

An overview of Madagascar's leaf tailed geckos (genus *Uroplatus*): species boundaries, candidate species and review of geographical distribution based on molecular data

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Abstract. The spectacular appearance of Malagasy leaf-tailed geckos (genus *Uroplatus*) makes them one of the most fascinating reptile groups of Madagascar. However, species delimitation in these nocturnal geckos is notoriously difficult due to a high intraspecific genetic variability and an insufficient knowledge of the distribution and taxonomy of the 14 recognized species. Numerous surveys with new records have been published over the last 20 years, and molecular analyses have demonstrated the existence of several candidate species in this genus. Apart from a compilation of locality records in a field guide, the distribution ranges and species boundaries have not been reviewed recently in a comprehensive manner. Because the various recent studies in part used DNA sequences from different, non-homologous gene fragments, and applied different provisional names to these candidate species, it remains a major challenge to understand how these correspond to each other. Here we provide an updated list of *Uroplatus* species and candidate species resulting from an integrative taxonomic approach that mainly relies on analysis of published as well as newly determined mitochondrial DNA sequences, combined with preliminary data on morphological characters including pigmentation of the oral mucosa, tail length and tail shape. The present study focuses on *Uroplatus* species diversity and distribution, in order to provide baseline data for future taxonomic revisions, spatial prioritisation of conservation efforts, and management of the pet trade. We recognize 14 named species and another 11 undescribed candidate species, and allocate them to five species groups: the *U. eburnai* group (*U. eburnai*, *U. finiavana*, *U. malama*, *U. phantasticus*, four confirmed candidate species, CCS, and six unconfirmed candidate species, UCS), the *U. alluaudi* group (*U. alluaudi*, *U. pietschmanni*), the *U. guentheri* group (*U. guentheri*, *U. malahelo*), the *U. lineatus* group (*U. lineatus*), and the *U. fimbriatus* group (*U. fimbriatus*, *U. giganteus*, *U. henkeli*, *U. sameiti*, *U. sikorae*, and one CCS). Certain species (e.g., *U. phantasticus*, *U. sikorae*) are further subdivided into deep conspecific lineages that require further taxonomic revision. The *U. eburnai* group is the most species-rich with numerous candidate species that are still in need of thorough investigation. Most of these candidate species are distributed in northern Madagascar and confined to mountain massifs including Marojejy, Anjanaharibe-Sud and Tsaratanana.

Key words. Squamata, Gekkonidae, *Uroplatus* species, integrative taxonomy, candidate species, geographical distribution, Madagascar.

Introduction

Madagascar's forests host a unique fauna and flora and rank among the most species-rich and endangered habitats of the world. Logging, slash-and-burn farming practice, social and political instability associated with generalized poverty and natural cataclysm have led to the loss of the greatest part of forest coverage on the island. Forest cover decreased by almost 40% between the 1950s and 2000, with a reduc-

tion of almost 80% in core forest (defined as forest more than 1 km from the edge) (HARPER et al. 2007). These landscape shifts imply threats to species, but a more detailed assessment requires reliable taxonomic and distributional data. Forest destruction and degradation involve fragmentation and habitat loss, which are sources of threat especially for strictly forest-dwelling species, fostering the risk of extinction. One group of such organisms is the leaf-tailed geckos of the genus *Uroplatus*, endemic to Madagascar.

Fourteen species of *Uroplatus* geckos are recognized so far (RATSOAVINA et al. 2011). These nocturnal geckos are characterized by their large eyes with a vertical pupil, their triangular head with a large mouth, and a flattened tail that often is leaf-shaped. Because of their spectacular body shape and appearance, *Uroplatus* are among the most coveted animals by hobbyists and therefore regularly commercialised in the pet trade. Overharvesting at specific sites of easy access might constitute an additional threat toward local extirpation, especially to species with restricted distribution ranges, in spite of a sustainable export quota system that is now well established for these and other reptiles.

Despite the general interest in these geckos, little is known about the ecology, biology, and distribution ranges of most of the recognized forms, and species diversity within *Uroplatus* remains rather poorly understood (GLAW et al. 2006, GREENBAUM et al. 2007, RAXWORTHY et al. 2008). Recent molecular studies revealed the presence of several distinct populations, characterized by deep divergences in mitochondrial genes and often also in nuclear genes. However, translating these complex data into a stable taxonomy is challenging, and a thorough conservation assessment for these newly discovered lineages is hampered by differing interpretations of the observations. A typical example is the case of the northern giant tailed gecko populations that are considered a separate species, *Uroplatus giganteus* (GLAW et al. 2006), or a deep genetic lineage within *U. fimbriatus* (RAXWORTHY et al. 2008).

Because of this taxonomic uncertainty and the morphological similarity of many species of *Uroplatus*, the delimitation of their geographical distribution is challenging. Some species appear to be endemic to small areas in Madagascar, such as *U. fnyiavana* in the Montagne d'Ambre National Park (RATSOAVINA et al. 2011), whereas others are considered to be widespread. Solving this conundrum is further complicated and sometimes even impossible through simple comparisons of the published molecular trees, because various authors have based their studies on different sets of genes and on samples from different localities.

After a small-scale data set of 16S rDNA sequences published by GLAW et al. (2006) focusing on *U. giganteus* and *U. fimbriatus*, the first comprehensive molecular multi-gene phylogeny of the genus *Uroplatus* was published by GREENBAUM et al. (2007). These authors used a combination of nuclear (RAG1 and PDC) and mitochondrial (COB and ND2) gene fragments. Their results corroborated the hypothesis of BÖHME & HENKEL (1995) concerning the distinction of *U. ebenau* from *U. phantasticus* and an overall complex taxonomy of the small-sized leaf-tailed geckos, which are in fact a group of cryptic species. This study also pointed to genetically divergent lineages being present especially in northern Madagascar, suggesting that this area is likely a centre of diversity and micro-endemism for several subgroups of *Uroplatus*. The most data-rich molecular work to date was subsequently published by RAXWORTHY et al. (2008). These authors studied the *Uroplatus* radiation on Madagascar by using mainly molecular data (nuclear genes: BDNF and 18S rRNA; mitochondrial genes: 12S

rRNA and COB). They identified eight unknown forms of *Uroplatus* in the northern montane areas of Madagascar. Additional molecular data on the *U. ebenau* group were published by RATSOAVINA et al. (2011, 2012).

Over the last decade, several studies have contributed to the definition of the distribution ranges of *Uroplatus* spp. (RASELIMANANA et al. 2000, ANDREONE et al. 2001, RAMANAMANJATO et al. 2002, RAKOTOMALALA & RASELIMANANA 2003; RABIBISOA et al. 2005, RAKOTONDRAVONY 2006, MORI et al. 2006, ANDREONE & RANDRIANIRINA 2007, RASELIMANANA & ANDRIAMAMPIONONA 2007, GLAW & VENCES 2007, PEARSON et al. 2007, BORA et al. 2007, 2010, D'CRUZE et al. 2007, 2008, RASELIMANANA 2008, ANDREONE et al. 2009, MEGSON et al. 2009, GEHRING et al. 2010). In numerous cases, the precise identity of these records remained uncertain because of the incomplete knowledge on species identity and species delimitation.

Integrative taxonomy has been proposed as an approach that is based on combining all available evidence in taxonomic practice (DAYRAT 2005, WILL et al. 2005, SCHLICK-STEINER et al. 2010, PADIAL et al. 2010), thus avoiding overestimation or underestimation of the real species diversity in nature. In the case of cryptic species in the genus *Uroplatus*, morphology alone can fail to delimit one species from another, but the combination of molecular and morphological evidence provides a more reliable resolution.

In this study, we provide a preliminary review of the taxonomy and species distribution of the genus *Uroplatus* as a baseline for future studies on their biogeography and conservation in Madagascar. For this purpose, we first sequenced fragments of one or several mitochondrial genes from all *Uroplatus* samples available to us. Second, we aligned these with the homologous sequences of *Uroplatus* available from previous studies, and used these data sets to infer phylogenetic trees. On the basis of samples clustering together in the various trees, we assess the distribution of mitochondrial lineages and we then integrate this evidence with information on some morphological key characters. Combining data allows us to propose preliminary delimitations of both nominal and candidate species, and present an updated summary of the distribution of *Uroplatus* lineages as a basis for future comprehensive taxonomic revision.

Material and methods

Geographical data

Distribution records cited in the present manuscript were obtained from scientific publications, unpublished reports, personal communications, and our own collections. The locality records for each species provided by GLAW & VENCES (2007) were used as a basis. We attempted to be as comprehensive as possible and discuss a large number of records from the literature and our own observations. However, given the recent intensity of research in Madagascar, our list will almost inevitably miss some records. Where morphological diagnosis is challenging, especially in complexes of morphologically similar species, we will

only consider localities to be verified if they are confirmed by a DNA sequence. Global Positioning System (GPS) coordinates from our own fieldwork and the literature, along with historical localities georeferenced using gazetteers, were verified in GoogleEarth and used to compile distribution maps. Some geographical coordinates may not exactly refer to the actual sampling site if more precise information is unavailable. Formal biogeographical regions are named according to BOUMANS et al. (2007) and start with an uppercase letter (e.g., North East) while geographical directions are given in lowercase (e.g., northern part of Madagascar).

Voucher specimens

Specimens were detected along forest transect lines or opportunistically during night walks using torches or headlamps. Grabbed by hand, specimens were either sampled for small tail clips and released, or euthanised by injecting an overdose of anaesthetic and then fixed with 95% ethanol and preserved in 70% ethanol. Most voucher specimens cited in this work are deposited in the collections of the Département de Biologie Animale de l'Université d'Antananarivo, Madagascar (UADBA) and the Zoologische Staatssammlung München, Germany (ZSM). Additional institutional acronyms cited in this work are as follows: KUZ, Zoological collection of the Kyoto University Museum, Japan; MNHN, Muséum Nationale d'Histoire Naturelle de Paris, France; MRSN, Museo Regionale di Scienze Naturali, Torino, Italy; UMMZ, Museum of Zoology, University of Michigan, USA; ZFMK, Zoologisches Forschungsmuseum A. Koenig, Bonn, Germany. Acronyms of field numbers (also used as identifiers of tissue samples) refer to the following persons; RAN (RONALD A. NUSSBAUM), RAX (CHRISTOPHER J. RAXWORTHY), ACZC (ANGELICA CROTTINI), DRV (DAVID R. VIEITES), FGZC (FRANK GLAW), ZCMV (MIGUEL VENCES), RATF (FANOMEZANA RATSOAVINA for laboratory identification of specimens), ZCSH (SUSANNE HAUSWALDT), AND/BET/URAN/ZAH/KIAN (FANOMEZANA RATSOAVINA and ED LOUIS), MPFC (MACIEJ PABIJAN). Recorded specimens or samples are given for each locality, and doubtful localities mentioned in some literature listed as well.

Molecular sampling and reconstruction of phylogeny

Tissue samples from the tail tip or thigh muscle (preserved in 99% ethanol) obtained during fieldwork across the full extent and accessible geographical distribution of the genus *Uroplatus* were used for molecular analysis. Genomic DNA was extracted using proteinase-K digestion and salt extraction following BRUFORD et al. (1992). We amplified three mitochondrial DNA fragments (12S rRNA, 12S; NADH-dehydrogenase subunit 4, ND4; and cytochrome *b*, COB) using standard PCR protocols with the following primers: a fragment (400 base pairs) of the 12S ribosomal RNA gene

(12S) with 12SAL 5'-AAACTGGGATTAGATACCCCATAT-3' and 16SBHnew 5'-CCTGGATTACTCCGGTCTGA-3' (sequenced in one direction only using 12SAL), a fragment (500 bp) of NADH dehydrogenase subunit 4 (ND4) with ND4 5'-CACCTATGACTACCAAAAGCTCATGTAGAAGC-3' and LeutRNA 5'-CATTACTTTTACTTTGGATTTGCACC-3' (ARÉVALO et al. 1994) and a section (310 bp) of cytochrome *b* (COB) with CytbF700 5'-CTTCCAACACCAYCAAACATCTCAGCATGATGAAA-3' and CytbR700 5'-ACTGTAGCCCCCTCAGAATGATATTTGTCCTCA-3' (BAUER et al. 2007). Sequences were resolved on an automated DNA sequencer (ABI 3130 XL, Applied Biosystems) and checked visually for quality and possible errors with CodonCode Aligner software (Codon Code Corporation).

Available *Uroplatus* sequences of the focal genes from the studies of GLAW et al. (2006), GREENBAUM et al. (2007), RAXWORTHY et al. (2008), and RATSOAVINA et al. (2011, 2012) were retrieved from GenBank and aligned with the newly generated data from this study that consisted of 5, 22, and 98 sequences of the 12S, COB, and ND4 genes, respectively. The new sequences were deposited in GenBank (accession numbers KF160342–KF160464).

Multiple DNA sequence alignments were carried out using MEGA 5 (TAMURA et al. 2011). For each mitochondrial gene, we performed a model-based phylogenetic analysis by Bayesian inference using MrBayes (HUELSENBECK & RONQUIST 2001), selecting substitution models under the AIC criterion with MrModeltest (POSADA & CRANDALL 1998, NYLANDER 2004). For the analysis in MrBayes, we implemented two simultaneous runs separately with four chains each at least for 10 million generations, and trees were sampled every 1000 generations. The average standard deviation of split frequencies and the effective sample size given by Tracer v1.5 (RAMBAUT & DRUMMOND 2009) were used to evaluate topological and branch-length convergence. The first 25–50% of the generations were discarded as conservative burn-ins according to empirical evaluation, in order to obtain only a stationary distribution for each run. Trees were summarized as 50% majority rule consensus trees. We emphasize that the goal of this study is not to clarify *Uroplatus* phylogeny, but to assign as many specimens and localities as possible to species and major mitochondrial lineages. Therefore, we did not attempt to combine the various DNA fragments for analysis, as such a combined analysis would have been very complicated, considering the large number of samples of which only one of the various fragments has been sequenced. The deep phylogenetic relationships among the majority of species and candidate species of *Uroplatus* have been resolved by GREENBAUM et al. (2007), RAXWORTHY et al. (2008) and RATSOAVINA et al. (2012).

