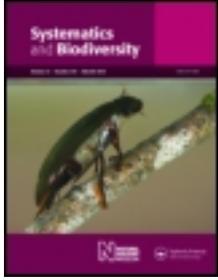


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### Endemic or exotic: the phylogenetic position of the Martinique Volcano Frog *Allobates chalcopis* (Anura: Dendrobatidae) sheds light on its origin and challenges current conservation strategies

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## Research Article

# Endemic or exotic: the phylogenetic position of the Martinique Volcano Frog *Allobates chalcopis* (Anura: Dendrobatidae) sheds light on its origin and challenges current conservation strategies

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Amphibian faunas of the Lesser Antilles are depauperate, with only a few species being endemic and generally threatened. *Allobates chalcopis* from the island of Martinique is a particularly enigmatic case being the only known dendrobatid endemic to an oceanic island. This species has previously been suggested as being introduced to Martinique. The question of its true origin remained unresolved because no individuals were found since its formal description in the 1990s. Twenty years after the last observation of the species, we succeeded in finding an isolated population of *Allobates chalcopis* in Martinique. The rediscovery allowed us to investigate the species' phylogenetic position, confirming that it is nested within a clade of lowland Amazonian *Allobates* but nonetheless distantly related to any known species of the group. The arrival of the species in Martinique likely corresponds to an overseas dispersal from South America during the late Miocene, as previously hypothesized for *Bothrops lanceolatus* and *Leptodactylus fallax*; two other species endemic to Martinique and surrounding islands. However, the species was not found in its type locality 500 m a.s.l. but 300 m higher in altitude, in herbaceous areas of the summit of Montagne Pelée. The possible range reduction and population decline in combination with the evidence of endemism of the species highlights the need for a reassignment of the current Red List status. Furthermore, a refined conservation strategy is needed to guarantee the long-term viability of *Allobates chalcopis* in its native range.

**Key words:** *Allobates*, amphibian, conservation, endemism, Lesser Antilles, overseas dispersal

## Introduction

The conservation of amphibians is of particular concern worldwide and the Caribbean region hosts one of the greatest proportions of amphibian species that are on the brink of extinction, mostly because of habitat destruction (Stuart *et al.*, 2004, 2008). The Caribbean is composed of two well-defined blocks: (1) the Greater Antilles forming the northern part of the archipelago and (2) the islands of the Lesser Antilles forming the eastern part. Whereas the former are islands of continental origin dating back to the Cretaceous,

the latter are oceanic (exception made of the continental islands of Trinidad and Tobago) and first emerged during the Eocene (Coney, 1982; Maury *et al.*, 1990). Truly oceanic islands never had physical contact with other landmasses as they are of complete volcanic origin and are surrounded by deep waters that make land connections through fluctuating sea levels impossible. Moreover, they are generally too young to assume vanished connections. Considering sea level fluctuations, biogeographical evidence and volcanic history of the southern part of the archipelago, the maximal age of the southern Lesser Antilles terrestrial biome can be estimated to be at around 20 million years ago (Ma) (Heinicke *et al.*, 2007; Germa *et al.*, 2011). Only 40 km

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separate the southern end of the Grenadines Bank from the edge of the South American continental shelf. However, seafloor depth in this short interval reaches 600 m b.s.l. (MacPhee *et al.*, 2000) and further north another > 600 m drop separates the Grenadines Bank from Martinique. A thorough study of the volcanic deposits that formed this island indicated that aerial deposits date back to a maximum of 16 Ma but most likely these first formations have been under sea level several times until the mid-Miocene ~9 Ma (Germa *et al.*, 2011).

Consequently, the faunal and floral communities of these islands originated from overseas dispersals or human-induced introductions. This is typically the case of the amphibian fauna of the Lesser Antilles that are depauperate compared with continental ones. This is related to the generally poor dispersal abilities of the vast majority of amphibians (Waldman & McKinnon, 1993; Blaustein *et al.*, 1994; Smith & Green, 2005) especially across salt water (Duellman & Trueb, 1986; Bossuyt & Milinkovitch, 2001; Inger & Voris, 2001; Brown & Guttman, 2002). Overseas dispersal of amphibians towards oceanic islands was evidenced via molecular data analyses for Comoros (Vences *et al.*, 2003, 2004). Additional examples in Sao Tomé (Measey *et al.*, 2007) and the Caribbean (Hedges *et al.*, 1992, 2008; Hedges & Heinicke, 2007; Heinicke *et al.*, 2007; Camargo *et al.*, 2009) were documented but these examples remain rare.

Most of the Lesser Antilles native amphibians belong to the genus *Eleutherodactylus* that radiated early in the Greater Antilles history and subsequently dispersed towards the Lesser Antilles (Heinicke *et al.*, 2007). Ancient overseas dispersals of amphibians from South America to the Lesser Antilles have also been documented via molecular data for *Leptodactylus fallax* (Heyer, 2005; Hedges & Heinicke, 2007), *Pristimantis euphronides* and *P. shrevei* (Kaiser *et al.*, 1994b; Hedges *et al.*, 2008) as well as in other groups of small terrestrial vertebrates, e.g. snakes (Wüster *et al.*, 2002; Rivera Rodríguez *et al.*, 2011), skinks (Hedges & Conn, 2012) or anoles (Alföldi *et al.*, 2011). Additionally, the Lesser Antillean amphibians have been complemented by two recent dispersion events in the genus *Leptodactylus* from South America and the Greater Antilles (*L. validus* and *L. albilabris*, respectively) (Yanek *et al.*, 2006; Hedges & Heinicke, 2007; Camargo *et al.*, 2009).

A species that remained particularly enigmatic is the dendrobatid frog *Allobates chalcopis* (Kaiser *et al.*, 1994a) partly because it was not found again (Breuil, 1997; Hedges & Diaz, 2011) since its discovery on Martinique in 1984 (M. Read, pers. comm.). The original description suggested that *A. chalcopis* could be the sister taxon of *Mannophryne* on the basis of (i) the shared occurrence of a dark throat collar and (ii) occurrence of *Mannophryne* in northern Venezuela and Trinidad and Tobago, i.e. directly facing the Caribbean. However, Grant *et al.* (2006) allocated the species to the genus *Allobates* based on morphology and karyology. This

allocation remains nonetheless to be tested via phylogenetic reconstruction. Likewise, the supposed endemicity of the species and its actual biogeographic history need to be clarified. *Allobates chalcopis* belongs to a speciose genus (~50 species) otherwise occurring in Amazonia, Atlantic Forest, Andes, and Chocó. Therefore, the exclusive presence of *Allobates chalcopis* in Martinique and its absence from any other Caribbean island is puzzling. It seems so exceptional that previous authors assumed that this species must have been introduced (Breuil & Ibénée, 2005; Breuil, cited in Stuart *et al.*, 2008; Breuil, 2009). Kaiser *et al.* (1994a) also acknowledged that a scenario of stepping-stone dispersal (Williams, 1989) with subsequent extinctions on the stopover islands is possible but without fossil evidence remains highly speculative. Confirming such overseas dispersal for *A. chalcopis* would therefore have important implications for the understanding of amphibian biogeography in the Caribbean as well as worldwide (De Queiroz, 2005; Samonds *et al.*, 2012).

Currently, *Allobates chalcopis* is only considered as vulnerable by the IUCN (Hedges *et al.*, 2010) and is not protected by any national conservation law (while some non-native species are). If *A. chalcopis* is in fact originating from an ancient oceanic dispersal and thus the only dendrobatid from an oceanic island and the only endemic frog of Martinique Island, its conservation would have to become a high priority and the current Red List assignment needs to be critically revised.

