apura	Suriname	05 11 00 N 55 39 00 W
	Scinax	boesemani	927 BPN	#######	#######	Scbo_H21	1-11	2-6	3-3	4-2	#######	Scbo_H20	Road to Apura	Suriname	05 11 00 N 55 39 00 W
	Scinax	boesemani	1370 BPN	#######	#######	Scbo_H01	1-1	2-1	3-1	4-1	#######	Scbo_H01	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Scinax	boesemani	1371 BPN	#######	#######	Scbo_H01	1-1	2-1	3-1	4-1	#######	Scbo_H01	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Scinax	boesemani	1374 BPN	#######	#######	Scbo_H01	1-1	2-1	3-1	4-1	#######	Scbo_H01	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Scinax	boesemani	1377 BPN	#######	#######	Scbo_H01	1-1	2-1	3-1	4-1	#######	Scbo_H01	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Scinax	boesemani	1376 BPN	#######	#######	Scbo_H01	1-1	2-1	3-1	4-1	#######	Scbo_H02	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Scinax	boesemani	1375 BPN	#######	#######	Scbo_H01	1-1	2-1	3-1	4-1	#######	Scbo_H04	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Scinax	boesemani	1531 BPN	#######	#######	Scbo_H01	1-1	2-1	3-1	4-1	#######	Scbo_H06	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Scinax	boesemani	1373 BPN	#######	#######	Scbo_H01	1-1	2-1	3-1	4-1	#######	Scbo_H10	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Scinax	boesemani	1555 BPN	#######	#######	Scbo_H01	1-1	2-1	3-1	4-1	#######	Scbo_H12	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Scinax	boesemani	1533 BPN	#######	#######	Scbo_H01	1-1	2-1	3-1	4-1	#######	Scbo_H13	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Scinax	boesemani	1536 BPN	#######	#######	Scbo_H01	1-1	2-1	3-1	4-1	#######	Scbo_H13	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Scinax	boesemani	1532 BPN	#######	#######	Scbo_H01	1-1	2-1	3-1	4-1	#######	Scbo_H16	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Scinax	boesemani	1534 BPN	#######	#######	Scbo_H01	1-1	2-1	3-1	4-1	#######	Scbo_H17	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Scinax	boesemani	301 CM	#######	#######	Scbo_H01	1-1	2-1	3-1	4-1	#######	Scbo_H08	Lac Toponowini	French Guiana	03 03 10 N 52 42 37 W
	Scinax	boesemani	13912 MTR	#######	#######	Scbo_H01	1-1	2-1	3-1	4-1	#######	Scbo_H04	Lourenço	Brazil	02 19 25 N 51 38 43 W
	Scinax	boesemani	13748 MTR	#######	#######	Scbo_H01	1-1	2-1	3-1	4-1	#######	Scbo_H02	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Scinax	boesemani	13737 MTR	#######	#######	Scbo_H01	1-1	2-1	3-1	4-1	#######	Scbo_H05	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Scinax	boesemani	13789 MTR	#######	#######	Scbo_H01	1-1	2-1	3-1	4-1	#######	Scbo_H14	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Scinax	boesemani	14 2001.0804484-5MNHN	#######	#######	Scbo_H02	1-1	2-1	3-1	4-1	#######	Scbo_H04	Pic Matecho	French Guiana	03 45 00 N 53 02 00 W
	Scinax	boesemani	1372 BPN	#######	#######	Scbo_H05	1-1	2-1	3-1	4-1	#######	Scbo_H12	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Scinax	boesemani	13746 MTR	#######	#######	Scbo_H06	1-1	2-1	3-1	4-1	#######	Scbo_H21	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Scinax	boesemani	13895 MTR	#######	#######	Scbo_H07	1-1	2-1	3-1	4-1	#######	Scbo_H04	Lourenço	Brazil	02 19 25 N 51 38 43 W
	Scinax	boesemani	13904 MTR	#######	#######	Scbo_H07	1-1	2-1	3-1	4-2	#######	Scbo_H04	Lourenço	Brazil	02 19 25 N 51 38 43 W
	Scinax	boesemani	13747 MTR	#######	#######	Scbo_H08	1-1	2-1	3-1	4-2	#######	Scbo_H08	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Scinax	boesemani	13736 MTR	#######	#######	Scbo_H08	1-1	2-1	3-1	4-1	#######	Scbo_H19	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Scinax	boesemani	13975 MTR	#######	#######	Scbo_H09	1-2	2-1	3-1	4-1	#######	Scbo_H09	Laranjal do Jari	Brazil	00 43 00 S 52 23 00 W
	Scinax	boesemani	13896 MTR	#######	#######	Scbo_H11	1-6	2-4	3-2	4-1	#######	Scbo_H15	Lourenço	Brazil	02 19 25 N 51 38 43 W
	Scinax	boesemani	13903 MTR	#######	#######	Scbo_H12	1-7	2-4	3-2	4-1	#######	Scbo_H04	Lourenço	Brazil	02 19 25 N 51 38 43 W
	Scinax	boesemani	1158 BPN	#######	#######	Scbo_H10	1-5	2-3	3-1	4-1	#######	Scbo_H04	Imbaimadai	Guyana	05 44 23 N 60 17 51 W
	Scinax	boesemani	379 CM	EF217453	EF217496	Scbo_H13	1-8	2-5	3-3	4-2	#######	Scbo_H08	Apatou	French Guiana	05 10 00 N 54 20 00 W
	Scinax	boesemani	1535 BPN	EF217453	EF217496	Scbo_H13	1-8	2-5	3-3	4-2	#######	Scbo_H01	Kaw2	French Guiana	04 43 00 N 52 08 00 W