Terminology used for candidate species

We follow VIEITES et al. (2009) and PADIAL et al. (2010) to classify deep genealogical lineages of *Uroplatus* as fol-

lows: first, we assigned the currently valid species names to lineages based on diagnostic morphological characters, current taxonomy, and assignment of sequences from populations close to or at type localities. Second, we categorised still-unnamed lineages as confirmed candidate species (CCS), unconfirmed candidate species (UCS), or deep conspecific lineages (DCL), depending on the amount of evidence available from other data sets. Our CCS refer to lineages that very probably represent distinct species that have not yet been scientifically named, as typically evidenced by a clear morphological distinctiveness compared to their sister lineage(s). UCS defines deep lineages for which such additional evidence is absent and the taxonomic status thus remains unclear. We classify those populations as DCL that differ by only moderate genetic distances from the nominal species, are geographically connected to those, and show no obvious morphological divergence. We name candidate species according to the scheme of PADIAL et al. (2010), by using the name of the phylogenetically closest (or morphologically most similar species, followed by Ca and a number in square brackets, together with a GenBank accession number of a representative sequence at first mention.

Results

By assembling information from previous studies and considering the new results obtained herein, we provide in the following accounts for the 14 recognized (nominal) species of *Uroplatus*, and for five CCS and six UCS, respectively. This taxonomy is based on phylogenetic trees calculated from the sequences of the 12S, COB and ND4 gene fragments presented in Figs. 1–5, while Figs. 6–11 depict specimens in life of most of the species and candidate species. Table 1 summarizes described species and undescribed forms assessed during this study, and Table 2 gives some very preliminary morphometric data taken from selected specimens of the *U. ebenau* group. Localities underlying the molecular data are assigned to species and candidate species in distribution maps (Figs. 12–13) and listed in detail in the online Supplementary Materials.

Altogether, as is discussed in more detail below, the genetic divergences found among species and lineages of *Uroplatus* were found to be high in comparison to those observed among species of many other groups of organisms.

Between the 14 nominal species, the average genetic divergence (given as uncorrected pairwise p-distance, in the following abbreviated UPD) in the ND4 gene was 28.4%. The highest UPD for this gene reached 37.8% between *U. pietschmanni* and *U. finivana*, and the lowest values were found between specimens of *U. sikorae* and *U. sameiti* (14–16%).

For the COB data, the average UPD is 27.2%, the highest distance value between described species is 33.0% between *U. guentheri* and *U. lineatus*, and the respective lowest value is 8.2% between *U. sikorae* and *U. sameiti*. For the can-

didate species defined in this work, the lowest distance is between *U. ebenau* [Ca3] and *U. ebenau* [Ca4] with 13.1%. The highest value is 35.3% between *U. ebenau* [Ca1] and *U. sameiti* from Zahamena.

The 12S sequences of nominal species show an average UPD of 18.1%, with the highest distance of 23.2% being found between *U. lineatus* and *U. ebenau* and the lowest of 6.3% between *U. sikorae* and *U. sameiti* (summary table S24 in online Supplementary Materials).

Taking into account that the evolutionary rates of each gene studied in this work are specific, UPD from the ND4 gene data matrix will generally be used as a threshold to help delimit candidate species. As mentioned above, ca. 14% is the minimum UPD value between two described species, and we will use this value as a minimum threshold for assigning the status of candidate species, but use additional evidence such as morphological traits to decide on its precise status (CCS, UCS, DCL).

Uroplatus ebenau group

Comprising four nominal species, this group has the largest distribution range of all *Uroplatus* species groups along a latitudinal axis. Representatives of the group have colonized many types of forest habitat and a wide altitudinal range. Species can be encountered in low- and mid-altitude rainforest, low-altitude dry deciduous forest, as well as in montane forests close to the tree line. GREENBAUM et al. (2007) and GLAW & VENCES (2007) asserted that, based on morphological and genetic data, several species in this group are in fact complexes that comprise undescribed species. This was confirmed by RAXWORTHY et al. (2008) who detected several additional undescribed forms of the group in the area of the Tsaratanana massif in northern Madagascar, and by the recent description by RATSOAVINA et al. (2011) of a new species from Montagne d'Ambre, *U. finivana*. The fact that some members of this group tolerate the rather cold climate of high altitudes is unique for nocturnal geckos in Madagascar; the confirmed candidate species *U. ebenau* [Ca2] from Tsaratanana has been recorded from as high as ca. 2,200 m a.s.l. Besides various other aspects of body shape, these geckos differ from other *Uroplatus* by a sexual dimorphism in tail shape, which at least in some species is laterally smooth in females and serrated in males, whereas the tail size appears to be rather species-specific with only limited variation between the sexes.

In total, ten candidate species are known in this group: eight forms are morphologically similar to *U. ebenau* while two others appear to be more similar to *U. phantasticus*.

Uroplatus ebenau (BOETTGER, 1879)

This species was named by BOETTGER (1879) from the small island Nosy Be off northern Madagascar, and the subsequently described *U. boettgeri* from the same locality (FISCHER 1884) is considered to represent a junior synonym of *U. ebenau*. The species has a very short tail of rhomboid shape that does not exceed 20 mm in length.

Diversity and distribution of the genus *Uroplatus*

Table 1. List of nominal species, confirmed and unconfirmed candidate species as assessed in this work plus previous names assigned to them in different publications. Note that the candidate species names used in RATSOAVINA et al. (2012) are consistent with the names used herein. Abbreviations: n.a. (not applicable), n.i. (not included or not explicitly mentioned in the respective paper).

Species in this study	GREENBAUM et al. (2007)	RAXWORTHY et al. (2008)	RATSOAVINA et al. (2011)	RATSOAVINA et al. (2012)	Morphologically most similar nominal species	Status
<i>U. ebenauai</i> group						
<i>U. ebenauai</i>	<i>U. ebenauai</i>	<i>U. ebenauai</i>	<i>U. ebenauai</i>	<i>U. ebenauai</i>	n.a.	valid taxon
<i>U. finiavana</i>	<i>U. "ebenauai"</i> Montagne d'Ambre	<i>Uroplatus</i> sp. B	<i>U. finiavana</i>	<i>U. finiavana</i>	n.a.	valid taxon
<i>U. phantasticus</i>	<i>U. phantasticus</i>	<i>U. phantasticus</i>	<i>U. phantasticus</i>	<i>U. phantasticus</i>	n.a.	valid taxon
<i>U. malama</i>	<i>U. malama</i>	<i>U. malama</i>	<i>U. malama</i>	<i>U. malama</i>	n.a.	valid taxon
<i>U. ebenauai</i> [Ca1]	<i>U. "ebenauai"</i> Tsaratanana	<i>Uroplatus</i> sp. F	<i>Uroplatus</i> sp. 1	<i>U. ebenauai</i> [Ca1]	<i>U. finiavana</i>	CCS
<i>U. ebenauai</i> [Ca2]	n.i.	<i>Uroplatus</i> sp. E	<i>Uroplatus</i> sp. 2	<i>U. ebenauai</i> [Ca2]	<i>U. ebenauai</i>	CCS
<i>U. ebenauai</i> [Ca3]	<i>U. "ebenauai"</i> Marojejy	<i>Uroplatus</i> sp. D	<i>Uroplatus</i> sp. 3	<i>U. ebenauai</i> [Ca3]	<i>U. ebenauai</i>	CCS
<i>U. ebenauai</i> [Ca4]	n.i.	<i>Uroplatus</i> sp. A	<i>Uroplatus</i> sp. 4	<i>U. ebenauai</i> [Ca4]	<i>U. ebenauai</i>	CCS
<i>U. ebenauai</i> [Ca5]	n.i.	n.i.	n.i.	n.i.	<i>U. ebenauai</i>	UCS
<i>U. ebenauai</i> [Ca6]	n.i.	<i>Uroplatus</i> sp. C	n.i.	n.i.	<i>U. ebenauai</i>	UCS
<i>U. ebenauai</i> [Ca7]	n.i.	<i>Uroplatus</i> sp. F	n.i.	<i>U. ebenauai</i> [Ca7]	<i>U. ebenauai</i>	UCS
<i>U. phantasticus</i> [Ca8]	n.i.	n.i.	n.i.	n.i.	<i>U. phantasticus</i>	UCS
<i>U. ebenauai</i> [Ca9]	n.i.	<i>Uroplatus</i> sp. G	n.i.	n.i.	<i>U. ebenauai</i>	UCS
<i>U. phantasticus</i> [Ca10]	n.i.	n.i.	n.i.	<i>U. phantasticus</i> [Ca10]	<i>U. phantasticus</i>	UCS
<i>U. lineatus</i> group						
<i>U. lineatus</i>	<i>U. lineatus</i>	<i>U. lineatus</i>	<i>U. lineatus</i>	n.i.	n.a.	valid taxon
<i>U. alluaudi</i> group						
<i>U. alluaudi</i>	<i>U. alluaudi</i>	<i>U. alluaudi</i>	<i>U. alluaudi</i>	n.i.	n.a.	valid taxon
<i>U. pietschmanni</i>	<i>U. pietschmanni</i>	<i>U. pietschmanni</i>	<i>U. pietschmanni</i>	n.i.	n.a.	valid taxon
<i>U. guentheri</i> group						
<i>U. guentheri</i>	<i>U. guentheri</i>	<i>U. guentheri</i>	<i>U. guentheri</i>	n.i.	n.a.	valid taxon
<i>U. malahelo</i>	<i>U. malahelo</i>	<i>U. malahelo</i>	<i>U. malahelo</i>	n.i.	n.a.	valid taxon
<i>U. fimbriatus</i> group						
<i>U. fimbriatus</i>	<i>U. fimbriatus</i>	<i>U. fimbriatus</i>	<i>U. fimbriatus</i>	n.i.	n.a.	valid taxon
<i>U. giganteus</i>	<i>U. giganteus</i>	<i>U. fimbriatus</i>	<i>U. giganteus</i>	n.i.	n.a.	valid taxon
<i>U. sikorae</i>	<i>U. sikorae</i>	<i>U. sikorae</i>	<i>U. sikorae</i>	n.i.	n.a.	valid taxon
<i>U. sameiti</i>	<i>U. sameiti</i>	<i>U. sameiti</i>	<i>U. sameiti</i>	n.i.	n.a.	valid taxon
<i>U. henkeli</i>	<i>U. henkeli</i>	<i>U. henkeli</i>	<i>U. henkeli</i>	n.i.	n.a.	valid taxon
<i>U. henkeli</i> [Ca11]	<i>U. henkeli</i>	<i>U. sp. H</i>	n.i.	n.i.	<i>U. henkeli</i>	CCS

Its total length can reach 85 mm, and the oral mucosa is pigmented (black). Tree topologies based on ND4, 12S and COB are congruent with the basal position of this lineage, which is sister to a large clade containing all other species and candidate species of the *U. ebenauai* group, except *U. malama*. The taxonomy followed herein fully agrees with the works of GREENBAUM et al. (2007), RAXWORTHY et al. (2008), and RATSOAVINA et al. (2011), who all referred to samples of this species in their molecular trees under the name *U. ebenauai*. This species is found in lowland areas in northern and western Madagascar of which several are confirmed by molecular data (Fig. 12, Table S1). Several of

these populations are differentiated by significant genetic distances, but they form a clear monophyletic group in the phylogenetic analyses. Several records such as Montagne des Français (D'CRUZE et al. 2007), Ampombofofo, (MEGSON et al. 2009), Tsingy de Bemaraha (BORA et al. 2010), and from low altitudes of the Marojejy massif (GLAW & VENCES 2007) might also refer to *U. ebenauai*, although no molecular data are thus far available from these populations.

Montagne d'Ambre and Forêt d'Ambre are two adjacent localities. Here, the recently described *U. finiavana* occurs on the Montagne d'Ambre above 750 m a.s.l., where it was

observed in sympatry with *U. ebenau* in a remnant of primary forest close to Joffreville, a village on the way to the national park's entrance. Most or all records of *U. ebenau* from Montagne d'Ambre National Park (e.g., D'CRUZE et al. 2008, RAXWORTHY & NUSBAUM 1994) probably refer to *U. finnavana*.

The localities Anjanaharibe-Sud, mid- to high-elevation sites in Marojejy (RAXWORTHY et al. 1998, RASELIMANANA et al. 2000, RAKOTOMALALA & RASELIMANANA 2003), Tsaratanana (including Antsahamanara and Manarikoba), Tsararano, Ambolokopatrika (ANDREONE et al. 2000, 2001, 2009), Makira and Ankarana (GLAW & VENCES 2007) have previously been ascribed to *U. ebenau*, but most likely do not belong to that species, and some are not vouchered by any genetic data. Therefore, they will in the following be discussed in the respective accounts of the candidate species known from these sites.

Uroplatus finnavana RATSOAVINA, CROTTINI, RANDRIANAINA, LOUIS, GLAW & VENCES, 2011

This species has previously been treated as *Uroplatus "ebenau"* Montagne d'Ambre by GREENBAUM et al. (2007) and *Uroplatus* sp. B by RAXWORTHY et al. (2008). Morphological or molecular differences compared to *U. ebenau* from Nosy Be were detected by GLAW & VENCES (1994), BÖHME & HENKEL (1995), GREENBAUM et al. (2007) and RAXWORTHY et al. (2008). The appearance of this species is similar to *U. ebenau*, but some morphological differences exist, especially in the size and shape of the tail, which is longer in *U. finnavana*. According to molecular data, the species is related to various candidate species from the mountain massifs of northern Madagascar.

Our data set confirms a high UPD in the ND4 gene (not less than 29%) between *U. finnavana* and all nominal species of the *U. ebenau* group (29.4% for *U. phantasticus*, 35.2% for *U. ebenau* and 35.7% for *U. malama*).

U. finnavana is encountered in the Montagne d'Ambre National Park rainforest, at altitudes of 750 m a.s.l. and higher. Its sympatric occurrence with *U. ebenau* has been recorded from its lower altitudinal limits, close to the town of Joffreville. So far, the species has not been reported from any sites other than Montagne d'Ambre.

Uroplatus phantasticus (BOULENGER, 1888)

The original description of this species by BOULENGER (1888) is based on a single gravid female without a tail and without exact locality data ("Madagascar"). The specimen was collected by Rev. BARON from the Northern Central East (for more details see RATSOAVINA et al. 2011). One junior synonym is *U. schneideri*, described on the basis of a single juvenile (holotype MNHN 1914.4) from the Manjakandriana forest (LAMBERTON 1913), which obviously refers to the region between Antananarivo and Moramanga where the long-tailed *Uroplatus* species considered to represent *U. phantasticus* is typically encountered. *Uroplatus phantasticus* is characterized by pigmented oral mucosa and a size that can reach 76 mm in snout-vent length (SVL). The length of an original tail can be more than

46 mm (about 2/3 of SVL), and the tail shapes of *U. phantasticus* and *U. malama* are similar, but the latter species differs by its larger size. Taxonomy followed herein fully agrees with the works of GREENBAUM et al. (2007), RAXWORTHY et al. (2008), and RATSOAVINA et al. (2011), who all referred to samples of this species in their molecular trees under the name *U. phantasticus*.