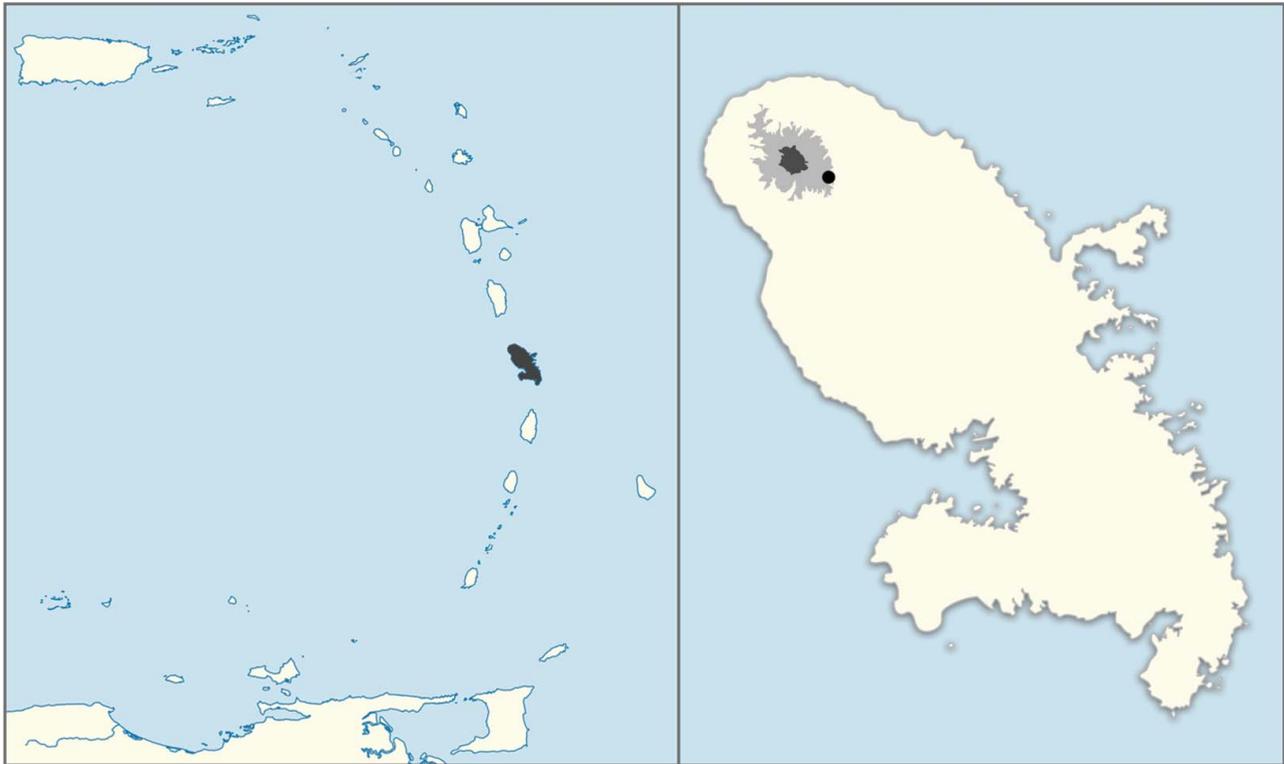
We therefore undertook fieldwork at the type locality of *Allobates chalcopis* and in its vicinity in order to (1) reconfirm the presence of the species, (2) assess its current distribution and (3) reassess its phylogenetic position using molecular data. Specifically, we tested the hypothesis of ancient overseas dispersal versus recent human introduction i.e. whether *A. chalcopis* is an endemic of Martinique or an introduced species. Based on these results, we evaluated the species' conservation status and the appropriateness of current conservation measures.

## Materials and methods

### Fieldwork

We undertook fieldwork between 3 and 15 October 2011 during the peak of the rainy season on the slopes of the Montagne Pelée. We spent approximately 52 h/person localizing calling males including 16 h/person in the 'ravines' and the elfin forest and 36 h/person for the summit.

We conducted a range-wide opportunistic survey in search of *A. chalcopis* covering the Montagne Pelée ecosystem and including the type locality (Ravine de la rivière cloche) and its vicinity 500 a.s.l. (Kaiser *et al.*, 1994a). Systematic searches aimed at delimiting altitudinal range distribution and habitat preference of the species were conducted in the core area of proven occurrence of the species (Fig. 1).



**Fig. 1.** Maps situating the Martinique Island in the Lesser Antilles and the distribution of *Allobates chalcopis* on the island. The black dot indicates the type locality. The light grey area delimits the estimated maximal distribution from the original records 20 years ago i.e. the area above 500 m asl. The dark grey area delimits the estimated maximal distribution from our data.

Calling males were detected by comparing their vocalization with a recording made by M. Read (<http://www.pond5.com/video-sound-effects-music-after-effects-photos-illustrations/1/8689347.html>) which was similar to the one described by Kaiser *et al.* (1994a) (analysed with R 2.14.1 (R Development Core Team, 2012) using the package Seewave (Sueur *et al.*, 2008)). We used playback to collect two calling individuals that were deposited at the Muséum National d’Histoire Naturelle de Paris (MNHN) under voucher numbers MNHN 2011.141 and MNHN 2011.142.

### Laboratory work

Newly collected tissues of *Allobates chalcopis* as well as those of *Allobates spumaponens* and that of an additional undescribed species from Guyana (collected by RE) were taken from thigh muscle and preserved in 95% ethanol. Genomic DNA was extracted using Promega DNA extraction kit. We targeted four mitochondrial (Cytb; COI; 12S; 16S) and one nuclear loci (TYR) that were already partly available for most Dendrobatidae lineages (*sensu* Pyron & Wiens, 2011), 14 other Hyloidea terminals and *Rana+Microhyla* considered as outgroup (Table 1).

Fragments were amplified by standard PCR techniques; detailed information is in supplementary Table 1 (see sup-

plementary material, which is available on the Supplementary tab of the article’s Taylor & Francis Online page at <http://dx.doi.org/10.1080/14772000.2013.764944>). Sequencing was performed using ABI Big Dye V3.1 (ABI Foster City USA) and resolved on an automated sequencer at IQUSP and Genomic Engenharia corp. (São Paulo Brazil). Sequences were edited and aligned with Codon-Code Aligner v.3.5.2. Novel sequences were deposited in Genbank.