	Scinax	boesemani	413 CM	EF217453	EF217496	Scbo_H13	1-8	2-5	3-3	4-2	#######	Scbo_H10	Lucifer	French Guiana	04 46 00 N 53 55 00 W
	Scinax	boesemani	232 BM	EF217453	EF217496	Scbo_H13	1-8	2-5	3-3	4-2	#######	Scbo_H02	St georges RN2/PK 165	French Guiana	03 52 00 N 51 48 00 W
	Scinax	boesemani	385 CM	EF217454	EF217497	Scbo_H18	1-8	2-5	3-3	4-2	#######	Scbo_H20	Apatou	French Guiana	05 10 00 N 54 20 00 W
	Scinax	boesemani	930 BPN	EF217459	EF217502	Scbo_H20	1-11	2-6	3-3	4-2	#######	Scbo_H01	Road to Apura	Suriname	05 11 00 N 55 39 00 W
	Scinax	boesemani	456 PG	EF217460	EF217503	Scbo_H03	1-3	2-2	3-1	4-2	#######	Scbo_H11	Mont Kotika	French Guiana	03 56 05 N 54 12 17 W
	Scinax	boesemani	T-2570 T	EF217460	EF217503	Scbo_H03	1-3	2-2	3-1	4-1	#######	Scbo_H01	Pic Matecho	French Guiana	03 45 00 N 53 02 00 W
	Scinax	boesemani	31 AF	EF217460	EF217503	Scbo_H03	1-3	2-2	3-1	4-1	#######	Scbo_H03	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Scinax	boesemani	1169 BPN	#######	EU201088	Scbo_H10	1-5	2-3	3-1	4-1	#######	Scbo_H04	Imbaimadai.	Guyana	05 44 23 N 60 17 51 W
	Scinax	boesemani	1022 BPN	#######	EU201089	Scbo_H23	1-12	2-7	3-4	4-2	#######	Scbo_H18	Sipaliwini	Suriname	02 02 00 N 56 07 00 W
	Scinax	boesemani	932 BPN	#######	EU201090	Scbo_H21	1-11	2-6	3-3	4-2	#######	Scbo_H02	Road to Apura	Suriname	05 11 00 N 55 39 00 W
	Scinax	boesemani	124 BM	EF217453	EF217496	Scbo_H13	1-8	2-5	3-3	4-2	EF364207	Scbo_H01	CD8/PK 6	French Guiana	05 30 10 N 53 33 00 W
	Scinax	boesemani	136 BM	EF217453	EF217496	Scbo_H13	1-8	2-5	3-3	4-2	EF364208	Scbo_H10	CD8/PK 6	French Guiana	05 30 10 N 53 33 00 W
	Scinax	boesemani	151 BM	EF217457	EF217500	Scbo_H19	1-10	2-5	3-3	4-2	EF364209	Scbo_H08	Savane Roche Virginie	French Guiana	04 11 00 N 52 09 00 W
	Scinax	boesemani	152 BM	EF217455	EF217498	Scbo_H14	1-9	2-5	3-3	4-2	EF364210	Scbo_H04	Savane Roche Virginie	French Guiana	04 11 00 N 52 09 00 W
	Scinax	boesemani	153 BM	EF217455	EF217498	Scbo_H14	1-9	2-5	3-3	4-2	EF364211	Scbo_H01	Savane Roche Virginie	French Guiana	04 11 00 N 52 09 00 W
	Scinax	boesemani	147 CM	EF217458	EF217501	Scbo_H17	1-8	2-5	3-3	4-2	EF364212	Scbo_H10	Guatemala	French Guiana	05 09 00 N 52 38 00 W
	Scinax	boesemani	232 CM	EF217454	EF217497	Scbo_H18	1-8	2-5	3-3	4-2	EF364213	Scbo_H08	Grand Santi	French Guiana	04 20 00 N 54 15 00 W
	Scinax	boesemani	233 CM	EF217459	EF217502	Scbo_H20	1-11	2-6	3-3	4-2	EF364214	Scbo_H20	Grand Santi	French Guiana	04 20 00 N 54 15 00 W
	Scinax	boesemani	39 CM	EF376040	EF376072	Scbo_H04	1-4	2-2	3-1	4-1	EF376146	Scbo_H02	Grand-Santi	French Guiana	04 20 00 N 54 15 00 W
	Scinax	boesemani	403 CM	EF217453	EF217496	Scbo_H13	1-8	2-5	3-3	4-2		Scbo_NA	Lucifer	French Guiana	04 46 00 N 53 55 00 W
	Scinax	boesemani	198 CM	EF217460	EF217503	Scbo_H03	1-3	2-2	3-1	4-2		Scbo_NA	Grand Santi	French Guiana	04 20 00 N 54 15 00 W
CGsp	Scinax	boulengeri	MVZ207215	AY843755	AY843755						AY844177		Guanacaste, ca. 0.2Km W Hyw 1 on fst paved rd 10Km N entrance Santa Rosa NP	Costa Rica	
CGsp	Scinax	catharinae	MCP3734	AY843756	AY843756								Rio grande do Sul, Pro-Mata	Brazil	
CGsp	Scinax	elaeochrous	MVZ149785	EF376045	EF376076						EF376151		Swamp on E edge of Cahuita Prov. Limon	Costa rica	9.750000; -82.816670
CGsp	Scinax	fuscovarius	JF1973	AY843758	AY843758						AY844179		Misiones, Guarani, San Vicente, Campo anexo	Argentina	
CGsp	Scinax	garbei	KU202764	AY326033	AY326033								Chimborazo, 6.7Km E Riobamba	Ecuador	
CGsp	Scinax	jolyi	3 CM	EF376035	6:AF467261						EF376141		Kaw1	French Guiana	04 31 00 N 52 02 00 W
CGsp	Scinax	nasicus	MACN38650	AY843759	AY843759						AY844180		Buenos Aires, Baradero, Estancia El retoño	Argentina	
CGsp	Scinax	nebulosusA1	258 CM	EF217470	EF217513								Mana	French Guiana	05 39 00 N 53 47 00 W
CGsp	Scinax	nebulosusA2	126 BM	EF217471	EF217514						#######		CD8/PK 6	French Guiana	05 30 10 N 53 33 00 W
CGsp	Scinax	nebulosusA3	318 AG	#######	#######								Kaw4	French Guiana	04 43 00 N 52 17 00 W
CGsp	Scinax	nebulosusB	394 BPN	#######	EU201094								Mabaruma	Guyana	08 12 00 N 59 46 48 W
CGsp	Scinax	nebulosusC	13838 MTR	#######	#######								Serra do Navio	Brazil	00 55 05 N 52 00 10 W
CGsp	Scinax	nebulosusD	CE616 ACC	#######	#######						#######		São Benedito, Queimadas, Sítio Genipapo	Brazil	04 02 00 S 40 52 00 W
CGsp	Scinax	nebulosusD	CE581 ACC	#######	EU201096						#######		Ibiapina, Sítio Pimentas, Vivenda Santa Rosa	Brazil	03 55 00 S 40 53 00 W
CGsp	Scinax	nebulosusE	AA95 ACC	#######	#######						#######		Timbaúba, Engenho Água Azul	Brazil	07 31 00 S 35 19 00 W
CGsp	Scinax	nebulosusE	AA900 ACC	#######	EU201095						#######		Timbaúba, Engenho Água Azul	Brazil	07 31 00 S 35 19 00 W
CGsp	Scinax	proboscideus	208 CM	EF217468	EF217511						#######		Kaw3	French Guiana	04 32 53 N 52 09 07 W
CGsp	Scinax	rostratus	247 CM	EF376039	EF376071						EF376145		Rio Caura	Venezuela	
	Scinax	ruber	89 AF	#######	#######	Scru_H07	1-5	2-2	3-1	4-1	#######	Scru_H02	St Georges	French Guiana	03 52 00 N 51 48 00 W
	Scinax	ruber	205 BM	#######	#######	Scru_H08	1-3	2-1	3-1	4-1	#######	Scru_H01	crique wapou	French Guiana	04 26 00 N 52 09 00 W
	Scinax	ruber	VOGT2131 MTR	#######	#######	Scru_H19	1-11	2-6	3-3	4-1	#######	Scru_H15	Cachoeirinha ME Rio Madeira	Brazil	05 29 40 S 60 49 23 W
	Scinax	ruber	382 PG	#######	#######	Scru_H11	1-7	2-4	3-2	4-1	#######	Scru_H01	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
	Scinax	ruber	13790 MTR	#######	#######	Scru_H18	1-10	2-5	3-2	4-1	#######	Scru_H16	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Scinax	ruber	13742 MTR	#######	#######	Scru_H18	1-10	2-5	3-2	4-1	#######	Scru_H17	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Scinax	ruber	13749 MTR	#######	#######	Scru_H18	1-10	2-5	3-2	4-1	#######	Scru_H17	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Scinax	ruber	13741 MTR	#######	#######	Scru_H18	1-10	2-5	3-2	4-1	#######	Scru_H18	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Scinax	ruber	13738 MTR	#######	#######	Scru_H18	1-10	2-5	3-2	4-1	#######	Scru_H19	Serra do Navio	Brazil	00 55 05 N 52 00 10 W
	Scinax	ruber	228 AF	#######	#######	Scru_H21	1-13	2-8	3-5	4-2	#######	Scru_H12	Angouleme	French Guiana	05 23 00 N 53 39 00 W
	Scinax	ruber	222 AF	#######	#######	Scru_H21	1-13	2-8	3-5	4-2	#######	Scru_H14	Angouleme	French Guiana	05 23 00 N 53 39 00 W
	Scinax	ruber	229 AF	#######	#######	Scru_H21	1-13	2-8	3-5	4-2	#######	Scru_H14	Angouleme	French Guiana	05 23 00 N 53 39 00 W
	Scinax	ruber	140 AF	#######	#######	Scru_H21	1-13	2-8	3-5	4-2	#######	Scru_H12	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Scinax	ruber	189 AF	#######	#######	Scru_H21	1-13	2-8	3-5	4-2	#######	Scru_H14	CD9 entre Mana et coswine	French Guiana	05 39 00 N 53 51 40 W
	Scinax	ruber	236 BM	#######	#######	Scru_H21	1-13	2-8	3-5	4-2	#######	Scru_H14	Maripassoula	French Guiana	03 39 00 N 54 03 00 W
	Scinax	ruber	354 CM	#######	#######	Scru_H21	1-13	2-8	3-5	4-2	#######	Scru_H10	St Laurent	French Guiana	05 32 00 N 54 01 00 W
	Scinax	ruber	333 CM	#######	#######	Scru_H21	1-13	2-8	3-5	4-2	#######	Scru_H14	Twenké	French Guiana	03 22 00 N 54 04 00 W
	Scinax	ruber	256 BM	#######	#######	Scru_H24	1-13	2-8	3-5	4-2	#######	Scru_H12	Maripassoula	French Guiana	03 39 00 N 54 03 00 W
	Scinax	ruber	174 AF	#######	#######	Scru_H24	1-13	2-8	3-5	4-2	#######	Scru_H14	Maripassoula	French Guiana	03 39 00 N 54 03 00 W
	Scinax	ruber	334 CM	#######	#######	Scru_H24	1-13	2-8	3-5	4-2	#######	Scru_H10	Twenké	French Guiana	03 22 00 N 54 04 00 W
	Scinax	ruber	12076 SMNS	#######	#######	Scru_H25	1-14	2-9	3-5	4-2	#######	Scru_H11	Mabura hill forest reserve	Guyana	05 09 19 N 58 41 59 W