With regard to the ND4 data matrix, UPD between *U. phantasticus* and other nominal species of the group is 27.9–29.7%, *U. malama* is the closest with 27.9%, followed by *U. finnavana* with 29.4% and *U. ebenau* with 29.7%. Between candidate species, UPD recorded for *U. phantasticus* [Ca8] from Ambohitantely is 22.7% and 24.2% for *U. phantasticus* [Ca10] from Zahamena.

This species has been recorded from the East, Northern Central East, and Southern Central East regions of Madagascar. It is the most widespread species of the *U. ebenau* group (see also RATSOAVINA et al. 2012), and inhabits only tropical rainforest, typically at low to mid-altitudes. The northernmost limit of its range is the Zahamena National Park and the southernmost genetically confirmed locality is Andringitra. In addition to the localities shown in Fig. 12 and listed in Table S3, more sites are mentioned in GLAW & VENCES (2007), RASELIMANANA & ANDRIAMAMPIONONA (2007), and RABISOA et al. (2005). Many of these additional sites are located within the range spanning from the northernmost and southernmost localities confirmed by genetics. The molecular data suggest that the nominal taxon *U. phantasticus* in fact contains several, rather deep mitochondrial lineages. No obvious morphological differences are found among the various populations here assigned to the different intraspecific lineages, and a more detailed analysis of the variation in *U. phantasticus* has recently been provided in a separate study (RATSOAVINA et al. 2012).

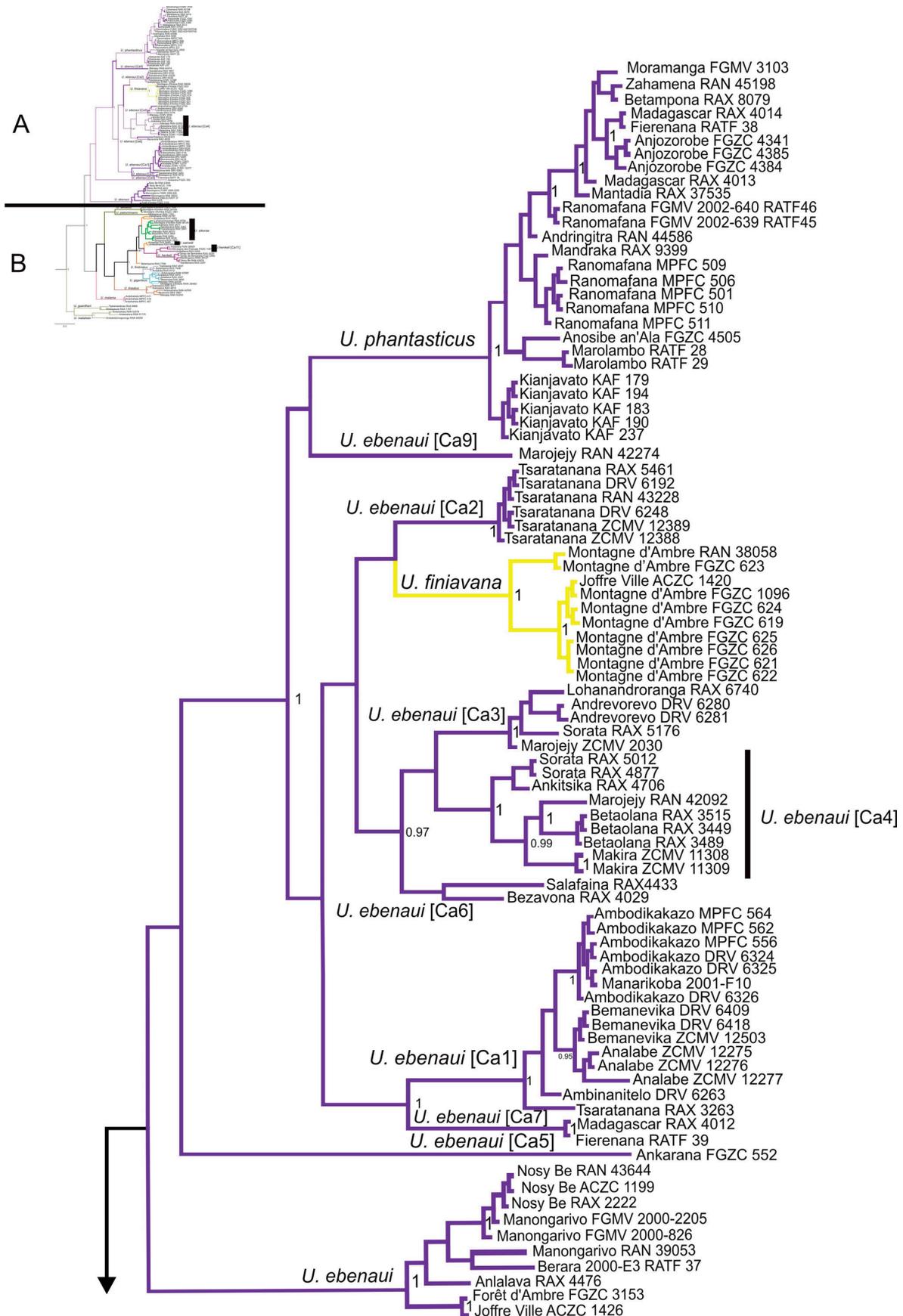
Specimens of small-sized *Uroplatus* from Zahamena sampled by ourselves were genetically divergent and are here considered as the candidate species *U. phantasticus* [Ca10] (see below). However, sequences from this locality by RAXWORTHY et al. (2008) clearly are placed within *U. phantasticus*, suggesting that these two taxa might occur sympatrically in this area.

Uroplatus malama NUSBAUM & RAXWORTHY, 1995

This species was described by NUSBAUM & RAXWORTHY (1995) from Ampamakiesiny, a site in the extreme South East of Madagascar. It is the largest species of the *U. ebenau* group, with a maximum SVL of up to 77.5 mm. The name *malama*, which means "smooth", refers to its appearance, lacking dermal spines on the head, neck and limbs, which characterize all other species of the group. This species is recognizable by its long (up to 56.1 mm) and wide (up to 18.4 mm) tail of strongly serrated shape in males (Fig. 7). Phylogenetically, it appears to represent the most basal species in the *U. ebenau* group (RATSOAVINA et al. 2011), and in the 12S tree, it is even placed apart from the group, without significant support. Clearly, the phylogenetic position of this species can be resolved only by using a comprehensive multigene data set.

Table 2. Summary of preliminary morphometric data, external characters and geographical range of species and candidate species of the *U. ebenau* group, with information merged for male and female adult specimens (juveniles are excluded). Data are preliminary, and details will be reported in forthcoming revisions.

Morphological characters													
Species and candidate species	Tail length (mm)			Tail width (mm)			SVL (mm)			Geographical distribution			
	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Oral mucosa pigmentation	Altitudinal range	List of localities	Specimens examined
<i>U. ebenau</i>	15.8	23	12	3.4	2.3	4.2	53.4	63	45	Black	up to 751 m (Manongarivo)	Northwestern range from probably Tsingy de Bemaraha through Montagne d'Ambre	10
<i>U. phantasticus</i>	41.6	46	38	10.9	12	9.6	61.2	76	52	Black	500 (Tsitola/ Kianjavato) – 1350 m	East (Betampona) and Southeast	9
<i>U. malama</i>	49.1	56	44	17	18	16	72.8	78	67	Black	600–1135 m (Befotaka-Midongy)	Andohahela, Befotaka-Midongy, Kalambatritra. Ivorona and Farafara	5
<i>U. finjavana</i>	30.4	35	23	6.7	7.6	5.6	58.1	65	52	White	800–1400 m	Montagne d'Ambre	12
CCS <i>U. ebenau</i> [Ca1]	17	23	11	4.8	6.7	3.6	65.5	71	56	White	1300–1550 m (Bemanevika)	Bemanevika, Analabe, Ambodikakazo, Ambinanitelo and Manarikoba	16
CCS <i>U. ebenau</i> [Ca2]	22.9	25	21	3.7	6.1	2.3	59.9	67	53	Black	2000–2200 m	Tsaratana (2000–2200 m)	7
CCS <i>U. ebenau</i> [Ca3]	19.4	21	18	4.6	5.2	3.8	61.1	64	57	Black	< 1000 m	Marojejy above 1506 m, Sorata, Lohanandroranga and Andrevorevo	3
CCS <i>U. ebenau</i> [Ca4] Makira	26.4	31	22	7.4	8.2	6.6	62.7	72	45	White	1000–1800 m	Sorata, Ankitsika, Marojejy and Betaolana (RAXWORTHY et al. 2008), Anjanharibe-Sud (RATSOAVINA et al. 2011), Marotondrano and Makira	4
UCS <i>U. ebenau</i> [Ca5]	Similar to <i>U. ebenau</i>			Similar to <i>U. ebenau</i>			Similar to <i>U. ebenau</i>			Black	80–200 m	Ankarana	–
UCS <i>U. ebenau</i> [Ca6]	not available			not available			not available			not known		Salafaina and Bezavona	–
CCS <i>U. ebenau</i> [Ca7]	20	25	18	3.8	4.3	3.5	66.5	79	56	White	900–1200 m	Fierenana	4
UCS <i>U. phantasticus</i> [Ca8]	Similar to <i>U. phantasticus</i>			Similar to <i>U. phantasticus</i>			Similar to <i>U. phantasticus</i>			not known	1550 m	Ambohitantely	–
UCS <i>U. ebenau</i> [Ca9]	not available			not available			not available			not known	1600 m	Marojejy	–
UCS <i>U. phantasticus</i> [Ca10]	Similar to <i>U. phantasticus</i>			Similar to <i>U. phantasticus</i>			Similar to <i>U. phantasticus</i>			Black		Zahamena	–



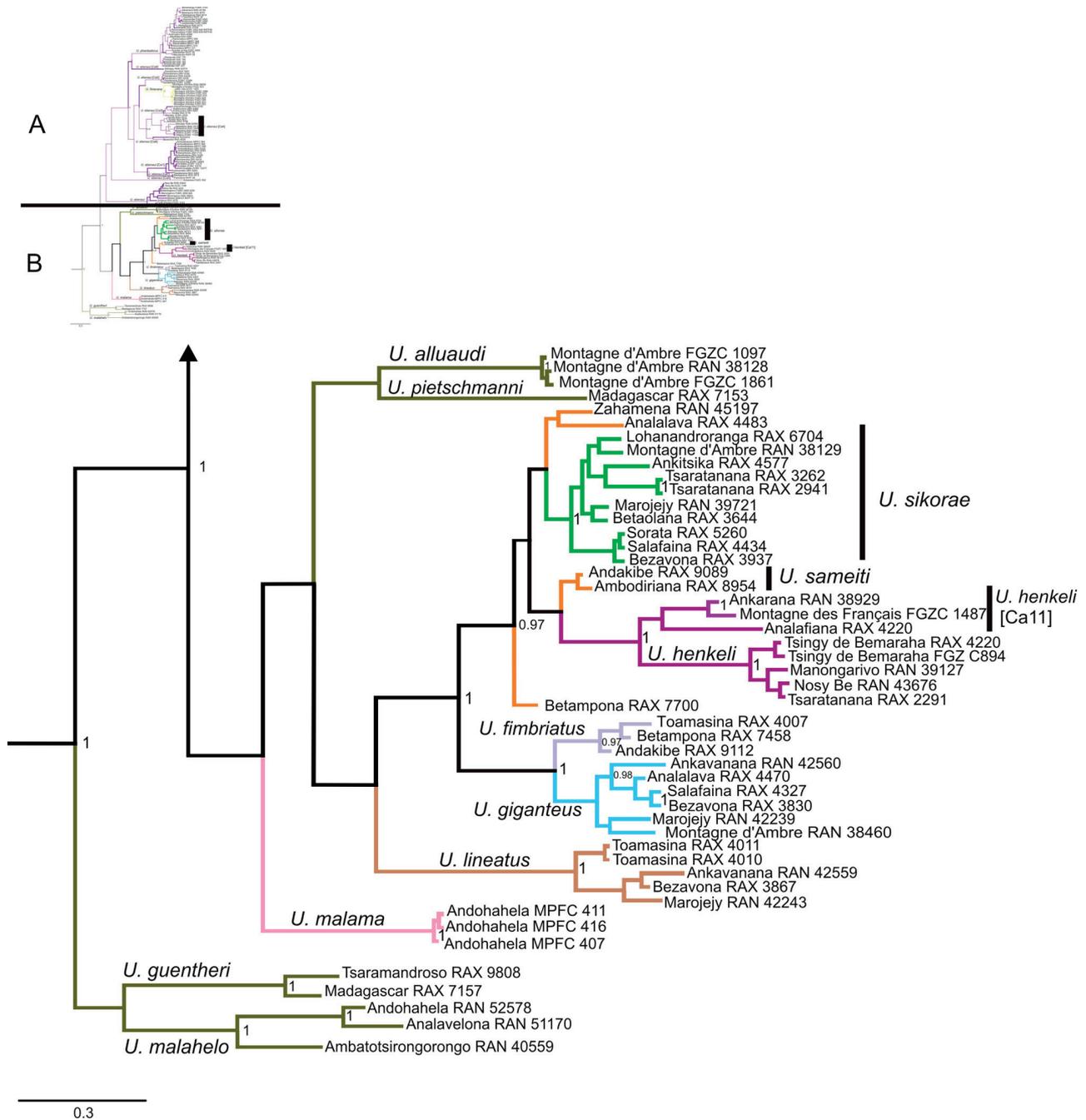


Figure 1a and 1b. Phylogenetic tree (50% majority-rule consensus with all compatible bifurcations shown) from a Bayesian analysis of DNA sequences of a fragment of the mitochondrial 12S rRNA gene of *Uroplatus* species. Values at nodes indicate posterior probabilities (PP) > 0.95. Besides sequences determined in this study, the analysis used sequences available from previous works retrieved from GenBank. Species are partially colour-coded.

The lowest ND₄ UPD of *U. malama* to nominal species is to *U. phantasticus* with 28.8%, followed by *U. ebenau* with 31.9%, and with the largest distance to *U. finiavana* with 35.8%.