### Matrix design and alignment

Newly generated sequence data were added to a matrix designed to comprise one terminal per species for which sequence data are available following Grant *et al.* (2006), Santos *et al.* (2009) and Fouquet *et al.* (2012). For family level taxonomy we choose to follow Santos *et al.* (2009) and Pyron & Wiens (2011) concurring with most of their objections against splitting dendrobatids into two different families. Most major other dendrobatid clades were also represented (*Anomaloglossus*, *Rheobates*, *Mannophryne*, *Aromobates*, *Dendrobates*, *Ameerega*, *Hyloxalus*) as well as one representative of each of most of the Hyloidea families (Bufonidae, Hylidae, Leptodactylidae, Hemiphractidae, Telmatobiidae, Cycloramphidae, Eleutherodactylidae)

**Table 1.** Sequence details including vouchers and accession numbers used for the Bayesian analysis.

Species	12S	16S	COI	Cb	TYR
<i>A. chalcopsis</i> MNHN 2011.141	KC520675/Alea1	KC520676/Alea1	KC520685/Alea1	KC520690/Alea2	KC520695/Alea1
<i>A. chalcopsis</i> MNHN 2011.142	KC520677/Alea2	KC520678/Alea2	KC520686/Alea2		
<i>A. algorei</i>	HQ290950/TNHCFSS551	HQ290950/TNHCFSS551	KC520688/MTD4771	HQ290530/TNHCFSS551	HQ290890/TNHCFSS551
<i>A. spumaponeis</i>	KC520681/MTD4771	KC520682/MTD4771	KC520682/MTD4771	KC520692/MTD4771	KC520697/MTD4771
<i>A. sp. Dueke</i>	DQ502115/MJH3988	DQ502115/MJH3988	DQ502824/MJH3988	DQ502547/MJH3988	
<i>A. granti</i>	JN690196/ E49-5	AY263233/ E49-5			JN691567/ E49-5
<i>A. paleovarzensis</i>	DQ502109/MJH3909	DQ502109/MJH3909		DQ502541/MJH3909	
<i>A. sp. PEG-M1</i>	DQ502136/LSUMZ17601	DQ502136/LSUMZ17601	DQ502843/LSUMZ17601	DQ502568/LSUMZ17601	
<i>A. sp. Rio Ituxi</i>	DQ502098/MPEG12978	DQ502098/MPEG12978		DQ502530/MPEG12978	
<i>A. sp. Manaus 1</i>	DQ502240/MPEG13827	DQ502240/MPEG13827		DQ502531/MPEG13826	
<i>A. trilineatus</i>	DQ502118/MJH7477	DQ502118/MJH7477	DQ502826/MJH7477	DQ502550/MJH7477	
<i>A. sp. Porto Walter</i>	DQ502198/OMNH36026	DQ502198/OMNH36026	DQ502894/OMNH36026	DQ502634/OMNH36026	
<i>A. sp. Iwokrama</i>	KC520679/MTD47884	KC520680/MTD47884	KC520687/MTD47884	KC520691/MTD47884	KC520696/MTD47884
<i>A. conspicuus</i>	DQ502135/OMNH35997	DQ502135/OMNH35997	DQ502842/OMNH35997	DQ502567/OMNH35997	
<i>A. insperatus</i>	AY364557/QCAZ16533	AY364557/QCAZ16533		HQ290539/QCAZ16533	HQ290899/QCAZ16533
<i>A. sp. Ecuador</i>	AY364561/QCAZ16609	AY364561/QCAZ16609			
<i>A. sp. Cuyabeno</i>	DQ502239/LSUMZ12948	DQ502239/LSUMZ12948	DQ502911/LSUMZ12948	DQ502671/LSUMZ12948	
<i>A. caeruleodactylus</i>	DQ502186/MPEG13808	DQ502186/MPEG13808	DQ502887/MPEG13808	DQ502622/MPEG13808	
<i>A. sp. PEG-M3</i>	DQ502139/MPEG13386	DQ502139/MPEG13386	DQ502844/MPEG13386	DQ502571/MPEG13386	DQ503164/MPEG13386
<i>A. gasconi</i>	DQ502209/OMNH36636	DQ502209/OMNH36636	DQ502898/OMNH36636	DQ502644/OMNH36636	
<i>A. sp. "Saul"</i>	E49-1/JN690215	MNHN 2000-653/AY263232			E49-1/JN691625
<i>A. sp. Curua-Una</i>	DQ502110/MJH3973	DQ502110/MJH3973	DQ502820/MJH3973	DQ502542/MJH3973	
<i>A. sp. Santa Maria 1</i>	JN690211/MTR10084	JN690935/MTR10084			JN691622/MTR10084
<i>A. sp. Santa Maria 2</i>	JN690210/MTR10054	JN690934/MTR10054			JN691624/MTR10054
<i>A. sp. PEG-M2</i>	DQ502271/ARA2394	DQ502271/ARA2394	DQ502933/ARA2394	HQ290540/TNHCFSS4978	HQ290900/TNHCFSS4978
<i>A. femoralis</i>	DQ502246/UTA A56478	DQ502246/UTA A56478	DQ502916/UTAA 56478	DQ502661-LSU12798/DQ523139- AtemBocMan22	JN691582/472PG
<i>A. sp. "Lago Cipotuba"</i>	JN690209/MTR10007	JN690933/MTR10007			JN691623/MTR10007
<i>A. nidicola</i>	DQ502210/MPEG13819	DQ502210/MPEG13819		DQ502645/MPEG13819	
<i>A. kingsburyi</i>	AY364550/QCAZ16613	AY364550/QCAZ16613		HQ290541/QCAZ16523	HQ290901/QCAZ16523
<i>A. brunneus</i>	DQ502238/OMNH34469	DQ502238/OMNH34469	DQ502910/OMNH34469	DQ502670/OMNH34469	
<i>A. sp. PEG-M2</i>	DQ502214/OMNH36993	DQ502214/OMNH36993		DQ502649/OMNH36993	DQ503169/OMNH36993
<i>A. talamancae</i>	DQ502166/SIUC7667	DQ502166/SIUC7667	DQ502868/SIUC7667	DQ502601/SIUC7667/DQ339073- C.tal.Nus.v4b	HQ290912/QCAZ16549
<i>A. niputidea</i>	DQ502272/MUJ3520	DQ502272/MUJ3520	DQ502934/MUJ3520	DQ502703/MUJ3520	
<i>A. undulatus</i>	DQ502028/AMNHA159141	DQ502028/AMNHA159141	DQ502755/AMNHA159141	DQ502458/AMNHA159141	
<i>A. sp. neblina</i>	DQ502074/AMCC106112	DQ502074/AMCC106112	DQ502795/AMCC106112	DQ502505/AMCC106112	DQ503149/AMCC106112
<i>A. offersioides</i>	DQ502126/MRT6031	DQ502126/MRT6031	DQ502833/MRT6031	DQ502557/MRT6031	
<i>Mannophryne</i>	<i>trinitatis</i> DQ502131/ MVZ199828	<i>trinitatis</i> DQ502131/ MVZ199828	<i>trinitatis</i> DQ502838/ MVZ199828	<i>trinitatis</i> DQ502562/ MVZ199828/DQ341164	<i>collaris</i> HQ290941/ TNHCFSS507
<i>Aromobates</i>	<i>nocturnus</i> DQ502156/ AMNHA130042	<i>nocturnus</i> DQ502156/ AMNHA130042	<i>nocturnus</i> DQ502860/ AMNHA130042	<i>saltauensis</i> HQ290548:TNHCFSS541/ DQ502592:AMNHA130042	<i>saltauensis</i> HQ290908: TNHCFSS541
<i>Rheobates palmatus</i>	EU342506/TNHCFSS4999	EU342506/TNHCFSS4999	DQ502925/MUJ 5003	DQ502694:MUJ5003/HQ290545: TNHCFSS4955	DQ503172:MUJ5003
<i>Anomaloglossus baobatrachus</i>	DQ501980/ PK-437-1	DQ501980/ PK-437-1	DQ502708/ PK-437-1	DQ502407/ PK-437-1	JN691674/2532T
<i>Anomaloglossus stepheni</i>	DQ502108/MJH3950	DQ502108/MJH3950	DQ502819/MJH3950	DQ502540/MJH3950	JN691731/10269MTR
<i>Anomaloglossus kaiei</i>	DQ502257/CP110209	DQ502257/CP110209	DQ502741/CP110209	DQ502446/CP110209	JN691805/1159PK
<i>Dendrobates tinctorius</i>	DQ502248/UTAA56495	DQ502248/UTAA56495	DQ502918/UTAA56495	DQ502680/UTAA 56495/ HQ290568/TNHCFSS4416	HQ290928/TNHCFSS4416