	Genus	species	Voucher			Hap						Hap	Locality	Country	Coordinates
	Scinax	ruber	1216 BPN	#######	#######	Scru_H26	1-15	2-9	3-5	4-2	#######	Scru_H14	Imbaimadai	Guyana	05 44 23 N 60 17 51 W
	Scinax	ruber	1276 BPN	#######	#######	Scru_H26	1-15	2-9	3-5	4-2	#######	Scru_H14	Imbaimadai	Guyana	05 44 23 N 60 17 51 W
	Scinax	ruber	12084 SMNS	#######	#######	Scru_H26	1-15	2-9	3-5	4-2	#######	Scru_H11	Iwokrama forest	Guyana	04 40 17 N 58 41 06 W
	Scinax	ruber	12086 SMNS	#######	#######	Scru_H26	1-15	2-9	3-5	4-2	#######	Scru_H11	Iwokrama forest	Guyana	04 40 17 N 58 41 06 W
	Scinax	ruber	12101 SMNS	#######	#######	Scru_H27	1-15	2-9	3-5	4-2	#######	Scru_H14	Georgetown	Guyana	06 09 34 N 58 09 29 W
	Scinax	ruber	12085 SMNS	#######	#######	Scru_H28	1-15	2-9	3-5	4-2	#######	Scru_H11	Iwokrama forest	Guyana	04 40 17 N 58 41 06 W
	Scinax	ruber	12087 SMNS	#######	#######	Scru_H29	1-15	2-9	3-5	4-2	#######	Scru_H14	Iwokrama forest	Guyana	04 40 17 N 58 41 06 W
	Scinax	ruber	362 CM	EF217430	EF217473	Scru_H01	1-1	2-1	3-1	4-1	#######	Scru_H01	Cacao	French Guiana	04 34 00 N 52 28 00 W
	Scinax	ruber	253 BM	EF217430	EF217473	Scru_H01	1-1	2-1	3-1	4-1	#######	Scru_H01	Comté Terrain	French Guiana	04 41 30 N 52 24 00 W
	Scinax	ruber	67 AF	EF217430	EF217473	Scru_H01	1-1	2-1	3-1	4-1	#######	Scru_H04	Petit-saut	French Guiana	05 04 00 N 53 03 00 W
	Scinax	ruber	207 BM	EF217430	EF217473	Scru_H01	1-1	2-1	3-1	4-1	#######	Scru_H01	RN1/PK 14	French Guiana	04 57 06 N 52 24 17 W
	Scinax	ruber	68 AF	EF217438	EF217481	Scru_H12	1-7	2-4	3-2	4-1	#######	Scru_H01	Petit-saut	French Guiana	05 04 00 N 53 03 00 W
	Scinax	ruber	4 AF	EF217442	EF217485	Scru_H14	1-8	2-4	3-2	4-1	#######	Scru_H01	Montjoly	French Guiana	04 55 00 N 52 16 00 W
	Scinax	ruber	KRE075 QCAZ18219	EF217444	EF217487	Scru_H30	1-16	2-10	3-6	4-3	#######	Scru_H21	Jatun sacha-parroquia ahuano-canton tena-Napo	Ecuador	01 04 03 S 77 36 55 W
	Scinax	ruber	164 AF	#######	EU201092	Scru_H23	1-13	2-8	3-5	4-2	#######	Scru_H14	Brownsberg	Suriname	04 56 31 N 55 10 33 W
	Scinax	ruber	IWK109	AY549365	AY549365	Scru_H28	1-15	2-9	3-5	4-2	AY844181	Scru_H11	Iwokrama, Muri scrub camp	Guyana	04 40 17 N 58 41 06 W
	Scinax	ruber	KRE487 QCAZ25301	EF217444	EF217487	Scru_H30	1-16	2-10	3-6	4-3	EF364155	Scru_H20	comunidad serena-northside Napo river-parroquia talag-canton tena-Napo	Ecuador	01 04 03 S 77 36 55 W
	Scinax	ruber	KRE486 QCAZ25874	EF217444	EF217487	Scru_H30	1-16	2-10	3-6	4-3	EF364156	Scru_H20	comunidad serena-northside Napo river-parroquia talag-canton tena-Napo	Ecuador	01 04 03 S 77 36 55 W
	Scinax	ruber	KRE361 QCAZ25275	EF217444	EF217487	Scru_H30	1-16	2-10	3-6	4-3	EF364157	Scru_H22	AUCA14rd-parroquia Dayuma- coca-Orellana	Ecuador	01 04 03 S 77 36 55 W
	Scinax	ruber	KRE073 QCAZ18217	EF217444	EF217487	Scru_H30	1-16	2-10	3-6	4-3	EF364158	Scru_H21	Jatun sacha-parroquia ahuano-canton tena-Napo	Ecuador	01 04 03 S 77 36 55 W
	Scinax	ruber	218 CM	EF376041	EF376073	Scru_H21	1-13	2-8	3-5	4-2	EF364160	Scru_H13	Apatou	French Guiana	05 10 00 N 54 20 00 W
	Scinax	ruber	1Fg RMNH35591	EF217430	EF217473	Scru_H01	1-1	2-1	3-1	4-1	EF364162	Scru_H01	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
	Scinax	ruber	9 BM	EF217430	EF217473	Scru_H01	1-1	2-1	3-1	4-1	EF364163	Scru_H01	Kaw3	French Guiana	04 32 53 N 52 09 07 W
	Scinax	ruber	59 BM	EF217430	EF217473	Scru_H01	1-1	2-1	3-1	4-1	EF364164	Scru_H01	Comté Terrain	French Guiana	04 41 30 N 52 24 00 W
	Scinax	ruber	114 BM	EF217430	EF217473	Scru_H01	1-1	2-1	3-1	4-1	EF364165	Scru_H01	Cacao	French Guiana	04 34 00 N 52 28 00 W
	Scinax	ruber	115 BM	EF217430	EF217473	Scru_H01	1-1	2-1	3-1	4-1	EF364166	Scru_H01	Cacao	French Guiana	04 34 00 N 52 28 00 W
	Scinax	ruber	137 BM	EF217433	EF217476	Scru_H04	1-1	2-1	3-1	4-1	EF364167	Scru_H01	Cacao	French Guiana	04 34 00 N 52 28 00 W
	Scinax	ruber	30 CM	EF217430	EF217473	Scru_H01	1-1	2-1	3-1	4-1	EF364168	Scru_H01	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Scinax	ruber	70 CM	EF217430	EF217473	Scru_H01	1-1	2-1	3-1	4-1	EF364169	Scru_H03	Camopi	French Guiana	03 20 00 N 52 17 00 W
	Scinax	ruber	71 CM	EF217434	EF217477	Scru_H05	1-4	2-2	3-1	4-1	EF364170	Scru_H02	Trois Sauts	French Guiana	02 14 00 N 52 52 00 W
	Scinax	ruber	74 CM	EF217435	EF217478	Scru_H06	1-1	2-1	3-1	4-1	EF364171	Scru_H01	Montagne d'Argent	French Guiana	04 23 00 N 51 42 00 W
	Scinax	ruber	83 CM	EF217430	EF217473	Scru_H01	1-1	2-1	3-1	4-1	EF364172	Scru_H01	Montjoly	French Guiana	04 55 00 N 52 16 00 W
	Scinax	ruber	176 CM	EF217432	EF217475	Scru_H03	1-1	2-1	3-1	4-1	EF364174	Scru_H02	Ouanary	French Guiana	04 15 00 N 51 40 00 W
	Scinax	ruber	177 CM	EF217431	EF217474	Scru_H02	1-2	2-1	3-1	4-2	EF364175	Scru_H02	Ouanary	French Guiana	04 15 00 N 51 40 00 W
	Scinax	ruber	193 CM	EF217430	EF217473	Scru_H01	1-1	2-1	3-1	4-1	EF364176	Scru_H01	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Scinax	ruber	194 CM	EF217430	EF217473	Scru_H01	1-1	2-1	3-1	4-1	EF364177	Scru_H01	Saül1	French Guiana	03 37 32 N 53 12 26 W
	Scinax	ruber	116 BM	EF217438	EF217481	Scru_H12	1-7	2-4	3-2	4-1	EF364178	Scru_H01	Cacao	French Guiana	04 34 00 N 52 28 00 W
	Scinax	ruber	130 BM	EF217441	EF217484	Scru_H16	1-9	2-4	3-2	4-1	EF364179	Scru_H01	Kourou	French Guiana	05 09 00 N 52 38 00 W
	Scinax	ruber	141 BM	EF217439	EF217482	Scru_H13	1-7	2-4	3-2	4-1	EF364180	Scru_H02	Petit Saut	French Guiana	05 04 00 N 53 03 00 W
	Scinax	ruber	148 BM	EF217440	EF217483	Scru_H17	1-9	2-4	3-2	4-1	EF364181	Scru_H01	Sinnamary Route CSG	French Guiana	05 12 29 N 52 44 40 W
	Scinax	ruber	149 BM	EF217442	EF217485	Scru_H14	1-8	2-4	3-2	4-1	EF364182	Scru_H01	Sinnamary Route CSG	French Guiana	05 12 29 N 52 44 40 W
	Scinax	ruber	150 BM	EF217438	EF217481	Scru_H12	1-7	2-4	3-2	4-1	EF364183	Scru_H01	Sinnamary Route CSG	French Guiana	05 12 29 N 52 44 40 W
	Scinax	ruber	151 CM	EF217438	EF217481	Scru_H12	1-7	2-4	3-2	4-1	EF364184	Scru_H01	Guatemala	French Guiana	05 09 00 N 52 38 00 W
	Scinax	ruber	250 CM	EF217438	EF217481	Scru_H12	1-7	2-4	3-2	4-1	EF364185	Scru_H01	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Scinax	ruber	282 CM	EF217443	EF217486	Scru_H15	1-8	2-4	3-2	4-1	EF364186	Scru_H02	Montsinery	French Guiana	04 53 00 N 52 29 00 W
	Scinax	ruber X sp. hybrid	18 CM	EF376041	AF467264	Scru_H21	1-13	2-8	3-5	4-2	EF376147	Scru_H06	Antecum Pata	French Guiana	03 19 00 N 54 04 00 W
	Scinax	ruber	40 CM	EF376041	EF376073	Scru_H24	1-13	2-8	3-5	4-2	EF376148	Scru_H14	Grand-Santi	French Guiana	04 20 00 N 54 15 00 W
	Scinax	ruber	192 AF	#######	#######	Scru_H21	1-13	2-8	3-5	4-2		Scru_NA	CD9 entre Mana et coswine	French Guiana	05 39 00 N 53 51 40 W
	Scinax	ruber	290 AF	#######	#######	Scru_H21	1-13	2-8	3-5	4-2		Scru_NA	Javouey	French Guiana	05 36 11 N 53 48 58 W
	Scinax	ruber	251 BM	#######	#######	Scru_H21	1-13	2-8	3-5	4-2		Scru_NA	Maripassoula	French Guiana	03 39 00 N 54 03 00 W
	Scinax	ruber	245 BM	#######	#######	Scru_H22	1-13	2-8	3-5	4-2		Scru_NA	Maripassoula	French Guiana	03 39 00 N 54 03 00 W
	Scinax	ruber	KU207622 WED56265	AY326034	AY326034	Scru_H20	1-12	2-7	3-4	4-1		Scru_NA	Cusco Amazonico	Peru	12 32 27 S 69 03 09 W
	Scinax	ruber	69 AF	EF217430	EF217473	Scru_H01	1-1	2-1	3-1	4-1		Scru_NA		Martinique	
	Scinax	ruber	249 CM	EF217438	EF217481	Scru_H12	1-7	2-4	3-2	4-1		Scru_NA	Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Scinax	ruber	279 AF	EF217438	EF217481	Scru_H12	1-7	2-4	3-2	4-1		Scru_NA	Nouragues1	French Guiana	04 05 00 N 52 41 00 W
CGsp	Scinax	ruber_cf.x-signatus	13993 MTR	#######	#######	Scru_H31					#######	Scru_H23	Macapa	Brazil	00 02 45 N 51 03 00 W
CGsp	Scinax	ruber_cf.x-signatus	13989 MTR	#######	#######	Scru_H31					#######	Scru_H24	Macapa	Brazil	00 02 45 N 51 03 00 W
CGsp	Scinax	ruber_cf.x-signatus	13990 MTR	#######	#######	Scru_H31					#######	Scru_H24	Macapa	Brazil	00 02 45 N 51 03 00 W
CGsp	Scinax	ruber_cf.x-signatus	13988 MTR	#######	#######	Scru_H31					#######	Scru_H26	Macapa	Brazil	00 02 45 N 51 03 00 W