Besides its type locality (Ampamakiesiny), the species has been reported from various sites in the South East of Madagascar. Molecular data are only available from two

sites (Befotaka/Midongy and Beampingaratra). However, because this species is rather easily recognized by its large tail, we also included in the map the other known records for it, i.e., Kalambatritra (ANDREONE & RANDRIANIRINA 2007), National Park of Andohahela, the type locality Ampamakiesiny, and two sites reported during the IUCN Red List assessment, Ivorona and Farafara. Among the species

in the *U. ebenau* group, *U. malama* is the only species restricted to the South East region of Madagascar. The locality Ivohibe reported by RASELIMANANA (1999) needs confirmation, because both *U. phantasticus* (close to the southernmost reliable locality, Andringitra) and *U. malama* (northernmost known locality: Befotaka/Midongy) might occur at this site.

Confirmed candidate species in the
U. ebenau species group

Uroplatus ebenau [Ca1 JN038123]

This form has previously been referred to as “*Uroplatus* sp. 1” by RATSOAVINA et al. (2011) and “*Uroplatus* sp. F” by RAXWORTHY et al. (2008). Morphologically, it shares several similarities with *U. finiavana*, such as the unpigmented oral mucosa and the relatively longer and wider tail compared to nominal *U. ebenau*.

According to our ND4 molecular data, *U. ebenau* [Ca1] has divergences of 24.4%, 31.5% and 33.4% UPD to *U. phantasticus*, *U. finiavana* and *U. ebenau*, respectively. Phylogenetically, it appears to be sister to *U. phantasticus* [Ca8] from Ambohitantely. The UDP for ND4 is 18.7% from its sister taxon.

In the 12S tree, *U. phantasticus* [Ca8] is not represented, and *U. ebenau* [Ca1] is placed sister to *U. ebenau* [Ca7] from Fierenana with a recorded UPD of 10.7%, which is also the lowest value.

For the COB tree, only one sample of *U. ebenau* [Ca1] from Manarikoba is available and it forms the sister group to *U. phantasticus* populations, with an UPD value of 27.8%, because *U. phantasticus* [Ca8] and *U. ebenau* [Ca7] are not represented.

A morphological comparison of *U. ebenau* [Ca1] and the nominal species in the *U. ebenau* group indicates a shorter and narrower tail as compared to *U. finiavana* (tail length 17 mm versus 30.4 mm; tail width 4.8 mm versus 6.7 mm in *U. finiavana*; Table 2). The non-pigmented oral mucosa is an evident character distinguishing this candidate species from the nominal *U. ebenau* and the candidate species *U. ebenau* [Ca3].

The combined evidence from diagnostic morphological characters cited above and genetic UPD values that are largely beyond the threshold for the formally named species, characterize this lineage as being distinct from *U. ebenau*, *U. finiavana*, *U. phantasticus* as well as related candidate species and thus warrant its categorisation as a CCS. We have used the name *Uroplatus ebenau* [Ca1 JN038123] from the first voucher’s GenBank accession number cited by RATSOAVINA et al. (2011).

All localities (Fig. 12; Table S5) are above 1,200 but below 1,700 m a.s.l. and located on the western slope of the Tsaratanana Massif except for Ambinanitelo, which is situated somewhat closer to the southern slope. These sites are characterized by similar climate and forest type, i.e., tropical humid forest.

Uroplatus ebenau [Ca2 JN038124]

This candidate species has previously been called “*Uroplatus* sp. E” by RAXWORTHY et al. (2008). It has so far been recorded only from the Tsaratanana Massif. This candidate species is morphologically similar to *U. ebenau*, with its pigmented oral mucosa and short tail, but with the tail being slightly less wide and having a spear-like shape. This CCS occurs at higher altitudes in montane forest around 2,000–2,200 m a.s.l. and thus is ecologically strongly differentiated from the lowland species, *U. ebenau*.

In terms of genetic distances for the ND4 gene, this CCS is divergent from the nominal species *U. ebenau* by a UPD of 32.3%, from *U. phantasticus* by 25.3%, from *U. finiavana* by 28.5%, and from *U. malama* by 29.7%. The lowest distance value to other candidate species is 24.6% to *U. ebenau* [Ca3].

In the 12S tree, the species is the sister group of *U. finiavana* with the lowest UPD value of 12.1%. Another candidate species, *U. ebenau* [Ca4], also shows a low UPD value of 12.4%. In the COB tree, the lowest UPD value is recorded between *U. ebenau* [Ca2] and *U. ebenau* [Ca6] from Salafaina.

The phylogenetic analyses based on 12S, ND4 and COB all agree in placing this CCS far from *U. ebenau* with high PP support. We classify *U. ebenau* [Ca2] as a distinct CCS, because of its morphological traits, namely the slightly larger SVL compared to *U. ebenau* (60 mm versus 53 mm in *U. ebenau*), a narrower tail compared to *U. finiavana* (3.7 versus 6.7 mm in *U. finiavana*), and a shorter tail compared to *U. phantasticus* and *U. malama* (half the length in *U. ebenau* [Ca2], with 23 mm versus 44–49 mm). Morphological differences to *U. ebenau* [Ca3], which is less strongly differentiated genetically, include a smoother body with less pronounced spine-like dermal extensions on the head, and a narrower tail in *U. ebenau* [Ca2]. Since this candidate species shows morphological affinities to *U. ebenau*, we have named it *U. ebenau* [Ca2 JN038124], with the respective GenBank accession number referring to a voucher specimen previously cited by RATSOAVINA et al. (2011).

Based on the various sequenced samples of *Uroplatus* from the Tsaratanana massif and surroundings, this CCS seems to be rather restricted to a certain habitat and was only found in one area of high altitude in the massif. No sympatry with other *Uroplatus* spp. has been recorded so far.

Uroplatus ebenau [Ca3 JN038126]

This candidate species has been called “*Uroplatus* sp. D” by RAXWORTHY et al. (2008). It has been recorded from localities in the eastern parts of the mountains of northern Madagascar (from Marojejy to Andrevorevo). Morphologically, *U. ebenau* [Ca3] is intermediate between *U. finiavana* and *U. ebenau*. This form resembles *U. ebenau* in its pigmented oral mucosa and can mainly be distinguished from that species by its rather long tail (19.4 mm versus 15.8 mm in *U. ebenau*) and slightly larger SVL (61 mm compared to 53 mm in *U. ebenau*). Compared to *U. finiavana*, the tail is

Diversity and distribution of the genus *Uroplatus*

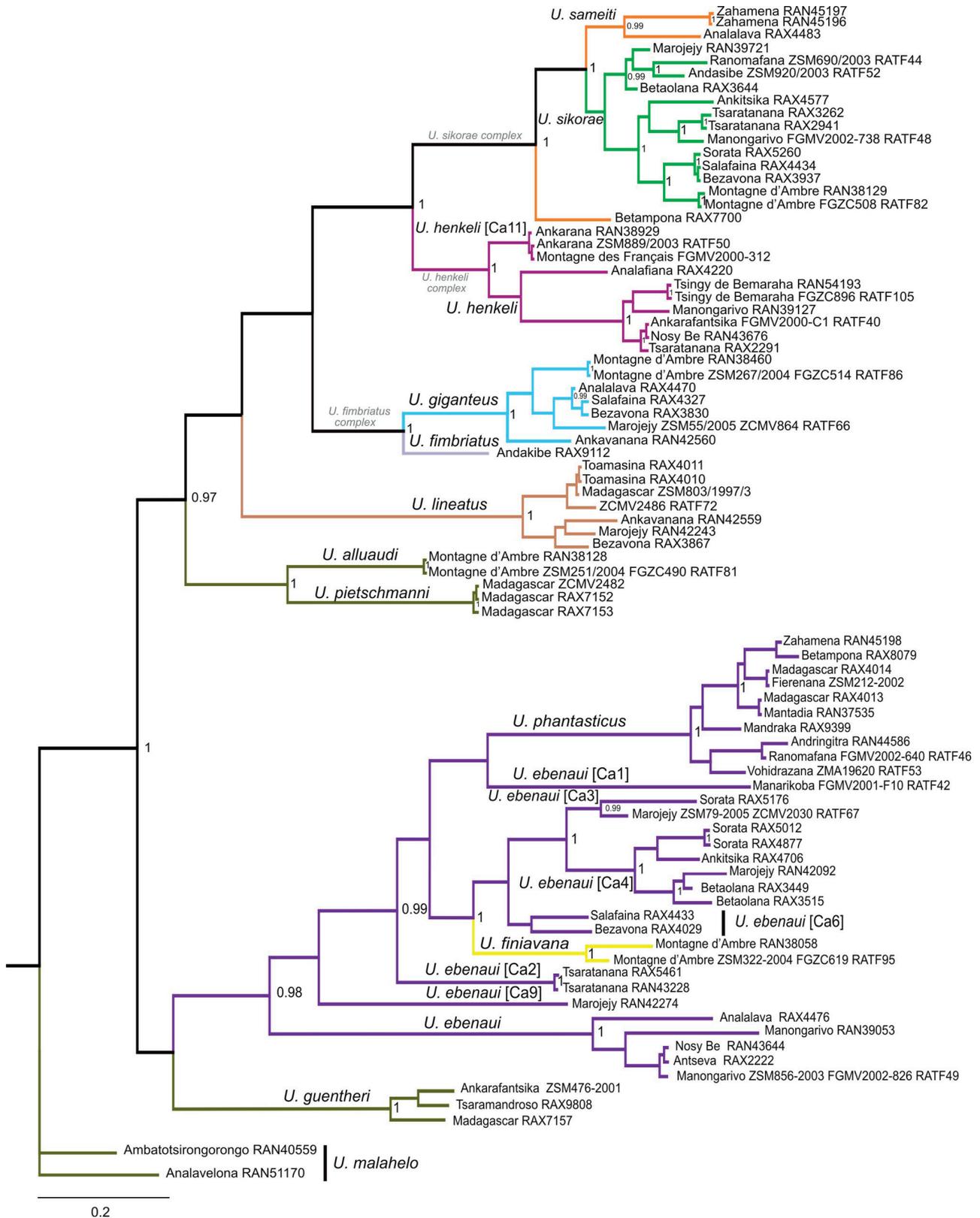


Figure 2. Phylogenetic tree (50% majority-rule consensus with all compatible bifurcations shown) from a Bayesian analysis of DNA sequences of a fragment of the mitochondrial cytochrome *b* (COB) gene of *Uroplatus* species. Values at nodes indicate posterior probabilities, PP > 0.95. Most of the sequences shown are from GREENBAUM et al. (2007) and RAXWORTHY et al. (2008).



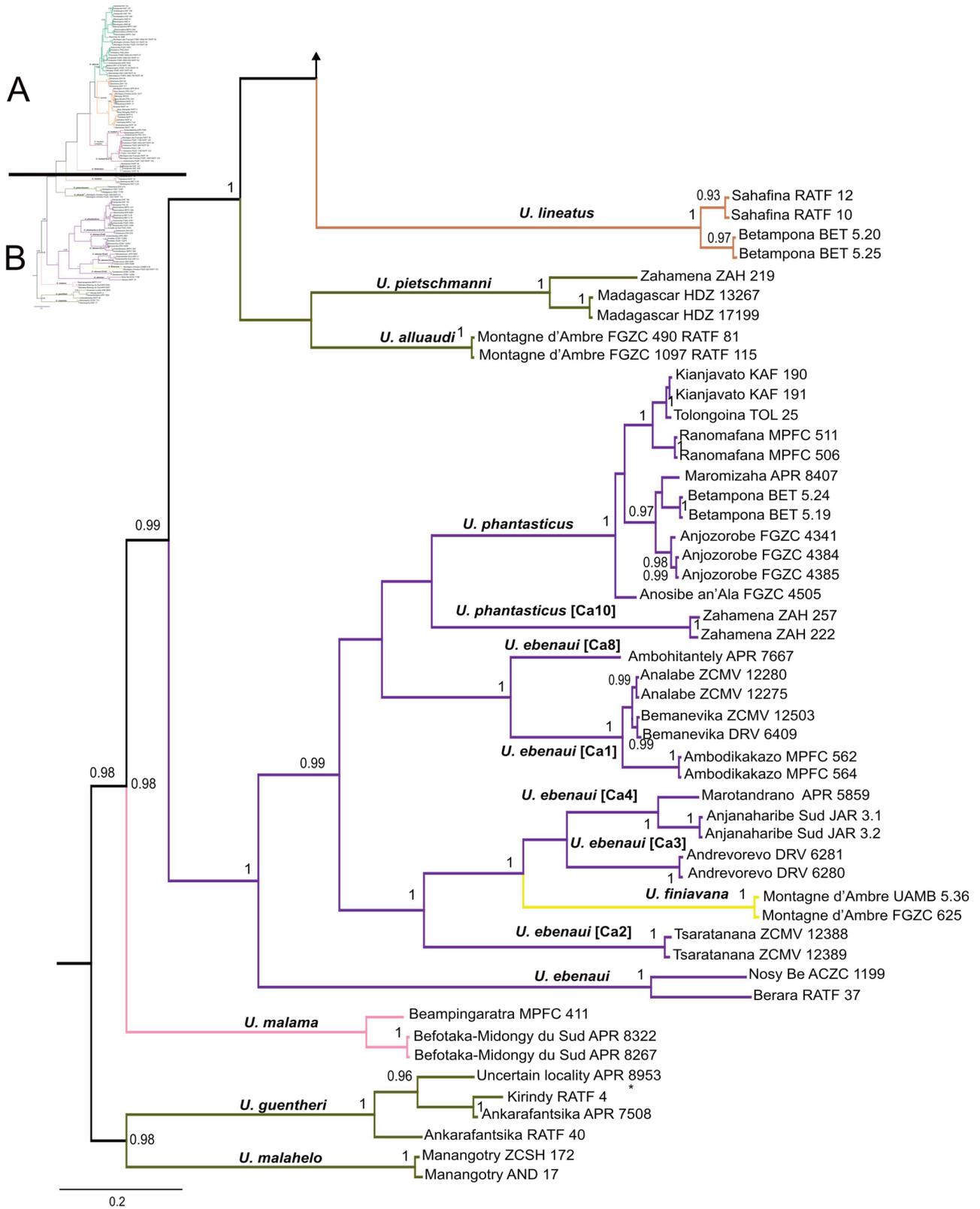


Figure 3a and 3b. Bayesian phylogenetic tree (50% majority-rule consensus with all compatible bifurcations shown) based on DNA sequences of a fragment of the mitochondrial ND4 gene of *Uroplatus* species. Values at nodes indicate posterior probabilities (PP) > 0.95. Samples marked with an asterisk are in need of confirmation of either the locality or sequence.