<i>Ameerega hahneli</i>	DQ502226/MPEG13844	DQ502902/MPEG13844	HQ290575/QCAZ19240	HQ290935/QCAZ19240
<i>Hyalotilus bocagei</i>	DQ502192/OMNH34072	DQ502890/OMNH34072	DQ502471/OMNH34072/ HQ290535/QCAZ37259	HQ290895/QCAZ37259
<i>Andenomera andreae</i>	317AF/KC520683	317AF/KC520689	317AF/JQ321766	317AF/KC520698
<i>Leptodactylus</i>	<i>savagei</i> FC13095/AY326017	<i>knudseni</i> 396MC/JX298373	<i>knudseni</i> 396MC/JX298414	<i>pentadactylus</i> 109MC/JX298243
<i>Telmatobius</i>	<i>vellardi</i> WED53381/ AY326018	<i>verrucosus</i> AMNHA165110/ DQ502743	<i>sanborni</i> MNCN 43526/GU060614	sp. FB-2006/DQ347182
<i>Centrolenidae</i>	<i>eurygnatha</i> CFBH 5729/ AY843595	<i>colymbiphyllum</i> KRL0852/ FJ766714	AY843814/ <i>uranoscopa</i>	<i>bejaranoi</i> MNK 5242/AY844029
<i>Thoropa miliaris</i>	<i>miliaris</i> CFBH 3239/ DQ283331	<i>miliaris</i> CFBH 3239/ DQ502874	MTR15819/JX298412	<i>miliaris</i> AF1434/JX298241
<i>Litoria</i>	<i>caerulea</i> DMH/AY326038	<i>aurea</i> ?/AY835904	DQ502607/ AF1434/FJ685662	<i>aurea</i> AM 52744/AY844130
<i>Phyllomedusinae</i>	<i>tomopterna</i> WED 55380/ AY326045	<i>callidryas</i> KRL 0917/ FJ766570	<i>aurea</i> AM 52744/AY843937 + <i>manya</i> DLS N-72386/EF125030	<i>aurea</i> AM 52744/AY844130
<i>Paratelmatobius</i>	aff. <i>cardosoi</i> CFBH 240/ EU224408	<i>mantiqueira</i> ITH0938/JX298372	GQ365966	<i>tomopterna</i> MJH 7076/ AY844157
<i>Pseudopaludicola</i>	<i>falciptes</i> MACN 38647/ AY843741	cf. <i>falciptes</i> 5468/KC520684	AY843987/ cf. <i>falciptes</i> 5468/KC520693	<i>mantiqueira</i> ITH0938/JX298242
<i>Engystomops</i>	<i>pustulatus</i> QCAZ 23420/ DQ337215	<i>pustulosus</i> KRL 0867/ FJ766703	<i>freibergi</i> 976875/KC520694	sp. 108BM/KC520701
<i>Gastrostecha</i>	<i>cornuta</i> KRL 799/AY843591	<i>cornuta</i> KRL 1163/FJ766705	<i>cornuta</i> KRL 799/AY843811	<i>cornuta</i> KRL 799/AY844040
<i>Rhinella</i>	cf. <i>margaritifera</i> USNM 268828/DQ158490	cf. <i>margaritifera</i> ROM40103/JX298367	cf. <i>margaritifera</i> ROM40103/JX298409	<i>martyi</i> MRT6313/JN692075
<i>Hypsiboas</i>	<i>geographicus</i> AMNH-A 141054/AMCC 101481/AY843628	<i>rufitelus</i> KRL 0798/FJ766740	AY843909/ <i>albomarginatus</i> ZUF RJ 8731/AF549303	cf. <i>fasciatus</i> 118MC/KC520699
<i>Eleutherodactylus</i>	<i>coqui</i> /USNM305421/ GQ345176	<i>auriculatus</i> GQ357659	<i>portoricensis</i> HM229995	<i>cooki</i> EF493455
<i>Microhyla</i>	<i>heymonsi</i> /cp/GEN/AY458596	<i>heymonsi</i> /cp/GEN/AY458596	<i>heymonsi</i> /cp/GEN/AY458596	<i>heymonsi</i> /MVZ236751/ EF395979
<i>Rana</i>	<i>nigromaculata</i> NC.002805	<i>nigromaculata</i> NC_002805	<i>nigromaculata</i> NC_002805	<i>nigromaculata</i> FMNH 232879/DQ282932

and *Rana + Microhyla* as outgroup. The final matrix comprised 60 terminals (Table 1). Missing data in *Allobates* terminals remained for the internal portion of the 12S-16S (eight terminals) for COI (14 terminals); for Cytb (seven terminals) and for TYR (18 terminals).

Most data consisted of coding regions and alignment was unambiguous. Reading frame was checked using MEGA 5.1 (Tamura *et al.*, 2011). For the 12S-16S fragment we performed an alignment with MAFFT v6 (Kato *et al.*, 2009) and default parameters except the use of the L-INS-i strategy which is adapted to sequences with one conserved domain and long gaps. We obtained a final 4612 bp alignment.

### Phylogenetic analysis

We used Bayesian analysis (BA) to investigate phylogenetic relationships among terminals. We divided the dataset into seven partitions: one for each codon position of the mtDNA (1390/3 bp) and the nuDNA coding genes (568 bp/3) and one for the 12S-16S fragment (2650 bp). Such partitioning was designed considering the coding nature of mtDNA (Cytb, COI) and nuDNA (TYR) loci and comparable rates

of evolution between Cytb and COI (Mueller, 2006). A more inclusive partitioning would have joined very different patterns of molecular evolution and more partitioning would likely result in overparameterization (Marshall, 2010).

We used the software jModeltest version 0.1.1 (Guindon & Gascuel, 2003; Posada, 2008) to select the substitution model that best fit each of these partitions under Akaike's Information Criterion (Akaike, 1981). The seven resulting models (supplementary Table 2, see supplementary material, which is available on the Supplementary tab of the article's Taylor & Francis Online page at <http://dx.doi.org/10.1080/14772000.2013.764944>) were employed in a BA with MrBayes 3.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). The BA consisted of a  $30 \times 10^6$  generations run starting with random trees and 10 Markov chains (one cold) sampled every 1000 generations. Adequate burn-in was determined by examining likelihood scores of the heated chains for convergence on stationarity as well as the effective sample size of values in Tracer 1.5 (Rambaut & Drummond, 2003). We considered relationships to be strongly supported when posterior probabilities were equal to or higher than 0.95.

**Table 2.** p distances using 16S calculated among selected *Allobates*, *Leptodactylus* and *Pristimantis* that occur in the Lesser Antilles and their continental relatives. Lowest distances are indicated in bold. Distances among *Allobates* of the *trilineatus* clade and their closest relative are indicated with grey cells.