														Locality	Country	Coordinates
CGsp	*Scinax*	*ruber_cf.x-signatus*	320 CM	EF217447	EF217490	Scru_H35					#######	Scru_H26		Bourda	French Guiana	04 56 00 N 52 17 00 W
CGsp	*Scinax*	*ruber_cf.x-signatus*	344 CM	EF217447	EF217490	Scru_H35					#######	Scru_H25		Montravel	French Guiana	04 54 42 N 52 15 39 W
CGsp	*Scinax*	*ruber_cf.x-signatus*	345 CM	EF217447	EF217490	Scru_H35					#######	Scru_H26		Montravel	French Guiana	04 54 42 N 52 15 39 W
CGsp	*Scinax*	*ruber_cf.x-signatus*	208 BM	EF217447	EF217490	Scru_H35					#######	Scru_H26		RN1/PK 14	French Guiana	04 57 06 N 52 24 17 W
CGsp	*Scinax*	*ruber_cf.x-signatus*	359 CM	#######	EU201091	Scru_H32					#######	Scru_H26		Montravel	French Guiana	04 54 42 N 52 15 39 W
CGsp	*Scinax*	*ruber_cf.x-signatus*	360 CM	#######	EU201091	Scru_H32					#######	Scru_H26		Montravel	French Guiana	04 54 42 N 52 15 39 W
CGsp	*Scinax*	*ruber_cf.x-signatus*	368 CM	#######	EU201091	Scru_H32					#######	Scru_H26		Montravel	French Guiana	04 54 42 N 52 15 39 W
CGsp	*Scinax*	*ruber_cf.x-signatus*	1 BM	EF217445	EF217488	Scru_H33					EF364134	Scru_H26		Kourou	French Guiana	05 09 00 N 52 38 00 W
CGsp	*Scinax*	*ruber_cf.x-signatus*	3 BM	EF217447	EF217490	Scru_H35					EF364135	Scru_H26		Kourou	French Guiana	05 09 00 N 52 38 00 W
CGsp	*Scinax*	*ruber_cf.x-signatus*	138 BM	EF217447	EF217490	Scru_H35					EF364136	Scru_H26		Kourou	French Guiana	05 09 00 N 52 38 00 W
CGsp	*Scinax*	*ruber_cf.x-signatus*	139 BM	EF217447	EF217490	Scru_H35					EF364137	Scru_H26		Kourou	French Guiana	05 09 00 N 52 38 00 W
CGsp	*Scinax*	*ruber_cf.x-signatus*	140 BM	EF217445	EF217488	Scru_H33					EF364138	Scru_H26		Kourou	French Guiana	05 09 00 N 52 38 00 W
CGsp	*Scinax*	*ruber_cf.x-signatus*	35 CM	EF217447	EF217490	Scru_H35					EF364139	Scru_H26		Montjoly	French Guiana	04 55 00 N 52 16 00 W
CGsp	*Scinax*	*ruber_cf.x-signatus*	75 CM	EF217447	EF217490	Scru_H35					EF364140	Scru_H26		Montravel	French Guiana	04 54 42 N 52 15 39 W
CGsp	*Scinax*	*ruber_cf.x-signatus*	76 CM	EF217447	EF217490	Scru_H35					EF364141	Scru_H26		Montravel	French Guiana	04 54 42 N 52 15 39 W
CGsp	*Scinax*	*ruber_cf.x-signatus*	210 CM	EF217446	EF217489	Scru_H34					EF364142	Scru_H26		Ile Royale	French Guiana	05 17 00 N 52 35 00 W
CGsp	*Scinax*	*sp._cf.ruber*	MRT285	#######	#######									Canavieiras	Brazil	15 38 00 S 38 57 00 W
	Scinax	*sp._hybrid*	349 CM	EF217437	EF217480	Scru_H09	1-6	2-3	3-1	4-1	#######	Scru_H07		Lucifer	French Guiana	04 46 00 N 53 55 00 W
	Scinax	*sp._hybrid*	365 CM	EF217437	EF217480	Scru_H09	1-6	2-3	3-1	4-1	#######	Scru_H07		Lucifer	French Guiana	04 46 00 N 53 55 00 W
	Scinax	*sp._hybrid*	22 BM	EF217436	EF217479	Scru_H10	1-6	2-3	3-1	4-1	EF364144	Scru_H05		Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Scinax	*sp._hybrid*	45 BM	EF217436	EF217479	Scru_H10	1-6	2-3	3-1	4-1	EF364145	Scru_H05		Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Scinax	*sp._hybrid*	142 BM	EF217436	EF217479	Scru_H10	1-6	2-3	3-1	4-1	EF364146	Scru_H07		Kaw3	French Guiana	04 32 53 N 52 09 07 W
	Scinax	*sp._hybrid*	143 BM	EF217436	EF217479	Scru_H10	1-6	2-3	3-1	4-1	EF364147	Scru_H05		Kaw3	French Guiana	04 32 53 N 52 09 07 W
	Scinax	*sp._hybrid*	144 BM	EF217436	EF217479	Scru_H10	1-6	2-3	3-1	4-1	EF364148	Scru_H08		Kaw3	French Guiana	04 32 53 N 52 09 07 W
	Scinax	*sp._hybrid*	145 BM	EF217436	EF217479	Scru_H10	1-6	2-3	3-1	4-1	EF364149	Scru_H07		Kaw3	French Guiana	04 32 53 N 52 09 07 W
	Scinax	*sp._hybrid*	259 CM	EF217436	EF217479	Scru_H10	1-6	2-3	3-1	4-1	EF364150	Scru_H05		Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Scinax	*sp._hybrid*	260 CM	EF217437	EF217480	Scru_H09	1-6	2-3	3-1	4-1	EF364151	Scru_H05		Aratai	French Guiana	03 59 41 N 52 35 45 W
	Scinax	*sp._hybrid*	86 CM	EF217436	EF217479	Scru_H10	1-6	2-3	3-1	4-1	EF364152	Scru_H09		Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Scinax	*sp._hybrid*	189 CM	EF217436	EF217479	Scru_H10	1-6	2-3	3-1	4-1	EF364153	Scru_H09		Kaw2	French Guiana	04 43 00 N 52 08 00 W
	Scinax	*sp._hybrid*	190 CM	EF217436	EF217479	Scru_H10	1-6	2-3	3-1	4-1	EF364154	Scru_H07		Kaw2	French Guiana	04 43 00 N 52 08 00 W
CGsp	*Scinax*	*sp.1A*	255 CM	EF217452	EF217495						EF364218			Aratai	French Guiana	03 59 41 N 52 35 45 W
CGsp	*Scinax*	*sp.1A*	173 BM	EF217450	EF217493						EF364221			Trinité	French Guiana	04 35 00 N 53 21 00 W
CGsp	*Scinax*	*sp.1B*	13734 MTR	#######	#######						#######			Serra do Navio	Brazil	00 55 05 N 52 00 10 W
CGsp	*Scinax*	*sp.1C*	1168 BPN	#######	#######									Imbaimadai	Guyana	05 44 23 N 60 17 51 W
CGsp	*Scinax*	*sp.2A*	61 AF	#######	#######						#######			Petit-saut	French Guiana	05 04 00 N 53 03 00 W
CGsp	*Scinax*	*sp.2B*	324 CM	#######	EU201093						#######			Antecum-Pata	French Guiana	03 19 00 N 54 04 00 W
CGsp	*Scinax*	*sp.3*	AA	EF217469	EF217512						EF364224			Municipality of Orocué, Casanare	Colombia	4.83187°N; -71.27214°W
CGsp	*Scinax*	*squalirostris*	MACN38241	AY843760	AY843760						AY844182			Entre Rios, Depto. Islas del Ibicuy, Ruta 12 vieja, entre brasos largo y arroyo luciano	Argentina	
CGsp	*Scinax*	*staufferi*	UTA-A50749	AY843761	AY843761						AY844183			Zacapa, 2.9Km S teculutan on road to Huit	Guatemala	
CGsp	*Scinax(Hyla)*	*uruguayus*	CFBH5788	AY843681	AY843681									Rio grande do Sul, Canbara do Sul	Brazil	
OGsp	*Sphaenorynchus*	*lacteus*	85 CM	EF217472	EF217515						EF364223			Kaw1	French Guiana	04 31 00 N 52 02 00 W
OGsp	*Sphaenorynchus*	*lacteus*	USNM268930	AY549367	AY549367									Madre de Dios, Tambopata Reserve	Peru	
OGsp	*Syrrophus*	*zeus*		EF493718							EF493477					
OGsp	*Trachycephalus*	*venulosus*		AY326048							DQ347161					
CGsp	*Xenohyla*	*truncata*		AY843775	AY843775											

Table S5.2: Ecological traits, molecular data description, Selection tests results and rates of molecular evolution estimates for each species species.

- Ecological traits are as follows: 1, Ranges are divided in two categories Guianan (G) and widespread (W). We considered the two *L. wagneri* group species included in the present study to be endemic to the Guiana Shield. 2, Habitats are segregated in four categories: Forest (F), Open (O), Wetland (W) and Artificial (A) following the GAA database and personal observations. For species that are predominantly found in a certain habitat but can be found in different adjacent habitat we indicated: assoc. For example *Adenomera andreae* is a forestrial species that can be found in associated clearings and open areas surrounded by forests. It is indicated: F, O and A assoc F. 3, Elevation range is indicated according to the GAA and personal observations.