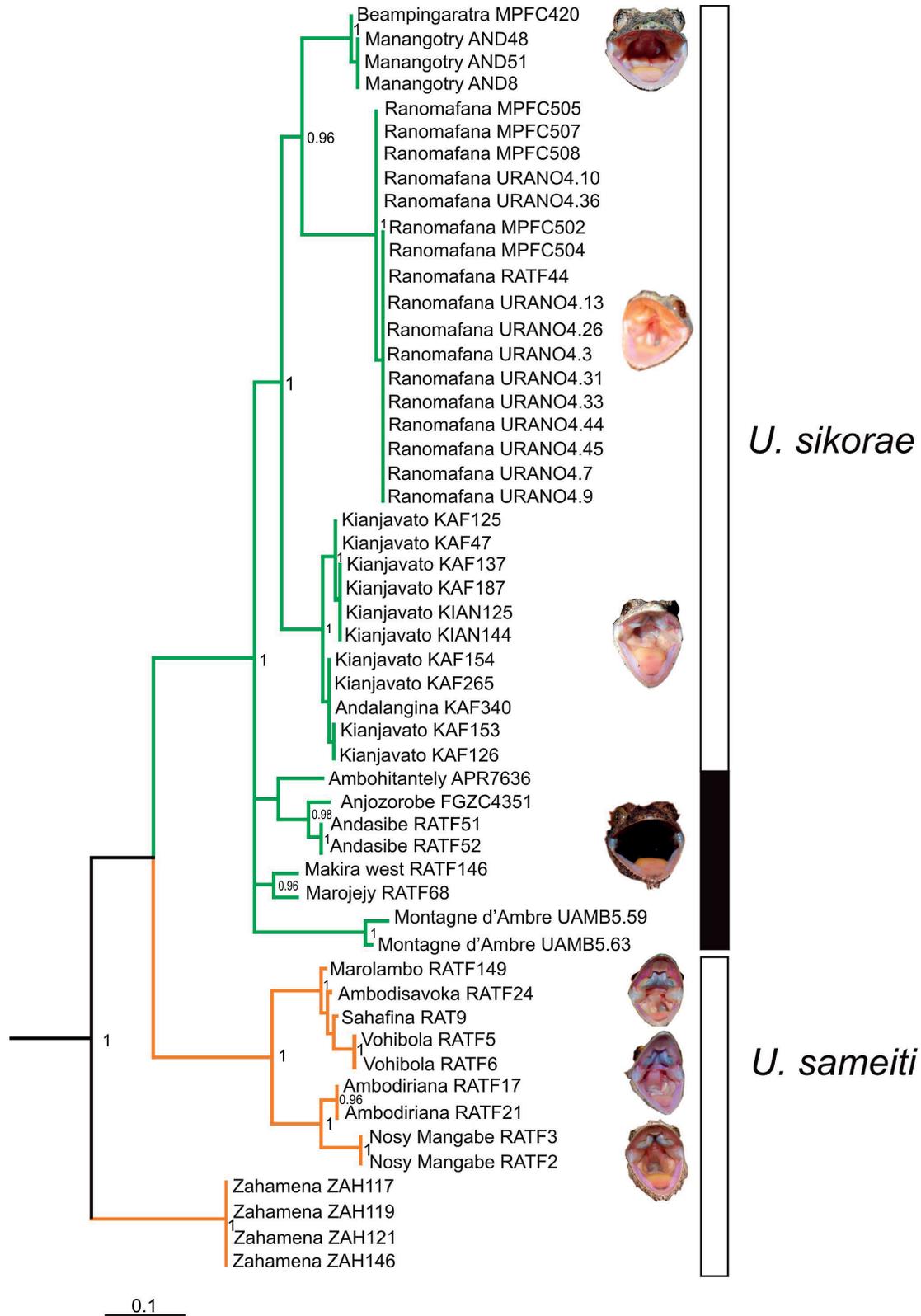


Figure 4. Bayesian phylogenetic tree (50% majority-rule consensus with all compatible bifurcations shown) from a 505 bp fragment of the mitochondrial ND4 gene of samples of the *Uroplatus sikorae* complex. The three major lineages are colour-coded; pictures of the oral mucosa are shown next to the population in which they were observed. Vertical bars indicate the colouration of the oral cavity, left empty for populations with an unpigmented oral mucosa and filled with black for a pigmented oral mucosa.

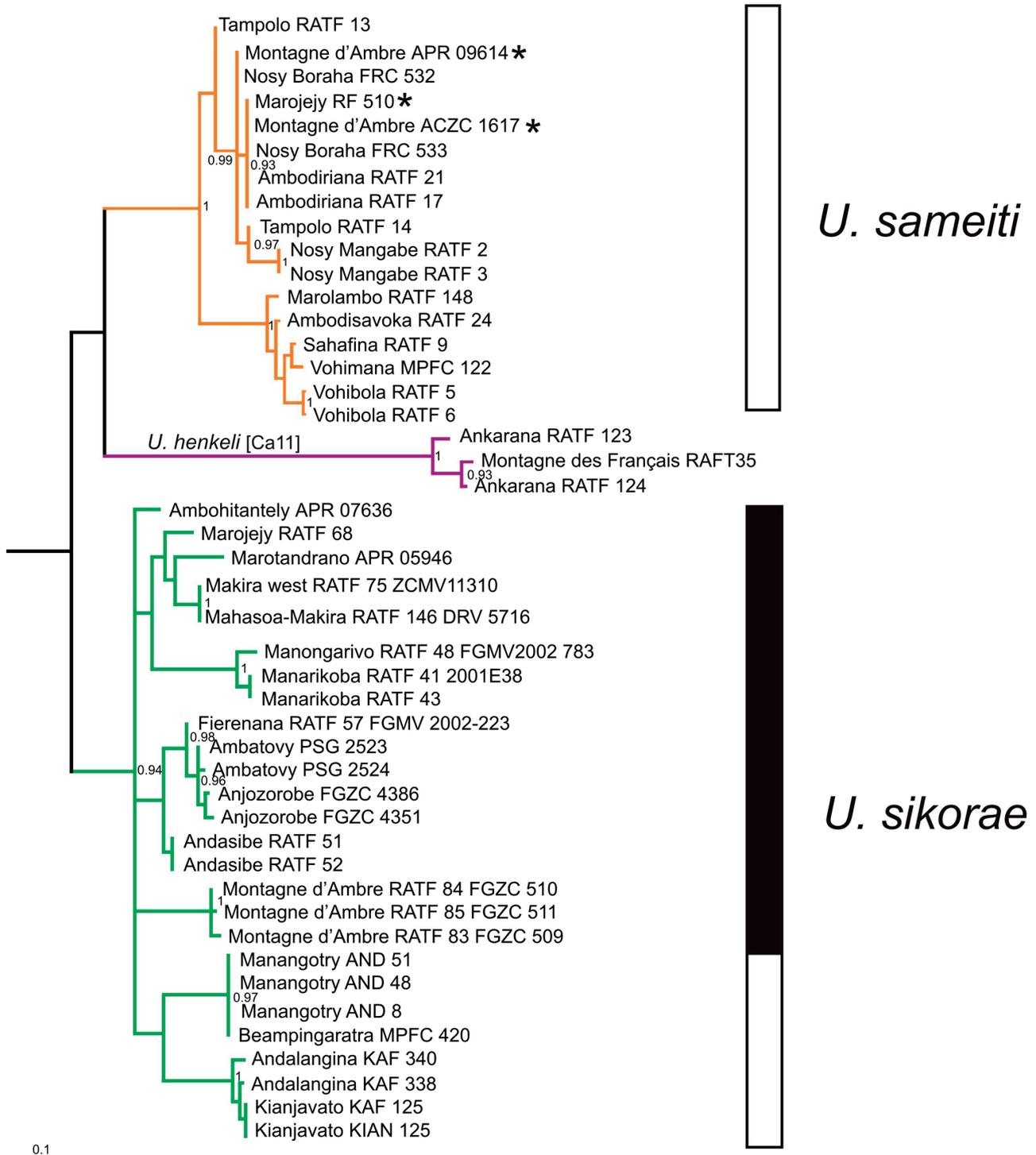


Figure 5. Bayesian phylogenetic tree (50% majority-rule consensus with all compatible bifurcations shown) from a part of the mitochondrial ND4 gene of samples of the *Uroplatus sikorae* complex. The analysis was performed for a reduced sequence length of 278 bp and a maximum number of samples available for this short fragment, in order to include the only two available sequences of *U. sameiti* from its type locality Nosy Boraha (= Sainte Marie). Vertical bars indicate the colouration of the oral cavity, left empty for populations with an unpigmented oral mucosa and filled with black for a pigmented oral mucosa. Sequences of samples marked with an asterisk are in need of confirmation.

shorter and the oral mucosa is pigmented. All three gene trees (ND₄, 12S and COB) are congruent in that this form is sister to *U. ebenau* [Ca4], another candidate species from an adjacent area in the North East of Madagascar (see below). Morphological comparison to its sister taxon indicates differences in tail length (19.4 mm versus 26.4 mm) and the pigmentation of the oral mucosa.

Based on the ND₄ gene, the UPD of this candidate species to nominal species in the *U. ebenau* group is 33.0% to *U. ebenau*, 24.8% to *U. phantasticus*, and 24.0% to *U. finiavana*. The lowest UPD value recorded in comparison to another candidate species is 17.6% to *U. ebenau* [Ca4].

In the 12S rRNA gene, the UPD values to the formally named species of the *U. ebenau* group are 20.4% for *U. ebenau*, 14.3% for *U. finiavana*, and 18.2% for *U. malama*. Compared to candidate species, the lowest UPD value corresponds to 9.7% for *U. ebenau* [Ca4].

In the COB distance data matrix, UPD values are 27.5% to *U. ebenau*, 18.5% to *U. finiavana*, 23.2% to *U. phantasticus*, and 13.1% to *U. ebenau* [Ca4].

RASELIMANANA et al. (2000) have reported the presence of *U. ebenau* from the eastern slope of the Marojejy massif, which possibly could refer to this candidate species. A further record of this CCS is probably the one by RAKOTOMALALA & RASELIMANANA (2003) from the western slope of Marojejy (as *U. ebenau*). These authors have mentioned the presence of two forms in this area, one of which (probably corresponding to *U. ebenau* [Ca3]) would occupy a broader altitudinal range, starting from 1,175 m a.s.l. According to our data, this candidate species occurs up to 1,576 m a.s.l. in Marojejy and 1,700 m a.s.l. in Andrevo-revo. One of the specimens listed as *U. ebenau* in RASELIMANANA et al. (2000) was caught at more than 1,875 m a.s.l., above the tree line in a isolated scrub in the otherwise open grassland along the trail to the summit.

Combining the above information, the high UPD (above the threshold) as compared to all described species, and the fact that this candidate species is not phylogenetically closely related to the morphologically most similar species, *U. ebenau*, support our classification as CCS.

This form has been recorded from various sites in northern and northeastern Madagascar at relatively high altitudes (ca. 1300–1800 m).

Uroplatus ebenau [Ca4] N038128

RAXWORTHY et al. (2008), based on molecular data, defined a candidate species, “*Uroplatus* sp. A”, in which they included individuals from Sorata, Ankitsika, Marojejy and Betaolana. RATSOAVINA et al. (2011) sequenced specimens from Anjanaharibe-Sud, and due to their high genetic divergence defined this lineage as UCS under the name “*Uroplatus* sp. 4”. Unfortunately, the Anjanaharibe sample was sequenced only for genes that are different from those used by RAXWORTHY et al. (2008). However, we here preliminarily group as *U. ebenau* [Ca4] all those small-sized *Uroplatus* specimens that cluster together with *U. ebenau* [Ca3] and represent its sister lineage in most trees. We are

aware that it is uncertain at this stage whether all these populations form a monophyletic group (they do not in the tree based on 12S rRNA), and the substantial genetic variation detected within this cluster renders it possible that it is actually a composite of divergent lineages.

The site Anjanaharibe-Sud has previously been mentioned by GLAW & VENCES (2007) and a survey by RAXWORTHY et al. (1998) recorded two different forms of small-sized *Uroplatus*, named *Uroplatus ebenau* and *U. cf. ebenau* in their biological assessment of the Marojejy-Betaolana-Anjanaharibe-Sud corridor. In their observations, the second type of these forms was restricted to Anjanaharibe-Sud and occurred around 1,200 m a.s.l. According to the 12S rRNA tree, the population from the western slope of the Makira massif also falls within *U. ebenau* [Ca4].

Morphological observations based on the Makira specimens indicate similarities to *U. finiavana* with respect to the non-pigmented oral mucosa and tail length (with 26.4 mm versus 30.4 mm in *U. finiavana*), but differences are found in the average SVL, which is slightly greater (62.7 mm versus 58.1 mm in *U. finiavana*) in the few specimens of the candidate species available to us (n = 4). Compared to *U. malama* and *U. phantasticus*, the specimens from the Makira population have a shorter tail and smaller SVL. Differences to *U. ebenau* are the oral mucosa pigmentation and the longer tail (26.1 mm versus 15.4 mm in *U. ebenau*). Compared to candidate species *U. ebenau* [Ca3], which is the sister taxon, morphological differences are found in what appears to be a wider and longer tail in *U. ebenau* [Ca4], with 7.4 and 26.4 mm, compared to *U. ebenau* [Ca3] with 4.6 and 19.4 mm.

For the ND₄ gene, the lowest UPD from nominal species of the *U. ebenau* group is found in *U. finiavana* with a distance value of 26.7%. The sister taxon *U. ebenau* [Ca3] is genetically divergent with an UPD value of 17.6%.

For the 12S gene, genetic distances to named species are as follows: 21.2% to *U. ebenau*, 15.1% to *U. phantasticus*, 12.4% to *U. finiavana*, and 19.5% to *U. malama*, while UPD is 9.7% to its sister taxon *U. ebenau* [Ca3]. In the COB data tree, the UPD value between *U. ebenau* [Ca4] and its sister taxon is 13.1%.

Combining information from UPD and the morphological distinctiveness compared to nominal and candidate species quoted above, even if only available for the population from Makira, we propose a status of CCS for *U. ebenau* [Ca4]. However, this CCS is genetically heterogeneous and comprises several genetically quite strongly differentiated populations. For instance, the ND₄ UPD between samples from Marotandrano and Anjanaharibe-Sud is 8.0%. Therefore the Marotandrano population should be considered as DCL of *U. ebenau* [Ca4] and several other populations possibly as well. Yet, we will refrain from formalizing such definitions until more samples and additional information become available.