(a)															
<i>Alca1</i>															
<i>Alca2</i>	0.012														
<i>A. trilineatus</i>	<b>0.093</b>	<b>0.090</b>													
<i>A. sp. Porto Walter</i>	<b>0.093</b>	<b>0.094</b>	0.036												
<i>A. sp. Iwokrama</i>	0.102	0.097	0.099	0.095											
<i>A. spumaponens</i>	0.103	0.098	0.097	0.108	0.119										
<i>A. sp. Duce</i>	0.101	0.095	0.094	0.097	0.108	0.041									
<i>A. granti</i>	<b>0.092</b>	0.097	0.085	0.088	0.098	0.072	0.077								
<i>A. algorei</i>	0.110	0.104	0.103	0.112	0.102	0.100	0.095	0.085							
<i>A. sp. Rio Ituxi</i>	0.112	0.107	0.108	0.107	0.120	0.106	0.103	0.081	0.108						
<i>A. sp. Manaus 1</i>	0.115	0.111	0.110	0.113	0.123	0.117	0.111	0.083	0.120	0.047					
<i>A. sp. PEGM1</i>	0.103	0.100	0.101	0.100	0.120	0.113	0.107	0.077	0.112	0.043	0.051				
<i>A. paleovarzensis</i>	0.107	0.101	0.107	0.113	0.115	0.092	0.095	0.077	0.112	0.114	0.119	0.112			
<i>A. conspicuus</i>	0.112	0.112	0.122	0.121	0.120	0.120	0.119	0.110	0.129	0.125	0.129	0.123	0.135		
<i>A. sp. Cuyabeno</i>	0.121	0.118	0.125	0.121	0.123	0.120	0.114	0.106	0.122	0.131	0.136	0.123	0.135	0.114	
<i>A. insperatus</i>	0.113	0.112	0.124	0.124	0.130	0.130	0.116	0.106	0.129	0.133	0.129	0.124	0.140	0.115	0.056
(b)															
<i>L. fallax</i>															
<i>L. myersi</i>	0.081														
<i>L. knudseni</i>	<b>0.080</b>	0.044													
<i>L. pentadactylus</i>	0.099	0.076	0.078												
<i>L. savagei</i>	0.088	0.054	0.072	0.058											
<i>L. rhodomereus</i>	0.097	0.096	0.091	0.081	0.067										
<i>L. labyrinthicus</i>	0.089	0.067	0.081	0.092	0.082	0.094									
<i>L. vastus</i>	0.118	0.089	0.100	0.122	0.104	0.112	0.107								
<i>L. paraensis</i>	0.118	0.089	0.100	0.122	0.104	0.112	0.107	0.002							
<i>L. stenodema</i>	0.143	0.113	0.111	0.116	0.106	0.123	0.128	0.126	0.126						
(c)															
<i>P. euphronides</i>															
<i>P. bipunctatus</i>	0.173														
<i>P. caprifer</i>	0.179	0.194													

## Divergence estimation

For molecular dating we modified the matrix focusing on the inclusive clade of *A. chalcopis* and discarding some terminals in order to reduce the impact of missing data. The Bayesian analyses revealed close affinity among some terminals that were incomplete and that were thus discarded. In other cases some closely related terminals were complementary and were fused to represent only one complete terminal representing the corresponding clade (supplementary Table 3; see supplementary material, which is available on the Supplementary tab of the article's Taylor & Francis Online page at <http://dx.doi.org/10.1080/14772000.2013.764944>). With this strategy we were able to obtain an almost complete matrix that included only one terminal for main lineages in *Allobates* and focusing on the inclusive clade of *A. chalcopis*. Missing data were therefore limited to only three terminals for COI and seven terminals for TYR.

Previous studies (Santos *et al.*, 2009) using large datasets and fossil/biogeographic calibrations to infer timing of diversification within dendrobatids provide a good estimation of the crown age of major groups that we used to calibrate our analyses. We used four time priors: (1) a uniform distribution bounded between 31.4 and 57.5 Ma for the root of the tree (Dendrobatidae); a normal distribution for the crown age of (2) the most inclusive clade containing *Allobates* and *Aromobates* set as 35 Ma for the mean (S.D. = 5.5); (3) its sister group set as 37 Ma for the mean (S.D. = 4.5); and (4) the crown age of the Amazonian *Allobates* (N233 in Santos *et al.*, 2009) set as a normal distribution with 19 Ma for the mean (S.D. = 3.7).

We used Beast 1.6.2 (Drummond & Rambaut, 2007) using relaxed Bayesian molecular clock with uncorrelated lognormal rates and the same models used in the previous BA. The tree prior used the Birth and Death Process with a randomly generated starting tree and the auto-optimize option for operators. We computed  $100 \times 10^6$  generations sampled every 1000 generations. We examined convergence on stationarity using Tracer 1.5 (Rambaut & Drummond, 2003). Effective sample sizes were  $> 200$  for all parameters except prior and posterior that were moving between alternative values. A few relative substitution rates were also with low ESS jumping from high values to zero (probably because no substitutions of these types are observed) rendering the prior on the rate invalid (Drummond *et al.*, 2002). Therefore, we computed additional  $100 \times 10^6$  generations run with the prior distribution of these relative rates changed from a gamma to a uniform distribution bounded between  $1.10^{-5}$  and 1. This resulted in ESS  $> 500$  for all parameters. The maximum clade credibility trees were computed with Tree Annotator 1.6.2.

We also compared the genetic distances (p distances) among Caribbean vs. closest continental relatives; *L. fallax* vs. the species of the *Leptodactylus pentadactylus* group, *Pristimantis euphonides* and its closest continental relatives according to Hedges *et al.* (2008) and Pyron & Wiens

(2011) and between *Allobates chalcopis* and its related species using 16S which was available for most documented species.

## Results

### Distribution and ecology

The species was found on the summit of Montagne Pelée from  $\sim 800$  to  $\sim 1400$  m a.s.l. which is well above the altitudinal zone from which the species was originally described (Kaiser *et al.*, 1994a). We failed to detect the species in its type locality, the 'ravines' along the Morne Rouge–Ajoupa Bouillon road and from the 'Elfin forests' (Fig. 1). These 'ravines' are around 500 m a.s.l. and are very steep slopes covered with a forest mostly consisting of Cyclanthaceae, Heliconiaceae, Piperaceae, ferns, bamboos, *Cecropia* sp. and a few sparse tall trees. The 'Elfin forests' are situated between 700–800 m and consist of small mossy trees with lianas and *Heliconia bihai*. These patches of forest are isolated from each other because connecting ridges are intensively cultivated.

The lower limit of occurrence of *Allobates chalcopis* was found to be at  $\sim 800$  m a.s.l. (Aileron Parking), a transitional site on the top of a 'ravine' between forest and a savanna dominated by ferns (*Dicranopteris* spp.) and Poaceae with a few Melastomataceae. Scattered calling males were located under 1–1.5 m of the very dense herbaceous vegetation. Calling male density increased with higher grounds with a maximum around 1200 m a.s.l. where savannas consist of Poaceae, Bromeliaceae (*Guzmania plumieri*, *Pitcairnia spicata*), lycopods and scattered mats of *Sphagnum* spp., and shrub (*Charianthus nodosus*) (Fig. 2). Dozens of individuals were heard up to the summit of Montagne Pelée ('Le Chinois' formations dating back to 1902 and 1929) that is 1390 m a.s.l. However, very few individuals were heard in the area that burned down in 2010. Based on the lowest and the highest altitudinal occurrence we calculated that the current range of *A. chalcopis* is approximately 3.7 km<sup>2</sup>. When including the type locality and all areas above 500 m a.s.l. on the Montagne Pelée the extent of the suitable habitat reaches 33 km<sup>2</sup> (Fig. 1).

Calls were heard throughout the day but intensity of the activity fluctuates with sunlight and a peak of activity was clear between 16:00 h and 17:00 h. A call voucher can be found at: <http://www.caribherp.org>.