- Molecular data description is as follows: 1, Number of individuals per species for the mtDNA dataset. Additional individuals are indicated: a, when data are available for only one of the two mtDNA fragment (for *D. leucophyllatus* according to Chek et al., 2001 and *L. wagneri* C), b, when additional distribution data were available (*Rhinella margaritifera* according to Fouquet et al., 2007c), and c, when they are corresponding to highly distant lineages considered different species. 2, Number of haplotypes in the network. 3, Number of haplotypes from DNASP. (without gaps). 4, Number of segregating sites (S). 5, Haplotypic diversity (Hd) and standard deviation (SD). 6, Nucleotidic diversity (Pi) and standard deviation (SD).

- Selection tests results are described as follows: 1, Tajima`s D. 2, Fu and Li's D. 3, Fu and Li's F

- Molecular rates of evolution estimates from Relaxed molecular clock analysis in substitution/site/my

(a) mtDNA

	Range	Habitat	Elevation	N mt DNA	add. 16S	H TCS	H DNAsp	S	Hd	SD	Pi	SD	Tajima's D	Fu and Li's D*	Fu and Li's F*	Mean rate BEAST	SD
Adenomera andreae	W	F. O. A assoc F	0 - 800m	91		69	49	108	0.976	0.006	0.023	0.00113	NS	NS	NS	0.0055167	0.001013
Adenomera heyeri	G	F	0 - 800m	32		17	16	33	0.927	0.024	0.015	0.0011	NS	NS	NS	0.005375	0.000506
Adenomera hylaedactyla	W	O. W. A assoc F	0 - 800m	25		16	15	53	0.947	0.025	0.0188	0.00217	NS	NS	NS	0.0054875	0.000724
Allobates femoralis	W	F	0 - 1000m	68		35	32	87	0.889	0.034	0.0209	0.00270	NS	NS	NS	0.0056	0.001109
Allobates granti 1	G	F	0 - 800m	32	+6	14	12	34	0.804	0.059	0.0145	0.00205	NS	NS	NS	0.00555	0.000354
Anomaloglossus baeobatrachus	G	F	0 - 800m	105		31	30	84	0.924	0.012	0.0263	0.00198	NS	NS	NS	0.0055	0.000847
Anomaloglossus degranvillei	G	F	0 - 800m	74		30	30	107	0.951	0.01	0.0345	0.00384	NS	NS	NS	0.0055	0.000632
Dendropsophus leucophyllatus	W	F. O. A assoc F	0 - 600m	28	+18	5	5	4	0.328	0.112	0.0005	0.00017	NS	NS	NS	0.0053	0
Dendropsophus minusculus	G	F	0 - 600m	50		22	22	45	0.938	0.015	0.0072	0.00108	NS	*. P < 0.05	*. P < 0.05	0.005275	0.000665
Leptodactylus mystaceus	W	F. O. A assoc F	0 - 1000m	53		37	33	84	0.97	0.012	0.0158	0.00212	NS	NS	NS	0.0054167	0.001026
Leptodactylus wagneri B	G	F*	0 - 600m	40		19	18	92	0.886	0.039	0.0367	0.00321	NS	NS	NS	0.0061333	0.000575
Leptodactylus wagneri C	G	F*	0 - 600m	11	+1	9	9	34	0.943	0.066	0.0161	0.00325	NS	NS	NS	0.005425	0.001424
Pristimantis chiastonotus	G	F	0 - 700m	61		17	16	31	0.896	0.019	0.0101	0.00113	NS	NS	NS	0.005525	0.000704
Pristimantis zeuctotylus	G	F	0 - 800m	54		18	17	49	0.884	0.028	0.0149	0.0007	NS	NS	NS	0.0055	0.000566
Rhinella castaneotica	W	F	0 - 600m	64		20	20	43	0.745	0.059	0.0052	0.00108	*. P < 0.05	NS	NS	0.005425	0.001504
Rhinella margaritifera	W	F	0 - 2400m	77	+7	34	33	75	0.864	0.035	0.0118	0.00139	NS	NS	NS	0.005575	0.000468
Scinax boesemani	W	O. W. A assoc F	0 - 650m	66		23	23	39	0.898	0.026	0.009	0.00044	NS	NS	NS	0.0055	0.000849
Scinax ruber	W	O. W. A assoc F	0 - 2600m	85	+21	30	29	80	0.922	0.014	0.0186	0.00114	NS	**. P < 0.02	*. P < 0.05	0.0059667	0.001435

(b) nuDNA

	N nuDNA	add. Tyr	N H mt TCS	N H mt DNAsp	S	Hd	SD	Pi	SD	Tajima's D	Fu and Li's D* test statistic	Fu and Li's F* test statistic
Adenomera andreae	89		35	8	8	0.212	0.058	0.00048	0.00015	*, P < 0.05	**, P < 0.02	**, P < 0.02
Adenomera heyeri	32		8	3	2	0.179	0.088	0.00032	0.00016	NS	NS	NS
Adenomera hylaedactyla	24		13	8	10	0.699	0.097	0.00299	0.00066	NS	NS	NS
Allobates femoralis	45		17	11	17	0.432	0.094	0.00293	0.00088	*, P < 0.05	*, P < 0.05	*, P < 0.05
Allobates granti 1	32	+4	8	3	2	0.232	0.094	0.00044	0.00018	NS	NS	NS
Anomaloglossus baeobatrachus	96		18	4	13	0.226	0.053	0.00439	0.00113	NS	NS	NS
Anomaloglossus degranvillei	69		14	10	21	0.475	0.068	0.00914	0.00161	NS	NS	NS
Dendropsophus leucophyllatus	23	+1	10	1	0	0	0	0	0	NS	NS	NS
Dendropsophus minusculus	45		13	3	4	0.088	0.057	0.00052	0.00038	*, P < 0.05	*, P < 0.05	**, P < 0.02
Leptodactylus mystaceus	52		11	3	4	0.113	0.060	0.00028	0.00016	NS	NS	NS
Leptodactylus wagneri B	38		10	3	2	0.437	0.072	0.00094	0.00017	NS	NS	NS
Leptodactylus wagneri C	11		5	2	1	0.327	0.153	0.00054	0.00025	NS	NS	NS
Pristimantis chiastonotus	58		8	6	6	0.284	0.076	0.00066	0.0002	*, P < 0.05	NS	*, P < 0.05
Pristimantis zeuctotylus	51		10	7	6	0.29	0.083	0.00055	0.00017	*, P < 0.05	NS	*, P < 0.05
Rhinella castaneotica	58		11	2	1	0.034	0.033	0.00008	0.00007	NS	NS	NS
Rhinella margaritifera	72		10	2	1	0.055	0.037	0.00011	0.00007	NS	NS	NS
Scinax boesemani	63		21	4	5	0.123	0.056	0.00036	0.0002	*, P < 0.05	*, P < 0.05	*, P < 0.05
Scinax ruber	81	+20	22	11	13	0.726	0.031	0.00451	0.00034	NS	NS	NS

Table S5.3: New Tyrosinase primers designed for this study

Leptodactylidae	Tyr I6 Adeno	CAACTCTCCTTTGGGTCCTC
Leptodactylidae	Tyr BtoC Adeno	CTGGAGATGGTTCTACTTGTGG
Leptodactylidae	Tyr H Adeno	ACATTGTTGGGCATCTCTCC
Leptodactylidae	Tyr E18 Adeno	CTGAGGAGAACAGTGCTGG
Leptodactylidae	Tyr E16 Adeno	GGCTGAGGAGAACAGTGCT
Aromobatidae	Tyr E Dendro12	GCTGGGCTGAGGAKATTATC
Aromobatidae	Tyr E Dendro16	GGCTGAGGAKATTATCRCTTA
Aromobatidae	Tyr I Dendro	CCTTTGGGTTCACARTTTC
Aromobatidae	Tyr I Dendro5	CCTCACCTTYGGGTTCACA
Pristimantis	Tyr E Eleu14	TGGGCTGAGTAGGAYGGTA
Pristimantis	Tyr E Eleu17	GCTGAGTAGGAYGGTACTGG
Pristimantis	Tyr I Eleu12	GTTGTATCTACCTCACCTTTGG
Leptodactylidae	Tyr I Lepto14	GTCSTGTCCAACTCTCCYGTG
Leptodactylidae	Tyr E Lepto29	CGTTGCTGGTTGGGTGGKTTC
Dendropsophus	Tyr I Dendrop17	GTCGTTGTGTCTACYTCACC
Dendropsophus	Tyr E Dendrop14	TGGGCTGAGGAGGACATTACTG
Aromobatidae	Tyr I Allob6	ACTCCCCTTCAGGTTCACA
Aromobatidae	Tyr I Dendrob+19	TCCCTTTAGYGGCATTGACGA
Aromobatidae	Tyr H Dendrob25	CAGAAGGGGATGGTGAAGTT
Scinax	Tyr E Scinax13	GCTGGGCTGAGGAGGACGAG
Scinax	Tyr E Scinax10	GATGCTGGGCTGAGGAGGAC
Scinax	Tyr J Scinax38	GCCTACRGTCTTCTACAACAG
Scinax	Tyr I Scinax+13	CCTCAGTTCCCCTTYAGTGGC

Table S5.4: Best models fitting the data for each genus estimated with Modeltest, alignements sizes of each dataset and outgroups used.

Models are also indicated for the mtDNA dataset used for relaxed molecular clock Bayesian dating.