Combining the evidence from the various genes, although somewhat ambiguous, we consider this candidate species to occur at the following localities: Sorata, Ankitsi-

ka, Marojejy and Betaolana (RAXWORTHY et al. 2008), Anjanaharibe-Sud (RATSOAVINA et al. 2011), Marotandrano and Makira (this study). As far as is presently known, most of the records are from mid-altitude rainforests. Sorata is a forested corridor north of Anjanaharibe-Sud and Marojejy that expands from 970–1,300 m a.s.l. The Makira forests are included in a large protected area of the same name in northeastern Madagascar. Our localities are on the western slope of the Makira massif and part of a vast rainforest area at altitudes between 900 and 1,200 m a.s.l., with a herpetofaunal composition that includes many species typical of other mid-altitude rainforests in eastern Madagascar. The locality Tsararano that is tentatively assigned to this CCS (no molecular data available) is part of a mountain chain with altitudes ranging from 400–1,269 m a.s.l., south of the Andapa basin, between Anjanaharibe-Sud and Masoala.

Unconfirmed candidate species in the *Uroplatus ebenau* group

Uroplatus ebenau [JX205421]

Specimens from Ankarana National Park are morphologically reminiscent of *U. ebenau*, with great similarities in tail shape, the pigmentation of the oral mucosa, and SVL. On the other hand, the two lineages are very divergent genetically, and they do not form a clade in the single gene tree available (12S). However, in multi-gene analyses (unpublished), we have found indications that this lineage might in fact be the sister group of *U. ebenau*, and because of a general scarcity of specimens from this site and apparent lack of morphological differentiation, we here treat it as UCS rather than CCS.

Molecular distances in the 12S gene to nominal species of the *U. ebenau* group are 25.7% to *U. ebenau*, 21.9% to *U. malama*, 20.7% to *U. phantasticus*, and 23.5% to *U. finiavana*. The lowest differentiation is found in the candidate species *U. ebenau* [Ca6] from Salafaina and Bezavona (UPD 20.1%), which does not appear to be a close relative according to the respective phylogenetic tree, however (Fig. 1).

Ankarana is an isolated karst massif with rather dry forest and numerous endemic species. Only two tissue samples (FGZC 552 and RF 408, the sequence of the latter was not included), and only one of these supported by a voucher specimen (ZSM 288/2004), were available to us. The general habitat agrees with that of *U. ebenau*, which occurs in forest fragments both north and south of Ankarana. The earliest records of this population were provided by BLOXAM & BARLOW (1987) and HAWKINS et al. (1990). A photograph of two specimens from Ankarana is shown in BÖHME & HENKEL (1995).

Uroplatus ebenau [Ca6 EU596636]

RAXWORTHY et al. (2008) reported the existence of one form they named “*Uroplatus* sp. C” from Salafaina and Bezavona, which is here included as *Uroplatus ebenau* [Ca6]. Genetic data is available to us only from the COB and

12S rRNA genes. Phylograms from these two genes place this lineage in the basal position to the clade comprising *U. ebenau* [Ca3] and *U. ebenau* [Ca4]. However, only the 12S tree provided PP support for this placement. 12S divergences between this candidate species and formally named species of the *U. ebenau* group are as follows: 13.9% to *U. finiavana*, 12.7% to *U. phantasticus*, 19.4% to *U. ebenau*, and 19.8% to *U. malama*. The lowest UPD value recorded to other candidate species is 8.7% to *U. ebenau* [Ca4].

COB distances were smallest to *U. finiavana* with 15.4% among the nominal species and with 14.1% to *U. ebenau* [Ca3] from Marojejy among candidate species.

Since no relevant morphological information exists and this form appears to be rather closely related to other candidate species such as *U. ebenau* [Ca3] and [Ca4] (Fig. 1), we suggest classifying *U. ebenau* [Ca6] as an UCS until more data will become available to clarify its status.

The vegetation at Salafaina consists of dense rainforest, at 80–790 m a.s.l. This area holds special microclimates at different altitudes. For instance, the valley close to the Salafaina River is covered with dry vegetation, whereas the hills harbour mostly primary rainforest. Bezavona Classified Forest is located on the extreme western limits of Madagascar’s eastern forests, and forms part of the Marovoalavo plateau, which comprises a mountain chain with peaks at Bezavona (1,050 m a.s.l.) and Berangompanihy (1,080 m a.s.l.). The main vegetation type is low- and mid-altitude, dense, humid evergreen forest with a closed canopy of 20 to 30 m in height (LOWRY et al. 1997). This UCS therefore seems to be living in low- to mid-altitude rainforest.

Uroplatus ebenau [Ca7 JX205405]

This lineage has been named “*U. ebenau* [Ca7]” by RATSOAVINA et al. (2012) and was included as one of two lineages in “*Uroplatus* sp. F” by RAXWORTHY et al. (2008), i.e., “*U. sp. F(2)*”. Concatenated DNA sequences from 16S rRNA, 12S rRNA, COI and ND4 have shown that this form is located at the basal position of the clade comprising the species *U. phantasticus*, *U. finiavana*, and some candidate species of the *U. ebenau* group (RATSOAVINA et al. 2012). Morphological observations show similarities of this candidate species to *U. finiavana*, *Uroplatus ebenau* [Ca1], and *Uroplatus ebenau* [Ca4], in particular the unpigmented oral mucosa.

Arguments to define this lineage as UCS are morphological characters that distinguish it from *U. ebenau*, namely the unpigmented oral mucosa, and from *U. phantasticus*, *U. malama* and *U. finiavana*, namely the rather short tail (20 mm in the candidate species compared to 30 mm in *U. finiavana* and > 44 mm in *U. phantasticus* and 49 mm in *U. malama*). *Uroplatus ebenau* [Ca7] resembles *U. ebenau* [Ca1] by its unpigmented oral mucosa and short tail, and the two of them were grouped as sister groups by RAXWORTHY et al. (2008) as well as in our 12S tree (Fig. 1), but not by RATSOAVINA et al. (2012). Therefore, the status of this form remains uncertain, and despite its deep genetic divergence, it might be conspecific with *U. ebenau* [Ca1]. Its sympatry with *U. phantasticus* is confirmed for the Am-



Figure 6. Photos of live individuals of species and candidate species of the *Uroplatus ebenauui* group.

batovy forest (J. RAFANOMEZANTSOA, pers. comm.) and around Fierenana.

As suggested by 12S rRNA data, this form differs strongly from *U. ebenau* in molecular distance (UPD 21.7%). Distances between the two morphologically most similar species are 15.4% for *U. finivana* and 10.7% for *Uroplatus ebenau* [Ca1].

Considering molecular distance, morphological distinctiveness and the sympatry with *U. phantasticus*, but unclarified status relative to *U. ebenau* [Ca1], we classify the lineage *U. ebenau* [Ca7] as a UCS. The GenBank accession number for a COI sequence reported in RATSOAVINA et al. (2012) is JX205405.

This form is only known with molecular support from Fierenana. In addition, one individual without precise locality from RAXWORTHY et al. (2008), RAX4012, also clusters with this form. These authors have referred to this specimen as “*U. sp. F*”, corresponding to our *U. ebenau* [Ca1].

Uroplatus phantasticus [Ca8 APR 7667]

Our ND4 tree contains a clade including a single sample (APR 7667) from Ambohitantely, which with high support is revealed as being sister to *U. ebenau* [Ca1], a candidate species known from middle to high altitudes in the Tsaratanana area.

Based on the ND4 fragment, the specimen from Ambohitantely differs from its sister lineage by 16.2–18.6% UPD. In its appearance, this individual from Ambohitantely is morphologically intermediate between *U. ebenau* and *U. phantasticus*. As more data are lacking, we preliminarily classify this lineage as an UCS because it represents a highly supported lineage within other populations of CCS status, but we lack morphological details to separate this population from *U. ebenau* [Ca1].

Ambohitantely is located on the central plateau of Madagascar where the vegetation type is largely mid-alti-

tude to montane rainforest. This is one of the rare reserves of the central highlands, but it is comparatively small and highly fragmented (VALLAN 2002, LANGRAND & WILMÉ 2000). *Uroplatus phantasticus* [Ca8] has been recorded at a site with the GPS coordinates -18.17167, 47.28167, 1,550 m a.s.l.

Uroplatus ebenau [EU596671]

RAXWORTHY et al. (2008) classified one specimen from the Marojejy massif as “*Uroplatus sp. G*”. In the 12S tree, the sequence of this specimen is sister to *U. phantasticus*, albeit without support. We cannot exclude the possibility that this form might be identical with our *Uroplatus phantasticus* [Ca10] listed below (see discussion in this account), because no sequences from homologous gene fragments are available for these two lineages. RAXWORTHY et al. (1998) might have at least in part referred to this form in their inventory of the forests of Marojejy and Betaolana.

The 12S gene reveals UPD values of 22.6% to *U. ebenau*, 17.6% to *U. phantasticus*, 18.1% to *U. finivana*, and 20.3% to *U. malama*. The lowest UPD to candidate species is 14.6% to *U. ebenau* [Ca6] from Bezavona.

Since no morphological observations are available to us, we refer to this form as UCS until more data will become available to update its status.

Marojejy is one of Madagascar’s national parks repudiated by its high degree of endemism, and characterized by diverse vegetation types including montane scrub where this UCS was spotted. The voucher specimen used for the genetic study is RAN 42274 by RAXWORTHY et al. (2008), its approximate GPS coordinates are -14.44000, 49.73500, 1,600 m a.s.l. (near the summit).

Uroplatus phantasticus [Ca10 JX205393]

While the molecular data of RAXWORTHY et al. (2008) suggest that specimens assignable to *Uroplatus phantasticus* occur in the Zahamena reserve (sample RAN 45198 as in-

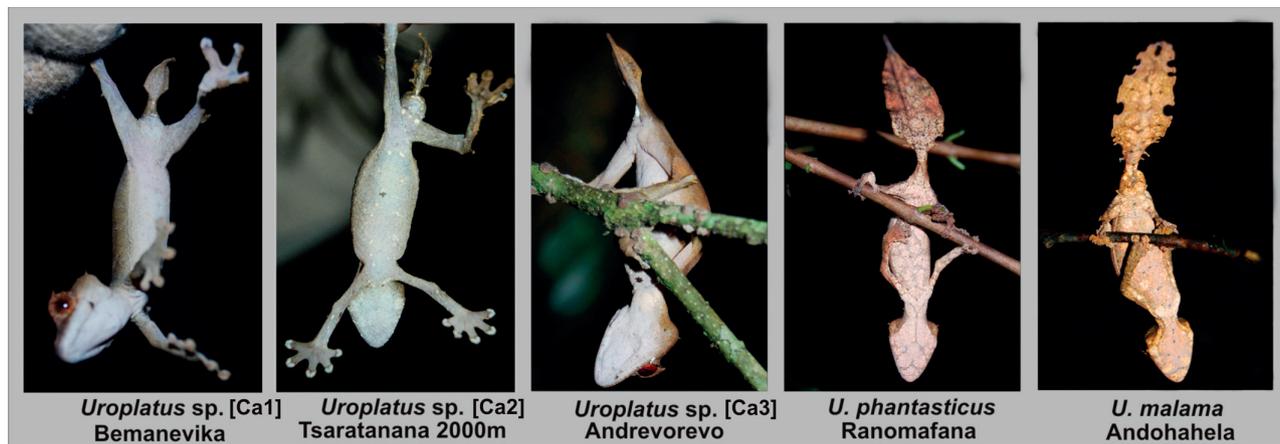


Figure 7. Ventral views of representatives of the *Uroplatus ebenau* group, showing the variation in shape, width and length of the tail. Note that males (with their typically serrated tail shape) are shown for *U. ebenau* [Ca2] and *U. malama*, whereas the other photos depict females (with a smoother tail shape).

cluded in the 12S and COB trees), our ND₄ data suggest the existence of another, deeply divergent mitochondrial lineage in this same reserve, which is sister to *U. phantasticus*. Unfortunately, no data from homologous DNA fragments are available for the two lineages that apparently occur in Zahamena, but it is evident that the ND₄ sequences cannot belong to the same lineage as the COB and 12S sequences. Already assessed as *U. phantasticus* [Ca10] by RATSOAVINA et al. (2012), this lineage is placed at the basal position of the clade comprising the nominal *U. phantasticus* populations from Anjozorobe and others incorporated in its distribution area.

The ND₄ genetic distance of what we here call the UCS *Uroplatus* sp. [Ca10] to *U. phantasticus* from Anjozorobe is 24.2%. Another uncertainty is whether this candidate species might be the same as *U. ebenau* [Ca9] as listed below. In the 12S tree, the latter is placed sister to *U. phantasticus* and the ND₄ data support the same placement for *U. phantasticus* [Ca10] in the respective tree. This again indicates that additional work is needed to solve the taxonomic conundrum of the lineages in the *U. ebenau* group. This lineage might also correspond to a form already mentioned by the rapid assessment of the corridor Zahamena-Mantadia by RABIBISOA et al. (2005) who refer to it as “*Uroplatus* sp. 2”, based on specimens encountered at mid-altitude areas around the study site Andriantantely. The sympatric occurrence of *U. phantasticus* [Ca10] with *U. phantasticus* at Zahamena as suggested by the data of the 12S rRNA tree compared to the ND₄ tree would suggest a status as CCS for the former, but we refrain from making this decision because of the general uncertainty surrounding this lineage and the complete lack of morphological data.

Zahamena forms one of the largest remaining blocks of rainforest on the east coast of Madagascar along with its southward corridor Ankeniheny. The area is very rich in terms of biodiversity; huge parts are still pristine due to difficult access. Tissue samples used in this study are ZAH 222 and ZAH 257 (RATSOAVINA et al. 2011), collected at -17.66666, 48.83333, 400–1,500 m a.s.l.

Uroplatus alluaudi group

The appearance of *U. alluaudi* and several similar species is less spectacular than that of other *Uroplatus* species. At first sight, they might be confused with other geckos since their head is not obviously triangular in shape and not distinctly set off from the body, although the flattened tail shape is typical of *Uroplatus*. In this work, based on molecular phylogenetic data (GREENBAUM et al. 2007, RAXWORTHY et al. 2008), we exclude the morphologically similar *U. malahelo* from this group, and distinguish two separate species groups as follows: on one hand, the *U. alluaudi* group, including *U. alluaudi* and *U. pietschmanni*, and the *U. guentheri* group, including *U. guentheri* and *U. malahelo*. Despite the morphological similarities of these species, previous phylogenetic work (e.g., GREENBAUM et al. 2007, RAXWORTHY et al. 2008) has shown that the four species

do not form a monophyletic group, while the two species pairs here included in either group usually are supported as clades. Consequently, the *U. alluaudi* group as defined here contains the two species *U. alluaudi* and *U. pietschmanni*.