### Phylogenetic position and molecular dating

*Allobates chalcopis* is unambiguously embedded within *Allobates* and nested within a well-defined clade comprising 10 additional species (Fig. 3). This clade corresponds to the 'trilineatus clade' of Grant *et al.* (2006) and is sister to a clade consisting of three species (*conspicuous*,

**Table 3.** *Allobates* spp. that belong or probably belong to the “*trilineatus* clade” sensu Grant *et al.* (2006) and other *Allobates* spp. that occur in the northern periphery of South America from where *Allobates chalcopsis* could have been translocated. We also indicated whether these species have been included in the molecular data matrix, their distributions; altitude range; whether the absence of black throat or presence of webbing allow clear distinction with *Allobates chalcopsis* and eventually the authors of the species of a redescription.

Species	DNA	Country	Distribution	Altitude	Morphology	Reference
<i>A. sp. Iwokrama</i>	X	Guyana	Iwokrama	~100 m	no black throat	NA
<i>A. granti</i>	X	French Guiana	French Guiana, Suriname	100–800 m	no black throat	Kok <i>et al.</i> , 2006
<i>A. sp. Duce</i>	X	Brazil	Manaus region	~100 m	?	NA
<i>A. sp. Rio Ituxi</i>	X	Brazil	Rio Ituxi	~100 m	?	NA
<i>A. sp. Manaus 1</i>	X	Brazil	Manaus region	~100 m	?	NA
<i>A. paleovarzensis</i>	X	Brazil	Manaus region	~100 m	no black throat	Lima <i>et al.</i> , 2010
<i>A. sp. PEG-M1</i>	X	Brazil	Rondonia; PE Guajara-Mirim	~100 m	?	NA
<i>A. trilineatus</i>	X	Brazil, Peru, Bolivia, Colombia	Western Amazonia	~100 m	no black throat	Boulenger, 1884
<i>A. sp. Porto Walter</i>	X	Brazil	Acre Porto Walter	~100 m	?	NA
<i>A. algorei</i>	X	Venezuela	Only known from Type Loc. and vicinity Andean foothills at the border with Colombia	400–1000 m	no black throat	Barrio-Amorós & Santos, 2009
<i>A. spumaponens</i>	X	Guyana	Mabura Hill Forest Reserve	~100 m	no black throat	Kok & Ernst, 2007
<i>A. sammaritini</i>	0	Venezuela	Las Majadas, Bolivar state	1000 m	no black throat	Rivero <i>et al.</i> , 1986
<i>A. cepedai</i>	0	Colombia	Meta, Villavicencio	600 m	dorsal colouration	Morales, 1994, 2002
<i>A. crombiei</i>	0	Brazil	Para, Alta Mira do Xingu	10 m	no black throat	Morales, 1994, 2002
<i>A. fraisenescus</i>	0	Ecuador	Pastaza, Rio Pastaza drainage	900–1100 m	no black throat	Morales, 1994, 2002
<i>A. fuscus</i>	0	Brazil, Peru, Bolivia, Colombia	western Amazonia	~100 m	dorsal colouration	Morales, 1994, 2002
<i>A. masniger</i>	0	Brazil	Para, Rio Tapajos	200 m	dorsal colouration	Morales, 1994, 2002
<i>A. melanolemus</i>	0	Peru	Loreto, lowe Napo drainage	~100 m	webbed feet	Grant & Rodriguez, 2001
<i>A. subfolionidificans</i>	0	Brazil	Acre, Rio Branco	136 m	no black throat	Lima <i>et al.</i> , 2007
<i>A. sumtuosus</i>	0	Brazil and Peru	Loreto and Para, north bank of the Amazon	100–200 m	no black throat	Morales, 1994, 2002
<i>A. pittieri</i>	0	Venezuela	Cordillera de la Costa and Cordillera de Mérida Venezuela	150–1700 m	no black throat	La Marca <i>et al.</i> , 2004
<i>A. mandelorum</i>	0	Venezuela	Cerro Turumiquire, a montane area northwest of tepui region, Monagas, Sucre	1900–2630 m	toes webbed	Schmidt, 1932
<i>A. “brunneus” venezuela</i>	0	Venezuela	Venezuelan Amazonia	?	no black throat	Cope, 1887; Lima <i>et al.</i> 2009 but different Venezuelan species
<i>A. “marchesianus” venezuela</i>	0	Brazil, Peru, Colo., Venez., Ecuad.	Western Amazonia	100–~1000 m	no black throat	Melin, 1941; Caldwell <i>et al.</i> 2002 but different Venezuelan species
<i>A. femoralis</i>	X	Amazonian	Amazonian	100–~1000 m	no black throat	Venezuelan species Boulenger, 1884
<i>A. sp. Saul</i>	X	French Guiana	Southern FG	100–800 m	no black throat	NA
<i>A. bromelicola</i>	0	Venezuela	Coastal Range of Venezuela, Aragua	> 1000 m	no black throat	Test, 1956
<i>A. caribe</i>	0	Venezuela	Peninsula de Paria Coastal Venezuela, sucre	> 1000 m	no black throat	Barrio-Amorós <i>et al.</i> , 2006
<i>A. humilis</i>	X	Venezuela	Eastern foothills of the Mérida Andes	600–1800 m	no black throat	Rivero, 1980



**Fig. 2.** On the left, pictures of the two collected specimens. Note the differences in colouration pattern of the specimens. On the right, two pictures of the herbaceous summit of Montagne pelée, habitat of *A. chalcopis*.

*insperatus* and sp. ‘Cuyabeno’). This more inclusive clade corresponds to the ‘*trilineatus* group’ *sensu* Santos *et al.* (2009). These 10 species cluster in five subclades of uncertain relationships within the ‘*trilineatus* clade’; one of them being formed by *Allobates chalcopis*. Interestingly, the two *A. chalcopis* specimens display notably distinct haplotypes with seven substitutions on 12–16S (0.12%; Table 2) and three substitutions on COI between them.

One of the two species from Guyana, included for the first time in any phylogenetic reconstruction i.e. *A. spumaponens* (Kok & Ernst, 2007), is also nested within the ‘*trilineatus* clade’. *Allobates spumaponens* clusters with *A. sp.* ‘Reserva Ducke’; genetic distance between them is low (16S 4.1%; Table 2), and they form with *Allobates granti* from French Guiana and *Allobates algorei* from coastal Venezuela one of the six main lineages of the ‘*trilineatus* clade’. The three remaining major subclades are (i) *A. trilineatus* + *A. sp.* ‘Porto Walter’ both from western Amazonia; (ii) *A. sp.* ‘Manaus’ + *A. sp.* ‘Rio Ituxi’ + *A. sp.* ‘PEG-M1’ all from central Amazonia; (iii) *A. paleovarzensis* also from central Amazonia. However, the other species from Iwokrama represents another highly divergent lineage related to *A. conspicuus* and *A. insperatus*.