	Model	Gamma	Subst. matrix	Pinvar	Base comp.	Align. mtDNA	Taxa mtDNA	Align. nuDNA	Taxa nu DNA	Outgroups
Adenomera	GTR+I+G	0.7662	0.2374,9.7214,2.4535,0.0785,4.4889,1	0.4235	0.2597,0.1737,0.2385,0.3281	807	107	584	152	*Leptodactylus gr. wagneri A, L. mystaceus, L. rhodomystax, Lithodytes lineatus*
Allobates	GTR+I+G	0.7493	0.2260,5.6390,1.2594,0.0800,2.6978,1	0.4379	0.2883,0.1573,0.2294,0.3250	807	81	549	87	*Aromobates nocturnus, Nephelobates sp.*
Anomaloglossus	GTR+I+G	0.3548	0.2091,8.7249,1.5651,0.0718,2.9267,1	0.1747	0.2613,0.1674,0.2386,0.3327	791	85	524	185	*Allobates granti 1 and 2, A. femoralis*
Dendropsophus	GTR+I+G	0.7147	0.3603,7.3531,1.2865,0.2704,2.7464,1	0.3946	0.2672,0.1676,0.2268,0.3384	817	62	582	87	*Pseudis paradoxa, Scarthyla goinorum*
Leptodactylus	GTR+I+G	0.6541	0.1683,7.3207,1.4646,0.1001,3.8140,1	0.3843	0.2549,0.1689,0.2473,0.3289	819	96	617	135	*Adenomera heyeri, Lithodytes lineatus*
Pristimantis	GTR+I+G	0.7586	0.2502,5.9063,1.2487,0.1596,3.3305,1	0.2550	0.2501,0.1357,0.2528,0.3614	866	130	576	135	*Phrynopus brunneus, P. peraccai, P. bracki, Eleutherodactylus dolops*
Rhinella	GTR+I+G	0.7779	0.1845,17.7267,3.6557,0.0001,7.7505,1	0.4938	0.2865,0.1822,0.2212,0.3101	790	68	539	152	*Chaunus chavin, C. nesiotes, Rhamphophryne festae*
Scinax	GTR+I+G	0.7511	0.2180,7.1337,1.3078,0.1762,2.8633,1	0.3486	0.2594,0.1694,0.2221,0.3491	812	93	561	187	*Pseudis paradoxa, Scarthyla goinorum, Dendropsophus leali, Sphaenorhynchus lacteus*
mtDNA dating	GTR+I+G	0.7216	0.412,8.019,1.6751,0.1781,4.6501,1	0.2763	0.2677,0.1139,0.2382,0.3802	843	97			

Table S5.5: Calibration point details used for the relaxed molecular clock Bayesian dating and corresponding references.

Node	Additional species included for mtDNA	Age (My)	SD	REF
Hyloidea (Root)		63	10	Roelants et al., 2007; San Mauro et al., 2005
Holartic Hyla	*Hyla arenicolor, Hyla arborea*	18.2	3	Roelants et al., 2007
Acris + Holartic Hyla	*Acris crepitans*	30.5	5	Roelants et al., 2007
Lophiohylini + Hylini	*Trachycephalus venulosus, Osteocephalus taurinus*	40.7	6	Roelants et al., 2007
Pelodryadinae + Phyllomedusinae	*Litoria caerulea, Phyllomedusa vaillanti*	43.2	8	Roelants et al., 2007
Dendrobates + Phyllobates	*Dendrobates auratus, Phyllobates vittatus*	18.9	4	Roelants et al., 2007
Dendrobates Phyllobates + Epipedobates	*Epipedobates tricolor*	26.6	5	Roelants et al., 2007
Rhinella + Cranopsis + Anaxyrus + Bufo	*Bufo bufo, Cranopsis coniferus, Anaxyrus boreas*	<43.3		interpreted from Roelants et al., 2007 and Pramuk et al 2007
Pristimantis	*Pristimantis cruentus, Pristimantis actites*	24.45	6	Heinicke et al., 2007
Pristimantis + Phrynopus bracki	*Phynopus bracki*	36.5	8	Heinicke et al., 2007
Carribean Eleutherodactylini	*Eleutherodactylus martinicensis, Syrrophus zeus*	29.4	6	Heinicke et al., 2007; Roelants et al., 2007
Carribean + other Eleutherodactylini		48.3	8	Heinicke et al., 2007; Roelants et al., 2007
Leptodactylidae		<54.8		interpreted from Roelants et al., 2007

Table S5.6: NCPA results with 1, Clade name for each species. 2, Chi square results. 3, Corresponding probability. 4, Inference chain. 5, Interpretation. 6, Potential interpretation

Species	Clade	chi square	p	Inference Chain	Interpretation	
Adenomera heyeri	1-1	28	0.1340	1,2,3,5,15,NO	Past fragmentation and/or Long distance colonization	
	2-4	18	0.0000	1,19,20,2,11,12,NO	Contiguous Range Expansion.	
	3-2	13	0.0300	1,19,20,2,3,4,9,NO	Allopatric Fragmentation	
Adenomera andreae	3-11	7	0.0485	1,19,20,2,3,4,9	Allopatric fragmentation	
	4-1	289.75	0.000	1,2,3,5,15,NO	Past fragmentation and/or Long distance colonization	
	4-2	9	0.0562	1,19,20,2,11,12,NO	Contiguous Range Expansion.	
	4-5	28	0.0001	1,19,20,2,11,12,NO	Contiguous Range Expansion.	
	5-1	189	0.000	1,19,20,2,11,12,NO	Contiguous Range Expansion.	
	5-2	40	0.000	1,19,20,2,3,5,15,NO	Past fragmentation and/or Long distance colonization	
	T	276	0.000	1,19,20,2,11,12,NO	Contiguous Range Expansion.	
Adenomera hylaedactyla	3-1	23.6167	0.0532	1,19,20,2,3,5,15,NO	Past fragmentation and/or Long distance colonization	
	4-1	18	0.0272	1,19,20,2,11,12,NO	Contiguous Range Expansion.	
	T	39.0476	0.0450	1,19,20,2,11,12,NO	Contiguous Range Expansion.	
Anomaloglossus baeobatrachus	1-1	59.9064	0.3388	1,2,3,5,6,7,YES	Restricted gene flow/dispersal but with some Long distance dispersal	
	1-3	16	0.0089	1,19,20,2,3,4,9,NO	Allopatric fragmentation	
	1-10	12	0.0092	1,19,20,2,3,4,9,NO	Allopatric fragmentation	
	2-1	19.1827	0.2202	1,2,11,12,NO	Contiguous Range Expansion.	
	2-2	17	0.057	1,19,20,2,3,4,NO	Restricted gene flow with IBD	
	2-6	17.5	0.0033	1,2,11,12,NO	Contiguous Range Expansion.	
	3-1	102	0.0000	1,19,20,2,11,12,13,YES-21...	Long distance colonization possibly coupled with subsequent fragmentation or past fragmentation followed by range expansion	Past gradual range expansion followed by fragmentation
	3-3	24.9167	0.3945	1,19,20,2,3,5,15, YES-21...	Long distance colonization and/or past fragmentation	Long distance movement
	4-2	32	0.0000	1,19,20,2,11,12,13,YES-21...	Long distance colonization possibly coupled with subsequent fragmentation or past fragmentation followed by range expansion	Past gradual range expansion followed by fragmentation
	T	143.5094	0.0000	1,19,20,2,11,12,NO	Contiguous Range Expansion.	
Anomaloglossus degranvillei	2-1	17.3333	0.0235	1,2,3,5,15,NO-21...	Past fragmentation and/or Long distance colonization	Past gradual range expansion followed by fragmentation
	3-1	18	0.0001	1,19,20,2,3,5,15,NO-21...	Past fragmentation and/or Long distance colonization	Past gradual range expansion followed by fragmentation
	3-2	15	0.0187	1,19,20,2,3,4,9,NO	Allopatric Fragmentation	
	3-3	26.6667	0.0000	1,19,20,2,11,12,13,YES-21...	Long distance colonization possibly coupled with subsequent fragmentation or past fragmentation followed by range expansion	Past gradual range expansion followed by fragmentation
	4-1	97.7556	0.0000	1,2,3,4,9,NO	Allopatric Fragmentation	
	T	124	0.0000	1,19,20,2,3,5,15, YES-21...	past fragmentation	
Allobates granti	1-2	29.0476	0.0028	1,2,3,4,NO	Restricted gene flow with IBD	
	2-2	16	0.1262	1,19,20,2,11,17,4,NO	Restricted gene flow with IBD	
	2-3	7	0.0563	1,19,20,2,11,12,NO	Contiguous Range Expansion.	
	3-1	30	0.0000	1,19,20,2,11,12,NO	Contiguous Range Expansion.	
Allobates femoralis	1-14	7	0.0280	1,19,20,2,3,5,15,NO-21...	Past fragmentation and/or Long distance colonization	Long distance movement
	2-1	27	0.0877	1,19,20,2,11,12,13,YES-21...	Long distance colonization possibly coupled with subsequent fragmentation or past fragmentation followed by range expansion	Long distance movement
	3-4	26	0.0370	1,19,20,2,11,17,4,NO	Restricted gene flow with IBD	
	4-1	68	0.0067	1,19,20,2,11,12,NO	Contiguous Range Expansion.	
	4-2	17	0.0043	1,19,20,2,3,5,15,NO	Past fragmentation	
	4-5	8	0.0199	1,19,20,2,11,12,NO	Contiguous Range Expansion.	
	5-1	180	0.0000	1,19,20,2,3,5,15,NO	Past fragmentation	
	T	68	0.0003	1,19,20,2,11,12,13,YES	past fragmentation followed by range expansion	
Dendropsophus minusculus	1-8	18	0.2816	1,19,20,2,11,12,NO	Contiguous Range Expansion.	
	2-1	47.8333	0.0114	1,2,11,12,NO	Contiguous Range Expansion.	
	3-1	35.7188	0.1740	1,19,20,2,11,17,4,NO	Restricted gene flow with IBD	
	3-2	8	0.0378	1,19,20,2,3,5,15,NO-21...	Past fragmentation and/or Long distance colonization	Long distance movement
	3-3	14	0.0010	1,19,20,2,3,5,15,NO-21...	Past fragmentation and/or Long distance colonization	Long distance movement
	4-1	98	0.0000	1,19,20,2,11,12,NO	Contiguous Range Expansion.	
Dendropsophus leucophyllatus	1-1	23.0609	0.8656		Inconclusive Outcome	
Leptodactylus mystaceus	1-1	17.8750	0.7810	1,2,3,4,NO	Restricted gene flow with IBD	
	2-3	6	0.0998	1,2,3,4,9,NO	Allopatric Fragmentation	
	3-1	15.7	0.0621	1,2,11,17,4,NO	Restricted gene flow with IBD	
	3-2	10.1250	0.0272	1,2,3,5,15,NO-21...	Past fragmentation and/or Long distance colonization	Past gradual range expansion followed by fragmentation
	3-4	14	0.0014	1,2,3,4,9,NO	Allopatric Fragmentation	
	4-2	25.5	0.1249	1,2,3,4,9,NO	Allopatric Fragmentation	
	4-3	6	0.0660	1,19,20,2,11,12,13,14,YES	Sampling design inadequate to discriminate between contiguous range expansion, L D colonization and past fragmentation	