Uroplatus alluaudi MOCQUARD, 1894

This species appears to be endemic to northern Madagascar. It is not easy to find at its type locality, Montagne d’Ambre National Park, although it can be locally moderately abundant at somewhat dry sites. All phylogenetic trees are congruent and place the species sister to *U. pietschmanni*, which is in agreement with the multi-gene analyses by GREENBAUM et al. (2007) and RAXWORTHY et al. (2008). Based on the ND₄ fragment, UPDs are 25.5% to *U. pietschmanni*, 26.8% to *U. malahelo*, and 28.2% to *U. guentheri*.

This species is encountered in mid-altitude humid forest; it is associated with patches of relatively dry vegetation in the Montagne d’Ambre (GLAW & VENCES 2007). We here also include in the map (Fig. 12) three localities not yet confirmed by molecular data: the humid forest of Binara in Daraina (RAKOTONDRAVONY 2006), Besariaka (ANDREONE & APREA 2006), and Marojejy (RAKOTOMALALA & RASELIMANANA 2003), all situated between 650 and 950 m a.s.l. (RAXWORTHY & NUSSBAUM 1994). The locality Besariaka is vouchered by the specimen MRSN R1630, caught in 1996. This locality represents the southern distribution limit of *U. alluaudi*, which is plausible as the forests of the western slopes of Marojejy around 810 m a.s.l. (RAKOTOMALALA & RASELIMANANA 2003) and Besariaka are connected by the corridor between Betaolana and Anjanaharibe-Sud. Molecular data are so far only available from samples collected at Montagne d’Ambre, and nothing is thus known about a possible genetic differentiation of the other populations.

Uroplatus pietschmanni BÖHLE & SCHÖNECKER, 2003

This gecko is morphologically unique and differs from other species of *Uroplatus* by its rough skin from which its common name derives: cork-bark leaf-tailed gecko. Originally described on the basis of this morphological peculiarity, the species is also genetically and probably ecologically differentiated, apparently inhabiting mainly the forest canopy.

Due to the morphological uniqueness of the species, we here list all of the known localities, even if not vouchered by genetic data. The type locality of *U. pietschmanni* is Fierenana, east of Amboasary Gara village, at around 1,041 m a.s.l. In Fierenana, huge patches of primary forest still exist, and part of this forest block is now included in a newly protected area, the Zahamena-Mantadia corridor. Few field records exist for the species and it was only in the beginning of the forest clearance at the Ambatovy mining site close to Moramanga that more individuals were collected (RASELIMANANA 2010). A conversation with an animal collector in Amboasary Gara (a village on the National Road 44, in 2009, by F. M. RATSOAVINA) revealed that this species is quite difficult to find and only occurs in intact forest where the canopy can be as much as 20 metres above the ground.

Uroplatus guentheri group

By the rationale given in the account of the preceding species group, the *U. guentheri* group comprises two species, *U. guentheri* and *U. malahelo*.

Uroplatus guentheri MOCQUARD, 1908

The holotype of this species was described by MOCQUARD (1908) from the imprecise type locality “Madagascar”, and it was only in 1970 that T. J. PAPENFUSS collected a second specimen at Ankarafantsika (RUSSELL & BAUER 1987). The species is well differentiated from all other *Uroplatus* both morphologically and genetically; its sister species is *U. malahelo* (RAXWORTHY et al. 2008).

From our ND4 data, UPD values recorded between *U. guentheri* populations (table not provided) range from

3.0 to 13.2%, with the highest UPDs between geographically distant populations such as Ankarafantsika and Kirindy.

As far as the COB gene is concerned, UPD values of 6.5–9.8% are recorded, with the highest value corresponding to a sample with no precise geographical location compared to the Ankarafantsika and Tsaramandroso populations.

Because the molecular data indicate that specimens from across the known range are always placed together in a clade, and the morphological identification of the species is not ambiguous, we consider all locality records (including the ones not vouchered by molecular data) as reliable. The species is mostly found in the North West and West of Madagascar in dry deciduous forest habitat. Recent information from a survey of the western region of Madagascar given by RAKOTONDRAVONY & GOODMAN (2011) indicates that this species is still encountered in some remnant for-

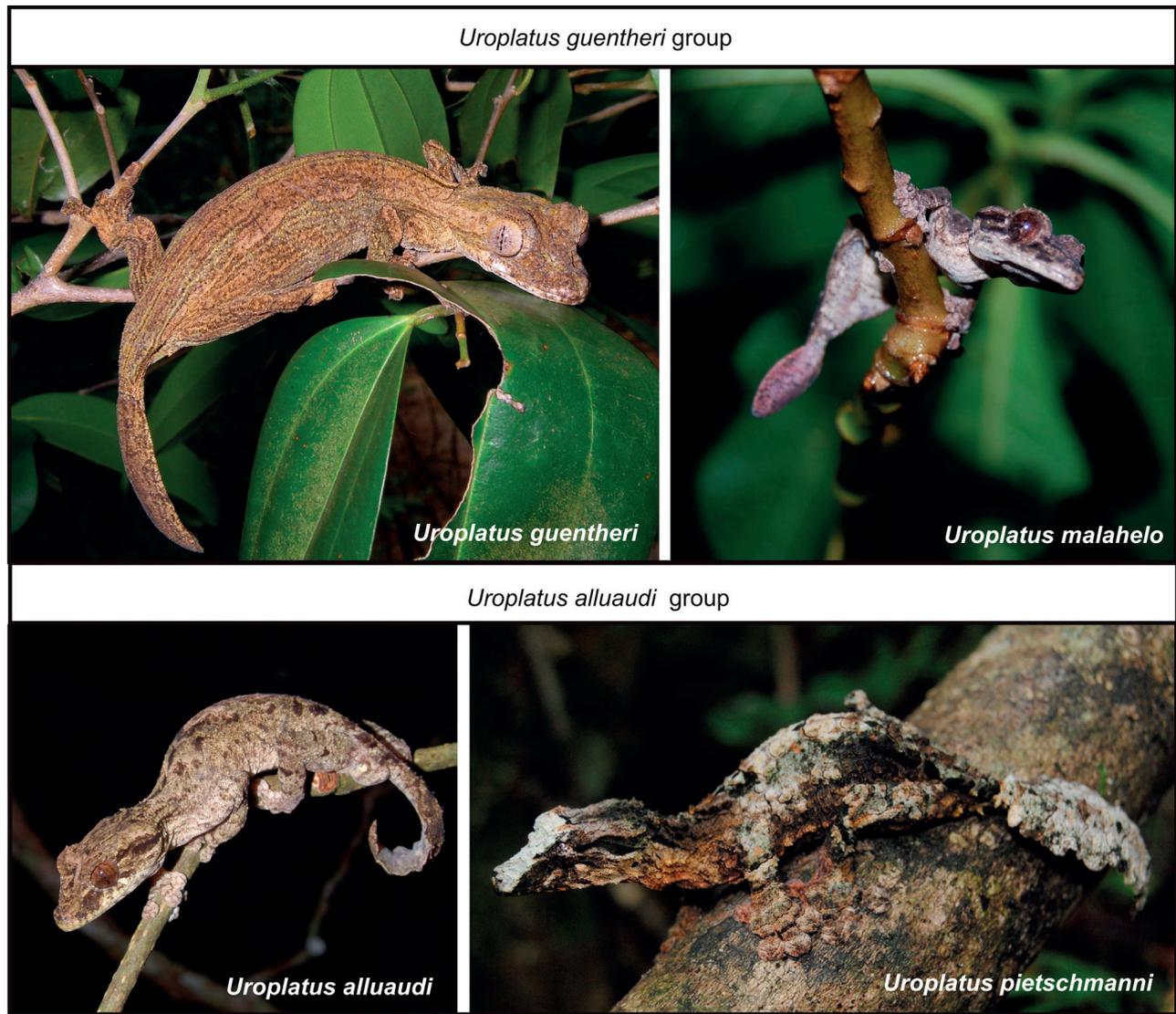


Figure 8. Photos of live representatives of the *Uroplatus guentheri* and *U. alluaudi* groups.

ests on the Kelifely plateau, between the Kirindy forest and Tsingy de Bemaraha.

Uroplatus malahelo NUSSBAUM & RAXWORTHY, 1994

The type locality of this species is a tiny forest patch in the South East of Madagascar, along the Anosy Chain (the forested part of the Ambatotsirongorongo Mountain). The future of this species was predicted to be “sad” in the original description, as indicated by its Malagasy name, “malahelo”, but thanks to several biological assessments in the area, more records have since been published. Originally described on the basis of morphological traits, subsequent molecular data supported the status of *U. malahelo* as an independent lineage. All data support its sister group relationship with *U. guentheri* (GREENBAUM et al. 2007, RAXWORTHY et al. 2008) and for the ND4 gene, the UPD between these two species is 26.0%.

The rapid decline of the forest in the southern part of Madagascar leaves the habitat of this species scattered. *Uroplatus malahelo* is not a common species. Until now, only a few individuals have been found, exclusively in primary forest at mainly low and middle altitudes. The localities Sakaraha and Kalambatritra still represent pristine forest and are now included in the protected area systems of Madagascar. The species reaches northward to Sakaraha and, according to specimens collected by A. RASELIMANANA and unpublished molecular data by K. TOLLEY and A. RASELIMANANA, the species is also present at Midongy du Sud. Our map incorporates all these localities, even if not vouchered by genetic data, because the species is rather easily identified by its morphology.

Although no morphological variation has so far been noted, our 12S and COB data suggest high genetic divergences between the population at the type locality Ambatotsirongorongo and those at Andohahela and Analavelona, although Andohahela is geographically closer to Ambatotsirongorongo. In the 12S data matrix, specimens from Ambatotsirongorongo were genetically divergent from the Andohahela and Analavelona populations by UPD values of 10.1 and 11.1%, respectively (table not included). Regarding their geographical distance, populations from Andohahela and Ambatotsirongorongo could be expected to differ by only small genetic distances, but this is not the case. However, given the small number of samples available, we cannot make reliable statements on the pattern of genetic structure among populations of this species for which more sampling effort and in-depth study are needed.

Uroplatus lineatus group

This group comprises only one species, which is morphologically rather unique and easily distinguishable from all other species of leaf-tailed geckos.

Uroplatus lineatus (DUMÉRIL & BIBRON, 1836)

This species inhabits lowland forests in eastern Madagascar. Morphologically, it constitutes a very distinctive tax-

on by its rather smooth appearance and peculiar yellow brownish body colouration and longitudinal stripes in females but usually light dots in males. Dermal fringes are missing in *U. lineatus*; however, the species has striking dermal spines above each eye. In the phylogenetic trees, its position is quite isolated, although it is congruently resolved as sister of the *U. fimbriatus* group.

Because of the unequivocal morphological characters of this species, we consider all published localities as reliable rather than only listing the sites vouchered by molecular data. Localities are listed in GLAW & VENCES (2007), GEHRING et al. (2010), and RASELIMANANA et al. (2000). The species can be encountered from sea level to 600 m a.s.l. The type locality is not precise. In their early systematic review, BAUER & RUSSELL (1989) examined one specimen from Lokobe, Nosy Be, but pointed out that this locality was doubtful. In our molecular data, we have representative populations from the North East of Madagascar, i.e., Ankavanana, Marojejy, Bezavona (included in the COB tree), and from the Northern Central East, i.e., Toamasina-Ivoloina, Betampona, Sahafina.

Some molecular differentiation of populations exists. In the ND4 sequences, the UPD between sequences from the nearby localities Sahafina and Betampona is 5% (table not provided).

In the 12S tree, a neat grouping into two clades is evident, one comprising populations from the North East and another one comprising populations from the Northern Central East. UPD between Ankavanana and Toamasina samples is 6%. This cluster is also supported by the COB tree, with a UPD of > 12%.

The type material of *U. lineatus* most likely originates from central eastern Madagascar (BAUER & RUSSELL 1989), and the uncorrected pairwise distance is quite substantial between the two main lineages, but no morphological differences have been noticed between these to date. This would support considering the North East populations as a UCS or DCL, but we refrain from such a step, awaiting more samples to become available to verify this genetic differentiation. There is no clear definition which populations would be included in either lineage, due to missing genetic data from many localities. We tentatively suggest to include Marojejy, Bezavona and Ankavanana in the North Eastern lineage.

Uroplatus fimbriatus group

This species group includes *U. fimbriatus*, *U. giganteus*, *U. sikorae*, *U. sameiti*, *U. henkeli* and one candidate species that is morphologically close to *U. henkeli* and named *U. henkeli* [Ca11]. The species included in this group are large-sized leaf-tailed geckos that can reach more than 30 cm in total length. They are characterized by dermal fringes along the lateral side of the body. The colouration is mostly a gradient of grey to black, but an almost completely white colouration can be displayed during daytime in the roosting place, for instance in *U. sameiti* from Vo-

hibola. In other individuals, a mimetic lichen-like colour pattern is observed, for instance in *U. sikorae* from Andasibe. Because of the morphological similarity among several of the species and candidate species in this complex, and the presence of deep genealogical lineages within what we consider constituting species, many misidentifications have occurred in past publications. Based on morphological similarity, three complexes can be distinguished in this group: the *U. fimbriatus* complex, including *U. fimbriatus* and *U. giganteus*; the *U. sikorae* complex, including *U. sikorae* and *U. sameiti*; and the *U. henkeli* complex, including *U. henkeli* and one candidate species *U. henkeli* [Ca11].

Uroplatus fimbriatus complex

This complex consists of two nominal species, *U. fimbriatus* from the east and *U. giganteus* distributed in northern and northeastern Madagascar. RAXWORTHY et al. (2008) confirmed the existence of two major clades, but did not accept the species status of *U. giganteus*, casting doubts on whether the population from the island Nosy Mangabe, the restricted type locality of *U. fimbriatus*, is referable to their eastern clade. We here provisionally follow GLAW et al. (2006) and GREENBAUM et al. (2007) who argued in favour of a separate species status of these specimens as *U. giganteus*. For a further discussion of this problem, see the species accounts below.

Uroplatus fimbriatus (SCHNEIDER, 1792)

This is historically the most widely known species of the genus *Uroplatus*, and it is among the largest species in the genus. It was originally described by SCHNEIDER (1792) although most subsequent authors considered the pub-

lication date as 1797. Remarkably, no other reptile species described by SCHNEIDER is dated as 1797 in the reptile database (UETZ & HOŠEK 2013), but a few other species (*Clemmys guttata*, *Hemidactylus platyurus*, *Platemys platycephala*) are dated as 1792 as well. KLUGE (1993) already suggested that 1792 was the correct publication date of *U. fimbriatus* and although we had no access to SCHNEIDER's (1792) work, all information available to us suggests that KLUGE (1993) is correct in this point. *Uroplatus fimbriatus* was described from the type locality "Madagascar" (ANGEL 1929), and is widespread all over eastern Madagascar. Due to the lack of precision of the type locality and some major problems with the holotype, BAUER & RUSSELL (1989) designated as neotype the specimen ZFMK 36503 from Nosy Mangabe and thereby restricted the type locality to this tiny offshore island in the North East of Madagascar. Most of the available records are from ancient literature and field reports.