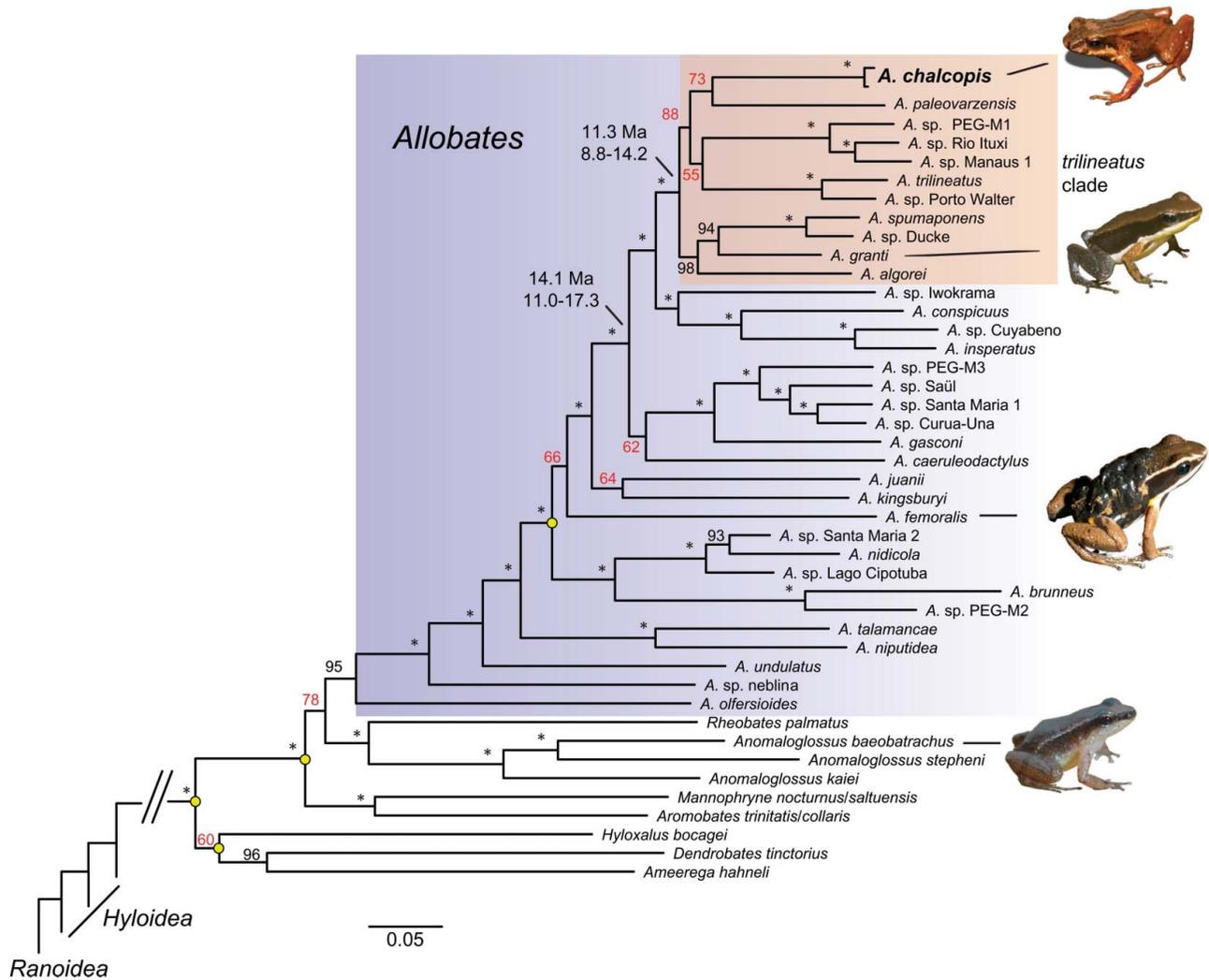
Using relaxed clock time calibrated BA, relationships remained ambiguous within the ‘*trilineatus* clade’ (supplementary Fig. 1, see supplementary material, which is available on the Supplementary tab of the article’s Taylor & Francis Online page at <http://dx.doi.org/10.1080/14772000.2013.764944>). Nevertheless, it confirms that *A. chalcopis* originated early within the ‘*trilineatus* clade’ (Fig. 3) which age is estimated around 11.3 Ma (95% CI: 8.8–14.2 Ma).

The 16S data examined showed a minimum genetic distance between *A. chalcopis* and *A. trilineatus* of 9% (Table 2). The lowest genetic distance between *L. fallax* and the other species of the *Leptodactylus pentadactylus* group is comparable (8% with *L. knudseni*). However, the genetic distances found between *Pristimantis euphronides* and its closest relatives on the continent according to Heinicke *et al.* (2007) and Pyron & Wiens (2011) are > 17%.

## Discussion

### *Allobates chalcopis* endemism

Thirty years after its discovery by M. Read in 1984 and 20 years after its formal description which corresponds to the last observation of the species we succeeded in finding



**Fig. 3.** Phylogenetic tree hypothesized from Bayesian analysis of 4612bp of mt and nuDNA of Dendrobatid frogs. Posterior probabilities \*100 are given aside the nodes above or under. Asterisks are standing for  $pp > 0.95$  and  $pp < 0.9$  are indicated in red. The calibration points used to estimate the age of two nodes are also indicated with yellow dots.

an isolated population of *Allobates chalcopsis* on the summit of Montagne Pelée. This ‘rediscovery’ allowed us to confirm that *Allobates chalcopsis* is unambiguously related to a well-defined clade of Amazonian *Allobates* (*trilineatus* clade) but is also highly divergent to its closest relatives. All the species of this clade occur in the lowlands of Amazonia; in the Guiana Shield, the Brazilian Shield and western Amazonia (Table 3); and all are morphologically distinct from *Allobates chalcopsis*. Ten additional species putatively belonging to the ‘*trilineatus* group’ (Table 3) remain undocumented in terms of molecular-based phylogenetic position. Among them, only males of *Allobates melanoaemus* from western Amazonia possess a black throat like *A. chalcopsis*. However, this species displays webbed feet and larger body size among other differences (Grant & Rodriguez, 2001) (Table 3). In fact, the species of the *trilineatus* clade display

an overall similar morphology and *A. chalcopsis* is one of the most conspicuously distinct ones. Therefore, even if the existence on the mainland of a still unknown species more closely related to *A. chalcopsis* cannot be completely rejected given that *Allobates* still contains many undescribed species (Grant *et al.*, 2006; Fouquet *et al.*, 2007), such a possibility remains extremely unlikely.

The altitudinal range and the ecology of the species also strengthen this point. *Allobates chalcopsis* occurs above 500 m and inhabits submontane formations while most of the species of the ‘*trilineatus* clade’ inhabit lowlands and all *Allobates* are otherwise forest dwelling. Moreover, such a habitat niche (i.e. mountainous areas that were not directly impacted by human activities such as forestry or agriculture) makes a human-mediated introduction extremely unlikely as previously suggested by Kaiser *et al.* (1994a).

Despite the fact that some *Allobates* species are known to thrive even in severely disturbed forest areas (Kok & Ernst, 2007), no species in the genus has been reported to be anthropophilic and neither have feral populations been reported previously (Lever, 2003).

Finally, the observed distinctiveness of the two *A. chalcopis* haplotypes provides further support. It seems highly unlikely that such a mitochondrial divergence could originate within the comparatively short time span (< 400 years) available since human introduction was realistically possible unless several females with highly distinct haplotypes had been introduced (Ficetola *et al.*, 2008). In most cases, introduced populations typically display low genetic diversity (Lee, 2002). A conclusive explanation would of course require additional sampling of individuals from different populations. However, at this point and based on the amount of substitutions between the two sampled haplotypes, the evidence speaks in favour of an ancient establishment of the population rather than a recent introduction.

Consequently, we conclude that there is no reasonable point not considering *A. chalcopis* as a microendemic to Martinique Island.