Species	Clade	χ^2	P	Inference chain	Biological inference	Notes
	T	92.4375	0.0000	1,19,20,2,3,5,15,NO-21...	Past fragmentation and/or Long distance colonization	Past gradual range expansion followed by fragmentation
Leptodactylus wagneri B	2-1	20	0.0066	1,19,20,2,3,5,15,NO-21...	Past fragmentation and/or Long distance colonization	Past gradual range expansion followed by fragmentation
	3-1	5.3333	0.5495	1,2,3,4,9,NO	Allopatric Fragmentation	
	3-3	10	1	1,2,3,4,9,NO	Allopatric Fragmentation	
	4-1	48	0.0010	1,19,20,2,11,12,NO	Contiguous Range Expansion.	
Leptodactylus wagneri C	3-1	4.95	0.4655	1,19,20,2,11,12,NO	Contiguous Range Expansion.	
Pristimantis chiastonotus	1-3	15	0.0016	1,19,20,2,3,4,NO	Restricted gene flow with IBD	
	2-1	23	0.0003	1,2,3,4,NO	Restricted gene flow with IBD	
	2-2	17	0.0302	1,19,20,2,11,12,NO	Contiguous Range Expansion.	
	3-1	43	0.0000	1,19,20,2,11,12,13,YES-21...	Long distance colonization possibly coupled with subsequent fragmentation or past fragmentation followed by range expansion	Past gradual range expansion followed by fragmentation
	3-2	17.7500	0.0050	1,2,3,4,NO	Restricted gene flow with IBD	
	T	122	0.0000	1,19,20,2,11,12,NO	Contiguous Range Expansion.	
Pristimantis zeuctotylus	1-10	7	0.0280	1,19,20,2,3,5,6,too few clades	Insufficient genetic resolution to discriminate between range expansion/colonization and restricted dispersal/gene flow	
	2-1	36	0.0008	1,2,11,12,NO	Contiguous Range Expansion.	
	2-2	13	0.0016	1,19,20,2,3,4,9,NO	Allopatric Fragmentation	
	2-7	9	0.1099	1,19,20,2,3,4,9,NO	Allopatric Fragmentation	
	4-1	123	0.0000	1,2,11,12,NO	Contiguous Range Expansion.	
	4-2	13	0.1533	1,19,20,2,11,17,4,9,NO	Allopatric fragmentation	
Rhinella castaenotica	1-1	89.4375	0.0148	1,2,3,4,NO	Restricted gene flow with IBD	
	1-5	16	0.0351	1,2,3,5,6,13,YES	Long distance colonization possibly coupled with subsequent fragmentation or past fragmentation followed by range expansion	Past gradual range expansion followed by fragmentation
	2-1	67.6056	0.0185	1,2,11,12,NO	Contiguous Range Expansion.	
	2-2	5.5714	0.5826	1,2,3,4,NO	Restricted gene flow with IBD	
	3-1	55	0.0000	1,19,20,2,3,4,9,NO	Allopatric Fragmentation	
	3-2	6	0.0998	1,2,11,12,NO	Contiguous Range Expansion.	
	4-1	37.8221	0.0768	1,2,11,17,4,9,NO	Allopatric Fragmentation	
Rhinella margaritifera	1-1	166.6	0.1483	1,2,3,4,NO	Restricted gene flow with IBD	
	2-1	142.8000	0.0495	1,2,3,4,NO	Restricted gene flow with IBD	
	2-2	6	0.0662	1,19,20,2,11,17,4,NO	Restricted gene flow with IBD	
	2-5	34	0.0002	1,19,20,2,11,12,13,YES-21...	Long distance colonization possibly coupled with subsequent fragmentation or past fragmentation followed by range expansion	Long distance movement
	3-1	41.8500	0.0045	1,19,20,2,11,12,NO	Contiguous Range Expansion.	
	T	148	0.0000	1,2,3,4,9,NO	Allopatric Fragmentation	
Scinax boesemani	1-1	51.6534	0.0128	1,2,11,17,4,NO	Restricted gene flow with IBD	
	1-8	32.2500	0.0446	1,2,11,17,4,NO	Restricted gene flow with IBD	
	2-1	26	0.1107	1,2,11,17,4,NO	Restricted gene flow with IBD	
	2-5	12.4242	0.8185	1,2,11,12,NO	Contiguous Range Expansion.	
	3-1	62.0654	0.0000	1,2,11,12,NO	Contiguous Range Expansion.	
	3-3	21.8667	0.0002	1,2,11,12,NO	Contiguous Range Expansion.	
	4-1	12.7273	0.2595	1,2,11,12,NO	Contiguous Range Expansion.	
	4-2	30	0.0002	1,2,11,12,NO	Contiguous Range Expansion.	
Scinax ruber	1-6	13	0.0026	1,19,20,2,3,4,NO	Restricted gene flow with IBD	
	1-13	21.0096	0.7837	1,2,3,4,NO	Restricted gene flow with IBD	
	2-1	27.9412	0.4510	1,2,3,4,NO	Restricted gene flow with IBD	
	2-4	19.1852	0.3340	1,2,3,4,NO	Restricted gene flow with IBD	
	3-1	60.6586	0.0000	1,2,11,12,NO	Contiguous Range Expansion.	
	3-2	19	0.0053	1,19,20,2,11,12,13,YES-21...	Long distance colonization possibly coupled with subsequent fragmentation or past fragmentation followed by range expansion	Past gradual range expansion followed by fragmentation
	3-5	28	0.0000	1,19,20,2,11,12,13,YES-21...	Long distance colonization possibly coupled with subsequent fragmentation or past fragmentation followed by range expansion	Past gradual range expansion followed by fragmentation
	4-1	148.3901	0.0001	1,19,20,2,3,5,15,NO-21...	Past fragmentation and/or Long distance colonization	Past gradual range expansion followed by fragmentation

Table S5.7: Time estimates summary with 1, the description of the divergence from NCPA and Phylogenetic reconstructions. 2, Coalescence time estimates for the gene and 95% CI. 3, Coalescence time estimates for the populations and 95% Credibility Intervals. 4, Corresponding time estimates from mean corrected pairwise distances estimates and 95% CI. 5, Corresponding Bayesian relaxed molecular clock estimates and 95% CI. Colours indicate the corresponding epoch (Yellow=Pleistocene, Green=Pliocene, Blue=Miocene).

	Divergence	Coalec. Gene	H 95%	L 95%	Coalec. Pop	H 95%	L 95%	Dist.	H 95%	L 95%	RMCB Beast	H 95%	L 95%
Adenomera andreae	4-9 vs ALL	3.974	4.867	3.357	3.070	3.760	2.593	3.640	4.458	3.075			
	4-2 VS 4-3	2.366	2.898	1.999	0.645	0.790	0.545	1.742	2.133	1.472	1.714	2.983	0.644
	4-4 VS 4-2 + 4-3	2.312	2.832	1.954	1.519	1.860	1.283	2.672	3.273	2.258	3.049	4.686	1.490
	4-6 VS 4-7	2.351	2.879	1.986	2.638	3.231	2.229	3.133	3.837	2.647			
	3-10 VS 3-11	0.393	0.481	0.332	0.165	0.203	0.140	0.477	0.585	0.403			
	3-13 VS 3-14+3-15	0.984	1.205	0.831	0.380	0.465	0.321	1.322	1.619	1.117			
	2-21 VS 2-22	0.851	1.042	0.719	0.848	1.038	0.716	1.062	1.300	0.897			
	3-9 VS 3-1 to 8	1.793	2.196	1.515	1.258	1.541	1.063	1.619	1.983	1.368			
Adenomera heyeri	3-1 VS 3-2	2.277	2.514	2.082	1.711	1.888	1.563	2.765	3.053	2.528	3.465	5.706	1.523
	2-1 VS 2-2	0.597	0.659	0.545	0.295	0.325	0.269	0.596	0.657	0.544			
	2-3 VS 2-4	0.826	0.911	0.755	0.534	0.589	0.488	0.939	1.036	0.858	1.336	2.527	0.366
	1-8+9VS1-10	0.298	0.329	0.272	0.200	0.221	0.183	0.370	0.408	0.338			
Adenomera hylaedactyla	4-1+4-2 VS 4-3	3.285	3.785	2.903	2.186	2.519	1.932	3.397	3.914	3.001	4.502	6.692	2.609
	4-1 VS 4-2	2.705	3.116	2.390	1.849	2.129	1.633	2.732	3.147	2.414	3.480	5.462	1.919
	3-1 VS 3-2	1.478	1.702	1.306	1.006	1.159	0.889	1.417	1.633	1.252	1.812	3.102	0.687
	2-1VS2-2	0.971	1.118	0.857	0.875	1.008	0.773	1.115	1.284	0.985			
Allobates femoralis	5-1 VS 5-2	4.869	6.071	4.064	3.491	4.352	2.914	5.713	7.123	4.769	7.236	10.514	4.588
	4-123 VS 4-4	2.792	3.481	2.330	1.859	2.318	1.552	2.886	3.599	2.409	4.479	6.537	2.632
	4-123 VS 3-7+8	2.135	2.662	1.782	1.615	2.013	1.348	2.015	2.512	1.682	2.604	3.875	1.470
	3-1VS3-3	0.286	0.357	0.239	0.192	0.239	0.160	0.852	1.062	0.711			
	4-1VS4-2	1.571	1.959	1.312	0.779	0.972	0.651	1.362	1.698	1.137			
Allobates granti 1	3-1 VS 3-2	2.662	2.843	2.502	2.288	2.444	2.151	3.302	3.527	3.105	3.564	6.042	1.414
	2-1 VS 2-2	0.940	1.004	0.884	0.645	0.688	0.606	1.090	1.164	1.024			
Anomaloglossus baeobatrachus	4-4 VS ALL	5.538	6.546	4.799	3.981	4.705	3.449	8.004	9.461	6.936	9.672	14.254	5.969
	4-1 + 4-3 VS 4-2	2.736	3.234	2.371	1.898	2.244	1.645	3.019	3.569	2.617	3.869	5.715	2.168
	2-1 VS 2-2 + 2-3	0.533	0.630	0.462	0.353	0.417	0.306	0.530	0.627	0.459			
	3-2 VS 3-3	1.090	1.289	0.945	0.661	0.781	0.573	1.291	1.526	1.119	2.363	3.924	0.844
	4-1 VS 4-3	2.416	2.856	2.094	1.645	1.945	1.426	2.850	3.369	2.470	2.679	4.214	1.293
	2-8+2-7 VS 2-6	0.694	0.820	0.601	0.001	0.001	0.001	0.882	1.043	0.765			
Anomaloglossus degranvillei	4-4 VS ALL	7.901	8.927	7.086	7.554	8.535	6.775	9.934	11.225	8.909	10.755	15.200	6.638
	3-1 VS 3-2	1.249	1.411	1.120	0.845	0.955	0.758	1.354	1.530	1.215			
	2-5 VS 2-6 + 2-7	0.800	0.904	0.718	0.518	0.585	0.465	0.756	0.855	0.678	1.048	1.897	0.344
	2-1 VS 2-2	0.600	0.678	0.538	0.318	0.359	0.285	0.587	0.663	0.526			
	3-1 VS 3-2 sp2	1.416	1.599	1.270	1.213	1.370	1.087	1.925	2.176	1.727	2.671	4.744	1.077
	4-3 VS 4-2	2.120	2.396	1.902	2.682	3.030	2.405	3.062	3.460	2.747			
	4-1 VS 4-2+4-3	2.637	2.980	2.365	1.833	2.071	1.644	2.758	3.117	2.474	4.409	6.661	2.547
	3-1+3-2VS 3-3	1.396	1.577	1.252	0.881	0.995	0.790	1.525	1.723	1.367	2.178	3.425	0.968
Dendropsophus	4-1 VS 4-2	2.876	3.292	2.554	1.754	2.007	1.557	3.313	3.792	2.942	4.534	7.453	2.069

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Species	Comparison												
minusculus	3-1 VS 3-3	1.067	1.221	0.948	0.615	0.704	0.547	0.833	0.953	0.740			
	2-6+2-7VS 2-5	0.788	0.902	0.700	0.319	0.365	0.283	0.784	0.898	0.697	1.791	3.322	0.589
	3-13+2-4VS2-3	1.219	1.395	1.082	0.482	0.552	0.428	0.695	0.795	0.617			
Dendropsophus leucophyllatus	1	0.182	0.182	0.182	0.019	0.019	0.019	0.195	0.195	0.195			
	1 VS 2							11.293	11.293	11.293	11.945	17.864	6.497
Leptodactylus mystaceus	4-5 VS ALL	5.899	7.278	4.959	3.821	4.715	3.212	6.140	7.576	5.162	8.637	12.806	4.990
	4-4 VS 4-123	5.427	6.696	4.562	3.360	4.146	2.825	6.208	7.659	5.219	6.956	10.600	3.964
	3-6 VS 3-12345	2.038	2.515	1.713	1.718	2.120	1.444	2.158	2.663	1.815	3.442	5.854	1.498
	4-1+4-2 VS 3-5	1.822	2.249	1.532	0.762	0.940	0.641	1.531	1.889	1.287			
	4-1 VS 4-2	1.804	2.226	1.517	1.157	1.428	0.973	1.784	2.202	1.500			
	2-35 VS 2-87	1.115	1.375	0.937	0.692	0.854	0.582	1.238	1.527	1.040			
	2-1VS 2-2	0.659	0.813	0.554	0.375	0.463	0.315	0.565	0.697	0.475			
	2-7VS2-8	0.656	0.809	0.551	0.406	0.501	0.341	0.570	0.703	0.479			
Leptodactylus wagneri C	4-1 VS 4-2	2.782	3.772	2.203	1.919	2.603	1.520	3.089	4.188	2.446	4.837	7.741	2.305
	3-1 VS 3-2	1.254	1.700	0.993	0.803	1.089	0.636	1.469	1.993	1.164	1.718	3.128	0.618
Leptodactylus wagneri B	5-1 VS 5-2	5.926	6.539	5.418	5.748	6.342	5.255	7.236	7.985	6.616	8.524	11.963	5.290
	3-1 VS 3-2	0.954	1.052	0.872	0.559	0.617	0.511	1.072	1.182	0.980			
	3-1+3-2VS 3-3	1.584	1.748	1.448	1.211	1.337	1.108	1.396	1.541	1.277	2.650	4.482	1.073
	2-65VS2-4	0.754	0.832	0.690	0.444	0.490	0.406	0.684	0.755	0.626			
Pristimantis chiastonotus	3-1 VS 3-2	1.529	1.752	1.356	1.302	1.492	1.155	1.811	2.075	1.606	1.995	3.412	0.751
	2-1VS2-2	0.427	0.489	0.378	0.268	0.308	0.238	0.408	0.468	0.362			
	2-34VS2-45	0.375	0.430	0.333	0.271	0.311	0.241	0.453	0.520	0.402			
	3-1+3-2VS3-3	2.051	2.351	1.820	1.616	1.852	1.433	2.179	2.497	1.933	3.126	5.062	1.556
Pristimantis zeuctotylus	4-1 VS 4-2	1.764	1.966	1.599	1.288	1.435	1.168	2.190	2.441	1.986	3.380	5.407	1.489
	3-5 VS 3-6	1.078	1.202	0.978	0.664	0.740	0.602	1.187	1.323	1.076			
	2-7VS2-8	0.496	0.552	0.449	0.357	0.398	0.323	0.557	0.620	0.505			
	1-3VS1-12	0.267	0.298	0.242	0.130	0.144	0.117	0.365	0.407	0.331			
	3-1+3-3+3-4 VS 3-2	1.346	1.501	1.221	0.732	0.816	0.664	1.421	1.584	1.289	1.933	3.367	0.744
Rhinella castaneotica	4-1+4-2 VS 4-3	2.206	3.052	1.727	1.201	1.661	0.940	2.428	3.360	1.901	3.665	5.541	1.960
	4-1VS 4-2	1.960	2.711	1.534	1.009	1.396	0.790	2.192	3.034	1.717	2.271	3.690	0.999
	2-1 VS 2-2	0.613	0.849	0.480	0.384	0.531	0.301	0.678	0.939	0.531			
	3-1 VS 3-2	0.876	1.213	0.686	0.619	0.856	0.484	0.769	1.064	0.602			
Rhinella margaritifera	4-1 VS 4-2	2.122	2.317	1.958	1.269	1.385	1.171	2.017	2.202	1.860	2.457	3.736	1.272
	2-1+2+3 VS 2-4	1.082	1.181	0.998	0.749	0.817	0.691	0.908	0.991	0.837			
	2-1+2 VS 2-3	1.121	1.224	1.034	0.602	0.657	0.556	0.988	1.079	0.912	1.588	2.700	0.620
	2-1 VS 2-2	1.021	1.114	0.941	0.608	0.664	0.561	0.941	1.028	0.868			
	9 10 11 VS 2-1	0.500	0.545	0.461	0.317	0.346	0.293	0.356	0.388	0.328			
	3-123VS ext	4.038	4.408	3.725	2.801	3.057	2.584	3.569	3.897	3.293	4.434	6.242	2.801
Scinax boesemani	3-2 VS 4-2	1.455	1.720	1.260	1.046	1.236	0.906	1.548	1.830	1.341			
	2-5+6 VS 2-7	0.783	0.925	0.678	0.493	0.582	0.427	0.712	0.842	0.617			
	2-1+2 VS 2-3	0.661	0.782	0.573	0.316	0.374	0.274	0.632	0.747	0.547			
	3-1 VS 3-234	1.604	1.896	1.389	1.023	1.210	0.887	1.416	1.674	1.226	2.386	4.133	0.863
Scinax ruber	5-1 VS 5-2	4.696	6.183	3.786	3.720	4.898	2.999	5.197	6.843	4.190	6.642	9.582	4.082
	4-1VS 4-2	2.972	3.913	2.396	2.111	2.779	1.701	3.292	4.334	2.654	3.643	5.451	1.966
	2-8 VS 2-9	0.553	0.727	0.445	0.442	0.581	0.356	0.753	0.991	0.607			
	3-1 + 2-4 VS 2-6+7	1.400	1.843	1.128	0.532	0.700	0.429	1.316	1.733	1.061	2.406	3.977	0.933