### A shift or shrinkage of range and habitat?

We found the species to occur well above 800 m. Kaiser *et al.* (1994a) as well as Read (pers. comm.) found *Allobates chalcopis* ~500 m a.s.l. in the ‘ravines’ along the Morne Rouge–Ajoupa Bouillon road and from the ‘Elfin forests’ where we were unable to detect the species despite intensive searches at peak call activity time of day. Kaiser *et al.* (1994a) mentioned ‘dozens of calling males’ along the side of the ravines. Given we failed to record a single calling male from these ravines while at the same time hearing numerous calling males at elevations well above 800 m during the exact same period, we consider the species to be likely locally extinct from the type locality.

As there were no major modifications of the habitats of Montagne Pelée during these last decades, a possible explanation for such range and elevation shift may be climatic changes leading to unfavourable conditions in its original habitat and causing an upward migration or dispersal. Even if such a hypothesis remains speculative and needs to be tested systematically in the future, the preponderance of upward range shifts leading to contraction of high-elevation species and expansions of low-elevation taxa matches the predicted impacts of climate warming (Rull & Vegas-Vilarrubia, 2006; Moritz *et al.*, 2008) and has been reported in several regions of the world and for a variety of organisms (Chen *et al.*, 2011). Raxworthy *et al.* (2008) reported upslope displacement for highland amphibians and reptiles in Madagascar matching predictions from global warming and concluded that extinctions are likely to happen within a period as short as 50–100 years.

Kaiser *et al.* (1994a) did not specifically mention whether they had searched for *Allobates chalcopis* above altitudes at which the species was first encountered. Therefore, two scenarios explaining the observed distributional pattern are possible: (i) a range reduction, i.e. the species originally occurred between 500 and 1400 m a.s.l. but the current lower occurrence limit is now raised to 800 m a.s.l. or (ii) a range shift from originally 500 m a.s.l. to above 800 m nowadays. Detailed habitat models including climatic parameters could shed more light on this question and would allow for predictions of future trends.

### Overseas dispersal

*Allobates chalcopis* clearly diverged very early from its closest relative in the ‘*trilineatus* clade’. Molecular dating suggests this happened after 11.3 Ma, a similar estimate to that of Santos *et al.* (2009) for the *trilineatus* clade. Such an estimate matches the early history of the Martinique island that emerged ~9 Ma (late Miocene). This period also corresponds to a low eustatic sea level with the establishment of the South Pole icecap. In South America it corresponds to the end of the Pebas system with the closure of the Andean chains and the establishment of the Amazon and Orinoco modern drainages (Hoorn *et al.*, 2010). Hypothetically, such a drastic topographic change and lower sea level could have resulted in massive fresh water discharge into the coastal sea of the Guiana Shield facing the Caribbean. Actually, a northward riverine connection between Amazonia and the Caribbean Sea has even been hypothesized between 10 and 8 Ma (Wilkinson *et al.*, 2010). Further south, that aquatic connection between Amazonia and the Caribbean may have persisted in a more easterly position along the exposed Guiana Shield margin (modern Orinoco course) even after local uplifts. Such fresh brackish water connection would have obviously favoured survival of migrants on rafts as documented in the ‘congo plume’ (Measey *et al.*, 2007). Surface seawater salinity can, depending on currents and precipitation regime, strongly decrease episodically thus increasing the survival probability of potential amphibian migrants (Measey *et al.*, 2007). The hypothesis of colonization via raft is in fact a longstanding one (Hedges, 1996a). Rafts formed of natural vegetation originating from the mouth of major South American rivers have been proposed as a mechanism to explain the scattered pattern of divergences of West Indian taxa from their South American ancestors throughout the Tertiary. Such a scenario matches well with the evolutionary history of the mabuyine skinks *Capitulum* spp., *Mabuya* spp. and *Spondylurus* spp. (Hedges & Conn, 2012), the snakes *Corallus hortulanus* (Henderson, 1997) and *Liophis melanotus* (Dixon & Michaud, 1992), the parthenogenetic lizards *Gymnophthalmus underwoodi* (Kizirian & Cole, 1999) and *Kentropyx borckiana* (Cole *et al.*, 1995). It is also a likely scenario for the arrival of *Lepidactylus fallax* in the Lesser Antilles and *Bothrops* spp.

that share a similar age with *Allobates chalcopis*. In fact, Hedges & Heinicke (2007) provided a much older time frame for the divergence between *L. fallax* and close relatives ( $> 25$  Ma) but their estimate was calibrated on unrealistic immunological distances given the age of the genus *Leptodactylus* was, according to their analysis, 70 million years old which corresponds to the age of the entire Hylaidea clade (San Mauro *et al.*, 2005; Zhang *et al.*, 2005; Marjanovic & Laurin, 2007; Roelants *et al.*, 2007; Santos *et al.*, 2009). Caribbean *Pristimantis* spp. have, however, diverged much before *A. chalcopis* and *L. fallax* from their closest continental relatives according to genetic distances (Table 2). However, *Pristimantis* is such a speciose and poorly documented genus that the occurrence of closer relatives on the mainland cannot be rejected.

Some groups seem more prone to disperse through salt-water than others and some areas are better configured to favour overseas dispersal depending on currents and salinity (Hedges, 1996b; Measey *et al.*, 2007; Samonds *et al.*, 2012). In the Caribbean, the genus *Eleutherodactylus* and the anoles have dispersed from island to island multiple times and the genus *Leptodactylus* seems also prone to overseas dispersal as it displays at least three examples of dispersal in the Caribbean. However, the unique dispersal of a dendrobatid frog, a group of forestial small-bodied species, is mystifying. Concomitant dispersals of *L. fallax*, *Bothrops* spp., *Capitellum* spp., *Mabuya* spp., *Spondylurus* spp. and *A. chalcopis* strengthen the idea that such events could have been favoured by punctual geomorphologic events during the late Miocene. Such dispersal could have happened by stepping stone dispersal via the island of the Grenadines, St Vincent and Ste Lucia or rafting directly from South America to Martinique.

### Conservation status

The IUCN Red List Categories are based upon five criteria (IUCN, 2011): (A) declining population, (B) geographic range size and fragmentation decline or fluctuations, (C) small population size and fragmentation decline or fluctuations, (D) very small distribution or very restricted distribution and (E) quantitative analyses of extinction risk. Only one of these criteria needs to be met to rank a particular taxon in any threat category. With an entire geographic range (area of occupancy) smaller than  $10 \text{ km}^2$  ('B2') and a single known isolated population ('B2a') the species can be considered to be facing an extremely high risk of extinction in the wild.

*Allobates chalcopis* was originally occurring from 500 to 1400 m a.s.l. or lower and currently from 800 to 1400 m a.s.l. Therefore, the species experienced either a range shift or severe reduction possibly associated with population decline during the last 20 years. If this putative range reduction, from  $33 \text{ km}^2$  (maximum range 30 years ago) to  $3.7 \text{ km}^2$  (current range), is associated with climate change

there is simply no higher ground available for the species. According to the criteria 'B2b(ii)' we thus argue that *Allobates chalcopis* should be considered Critically Endangered B2ab(ii).

The current geographic range of *Allobates chalcopis* (800–1400 m) entirely lies on the Réserve biologique intégrale de la Montagne Pelée (IUCN Cat. I), a protected area managed by the ONF (Office National des Forêts – Direction régionale de la Martinique). Nonetheless, it is possible that other populations will be discovered outside any protected areas. Currently, *Allobates chalcopis* is not protected by any national conservation law (while some non-native species on Martinique are). To prevent destruction of hypothetical populations in non-protected surrounding areas and also to prevent wildlife traffic we argue that on top of changing the IUCN status a national conservation programme should also fully protect this species.

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