The taxonomy of this species is in need of confirmation due to the absence of crucial sequences from the type locality Nosy Mangabe, which would allow a comparison with other populations from eastern and northern Madagascar in a multigene phylogeny. All of our molecular data from the three genes analysed suggest that there is a major subdivision into two lineages in the *U. fimbriatus* complex. We here regard the lineage containing samples from northeastern Madagascar as *U. giganteus* (see below) and the lineage with samples from Nosy Mangabe southwards as *U. fimbriatus*. In the dry forests of western Madagascar, large-sized *Uroplatus* occur, which can be mistaken for *U. fimbriatus* or *U. giganteus*, but they all belong to *U. henkeli* genetically, and therefore are not considered any further here or in the account of *U. giganteus*.



Figure 9. Photos of live *Uroplatus lineatus* and representatives of the *Uroplatus fimbriatus* complex.

Because the distinction of the *U. fimbriatus* complex from the species occurring sympatrically especially along Madagascar's east coast is straightforward, we consider all locality records (as summarized by GLAW & VENCES 2007) from the region south of Maroantsetra as valid even if not vouchered by molecular data. The locality Marojejy is here assigned to *U. giganteus*, and we cannot exclude that some of the northernmost sites listed here for *U. fimbriatus* might be assignable to *U. giganteus* instead.

The distribution records from Eminiminy, Vohipeno and Vondrozo by ANGEL (1942) are doubtful because this author did not distinguish *U. sikorae/U. sameiti* from *U. fimbriatus*. Numerous recent surveys in the Anosy Chain and the surrounding forest such as Ivohibe (RASELIMANANA 1999), Kalambatritra (ANDREONE & RANDRIANIRINA 2007), Midongy du Sud (BORA et al. 2007), and Andohahela (ANDREONE & RANDRIAMAHAZO 1997, NUSSBAUM et al. 1999, RAMANAMANJATO et al. 2002) did not yield records of *U. fimbriatus*.

Summarizing, *U. fimbriatus* appears to be mainly a species of low-altitude rainforest and littoral forest.

Uroplatus giganteus GLAW, KOSUCH, HENKEL, SOUND & BÖHME, 2006

Based on morphology, colouration, hemipenis structure, and a substantial genetic distance to *U. fimbriatus*, GLAW et al. (2006) described this form as a new species from Montagne d'Ambre, northern Madagascar, where specimens are particularly large-sized. The original description (GLAW et al. 2006) also relied on the differentiation in a fragment of the mitochondrial 16S rRNA gene, with 4.8% UPD in this gene between *U. giganteus* and *U. fimbriatus* from the type locality Nosy Mangabe to support the species description.

In the 12S data, the highest molecular divergence within the *U. fimbriatus* complex is the 7% UPD found between a *U. fimbriatus* sequence from Betampona versus *U. giganteus* from the type locality Montagne d'Ambre and from Analava, Salafaina, and Bezavona.

In the COB tree, the highest UPD value in the *U. fimbriatus* complex is between *U. fimbriatus* from Andakibe and *U. giganteus* from Marojejy, with an UPD of 17.6%. A strikingly high UPD value, 11.1%, is found between *U. giganteus* from the type locality Montagne d'Ambre and the population from Marojejy that was already noticed in the description of *U. giganteus*. Unfortunately, we have no representatives of the latter population in the ND4 tree.

The species occupies the mid-altitude rainforest of the Montagne d'Ambre National Park, and based on mtDNA data, is also found in some other localities in northeastern Madagascar. A more in-depth study that includes mitochondrial and nuclear DNA as well as morphology from more sites is needed for a better understanding of the variation of *U. giganteus*.

Uroplatus sikorae complex

Prior to 1989, it was disputed whether *U. sikorae* represents a species separate from *U. fimbriatus*. *Uroplatus sikorae* was described by BOETTGER (1913) on the basis of its smaller

size and some scalation features, but several subsequent authors did not consider these characters significant. The systematic revision of *Uroplatus* by BAUER & RUSSELL (1989) resurrected *U. sikorae* and considered it a distinct species based on morphological characters, i.e., differences in dermal flaps and colouration, and sympatric occurrence with *U. fimbriatus*. Subsequently, BÖHME & IBISCH (1990) found evidence for two subspecies: *U. sikorae sikorae* (type locality near Andrangoloaka) represented by the population near Périnet (same as Andasibe, close to Analamazaotra reserve) and other, mainly mid-altitude localities, and *U. sikorae sameiti*, with the type locality Nosy Boraha (or Sainte Marie) from mainly lowland localities. These two subspecies were subsequently elevated to species status based on their molecular differentiation by RAXWORTHY et al. (2008). The original study by BÖHME & IBISCH (1990) distinguished the two subspecies mainly based on one distinct character, i.e., the pigmentation of the oral mucosa: black in *U. sikorae* and unpigmented (pinkish in life) in *U. sameiti*.

The taxonomic situation in the *U. sikorae* complex is quite difficult, because on the one hand, there are numerous deep mitochondrial lineages and on the other, the main genetic subdivision does not correspond fully with the pigmentation of the oral mucosa, which is supposed to be a diagnostic character to distinguish the two species. The *U. sikorae* complex, based on our data and those previously published (GREENBAUM et al. 2007, RAXWORTHY et al. 2008) is clearly monophyletic. Our taxonomy largely follows the proposal by RAXWORTHY et al. (2008), in which two major subclades in the *U. sikorae* complex correspond to *U. sikorae* and *U. sameiti*.

Uroplatus sikorae BOETTGER, 1913

In our trees, mid-altitude samples represent the following localities: Andasibe, Fierenana, Ambatovy, Maromizaha and Anjozorobe. As far as assessed by us, specimens from these localities in their majority are characterized by a pigmented oral mucosa. Samples from most of the localities included in *U. sikorae* and separated by a relevant geographical distance are genetically strongly differentiated, which makes it difficult to define DCLs. In fact, the ND4 tree would indicate the presence of at least five DCLs (only loosely defined here) besides the one from the Andasibe region. The populations from the Southern Central East and South East form a highly supported clade based on ND4 and contain pink-mouthed populations that occur between Ranomafana and Andohahela, with a strong additional differentiation into at least three distinct deep lineages. In the North East, at least two deep lineages occur (from Montagne d'Ambre, and Marojejy, Manongarivo, Tsaratanana, and Makira, respectively), and as far as is known, these populations are black-mouthed. UPD among representative individuals in the ND4 sequences is, for instance, 13.2% between Ranomafana and Manongarivo.

Records of *U. sikorae* are mainly located in mid-altitude rainforest. In some cases, the records require confirmation, which is especially true for Montagne des Français even though it is vouchered by a ND4 sequence.

Uroplatus sameiti BÖHME & IBISCH, 1990

Originally described as a subspecies of *U. sikorae*, this species was elevated to species rank by RAXWORTHY et al. (2008). Mostly recorded from lowland rainforest, it is one of the most abundant and widespread species of the genus *Uroplatus*. We assign to this species those populations that in our trees are in the same major subclade of the *U. sikorae* complex as specimens from the type locality Nosy Boraha.

All of these have an unpigmented (pink) oral mucosa. UPD between *U. sameiti* and *U. sikorae* is approximately 6% for 12S sequences, and 15% for ND4 sequences. In addition, we also regard two remarkably divergent lineages (Figs. 1–5) from Zahamena and Betampona, respectively, as representing *Uroplatus sameiti*, because these two populations have only moderate UPD values to typical *U. sameiti* (see below), are nested in *U. sameiti* in the multigene tree



Figure 10. Photos of live representatives of the *Uroplatus sikorae* complex.

of RAXWORTHY et al. (2008), and their geographic distribution within the range of *U. sameiti* makes it unlikely that they represent distinct taxa.

The samples from Zahamena are placed as a separate deep subclade in the *U. sikorae* complex and supported by all phylogenetic trees (Figs. 1–5), but no data are available on a possible morphological differentiation of this population. In the 12S gene, this population has a UPD to *U. sameiti* from Ambodiriana of 5.4%. In the COB and the ND4 genes, the respective UPD values are 11.8% and 15.1%. In addition to Zahamena, molecular data also suggest the presence of a related mitochondrial lineage at Analalava.

The only sample from Betampona (RAX 7700) takes a place as a separate deep subclade within the *U. sikorae* complex in our phylogenetic trees based on 12S and COB sequences, but there is no information available on its possible morphological differentiation. Its genetic divergence in the 12S gene to *U. sameiti* from Ambodiriana is 4.1% UPD, and its divergence to the Zahamena population is 4.4% UPD. So far, this form has only been recorded from Betampona, a protected area with one of the few preserved lowland forests along the east coast. In spite of its small size of 2,228 ha, this nature reserve hosts a rather high degree of endemism with 24 species of amphibians and reptiles being potential endemics (ROSA et al. 2012).

The range of *Uroplatus sameiti* is restricted to the humid and littoral forests in the lowlands along Madagascar's east coast. The most inland locality within the known range is Marolambo where the vegetation type is rather similar to mid-altitude forests. In the ND4 tree, one sample from Marojejy (RF 510) and especially two from Montagne d'Ambre (APR 9614, ACZC 1617) are nested within *U. sameiti*, and we consider these biogeographically unexpected results in need of confirmation as they might be based on sample confusion or contamination. Possible records from Andohahela, as reported in the IUCN Red List, lack confirmation from genetic data and might be in error.

Uroplatus henkeli complex

Two taxa are here included in this group, *U. henkeli*, which is distributed in the Sambirano region and along the western coast, and a confirmed candidate species that inhabits the far North of Madagascar, *U. henkeli* [Ca11].

Uroplatus henkeli BÖHME & IBISCH, 1990

Originally described from Nosy Be, this species is known from the Sambirano region and localities in the West of Madagascar. The total length of *U. henkeli* can reach 30 cm as recorded by GLAW & VENCES (2007) for a specimen from the Tsingy de Bemaraha. Some animals show vermiculated dark dots on the back.

Recorded sites other than the type locality Nosy Be are as follows: Ankarafantsika, Benavony, Berara forest, Manongarivo, Tsarakibany, Sahamalaza, Ambohimarina, Kelifely, Ankara and Tsingy de Bemaraha (data compiled from GLAW & VENCES 2007, RAKOTONDRAVONY & GOODMAN 2011). Records from Ankarana, Montagne des

Français, Ampombofofo, and Forêt d'Ambre in northern Madagascar (D'CRUZE et al. 2008, MEGSON et al. 2009, DURKIN et al. 2011, LABANOWSKI & LOWIN 2011) are here assigned to the candidate species *U. henkeli* [Ca11] (see below). On Nosy Be, the species occurs in the protected area Lokobe and in Ambatozavavy, a forest managed by local people. Its presence in gallery forests surrounding some of the volcanic lakes in Nosy Be is possible.

Recent records of *U. henkeli* from Kelifely and Ankara in western Madagascar support a continuous western distribution to Tsingy de Bemaraha, which is also supported by the molecular data that include Bemaraha as the southernmost locality and show only a limited genetic differentiation across the rather extensive range.

Based on 12S sequence data, molecular genetic distances are 2.5% UPD between *U. henkeli* from Nosy Be and the Tsingy de Bemaraha sample. The lowest molecular distance is found between the population from Tsaratanana and that from Nosy Be with 0.3% UPD. In the COB gene, UPD among *U. henkeli* populations is up to 7.2%, with this highest value being recorded between populations from Tsingy de Bemaraha and Manongarivo.

Confirmed candidate species in the *U. henkeli* complex

Uroplatus henkeli [Ca11]

For populations assigned to *U. henkeli* occurring north of the type locality Nosy Be, i.e., in the area comprising Montagne des Français and Ankarana, GLAW & VENCES (2007) have asserted a possibly smaller body size. Based on their genetic divergence together with putative morphological differences (at least the smaller SVL), we here define this form as CCS, *Uroplatus henkeli* [Ca11]. This SVL variation has also been reported by DURKIN et al. (2011) for animals found in Tsarakibany, and these authors called the form "*Uroplatus* sp. aff. *henkeli*". RAXWORTHY et al. (2008) referred to this lineage as "*U. sp. H*" while GREENBAUM et al. (2007) regarded it as *U. henkeli*.

In the ND4 gene, a UPD value of 13.8% is found between the CCS (from Ankarana) and *U. henkeli* (from Ambohimarina, a lowland forest close to Maromandia). In the 12S gene, samples from Analafiana and Ankarana representing *U. henkeli* [Ca11] show UPD values between 8.8–10.9% compared to populations representing the nominal *U. henkeli*, which among them display genetic distances of 0.3 to 2.5%. In the COB gene, the divergence between *U. henkeli* and the CCS is 15.2% UPD. No significant genetic divergences were found between populations from Ankarana and Montagne des Français, but samples from these two sites differed strongly from Analafiana (UPD 12.4%).

Discussion

Taxonomy of *Uroplatus*

DE QUEIROZ (2007) has argued that at the root of all modern species concepts, there is general agreement on the fun-

damental nature of species: species are separately evolving meta-population lineages. Still, this author has proposed that the greater the number of species criteria satisfied by a group, the more likely it becomes that the group is a distinct lineage. In the present work, we have combined preliminary information on morphological traits and phylogenetic data to delimit species in the genus *Uroplatus*. We emphasize that while this new classification is not definitive by pointing more precisely than previous assessments to the specific questions that need to be addressed in future taxonomic revisions, it makes the whole genus *Uroplatus* more accessible for such revisionary work. Especially the morphological data presented here are far too incomplete for satisfying the requirements for well-founded species descriptions.

In total, we suggest that six lineages be assigned the status of confirmed candidate species (CCS), i.e., potentially new species that are likely to be upgraded and described as nominal species once more detailed data become available. A further five unconfirmed candidate species (UCS) are proposed in the *U. ebenauai* and *U. fimbriatus* groups. A rather large number of additional deep genealogical (mitochondrial) lineages were identified, which can be defined as DCL; it is difficult to precisely quantify these, as different samples were included in the different gene trees. An important point to consider when interpreting the genetic variation observed is that, in general, all individuals of *Uroplatus* from one population show at least some mitochondrial differentiation from the most closely related lineage from another site, with almost no instance of haplotype-

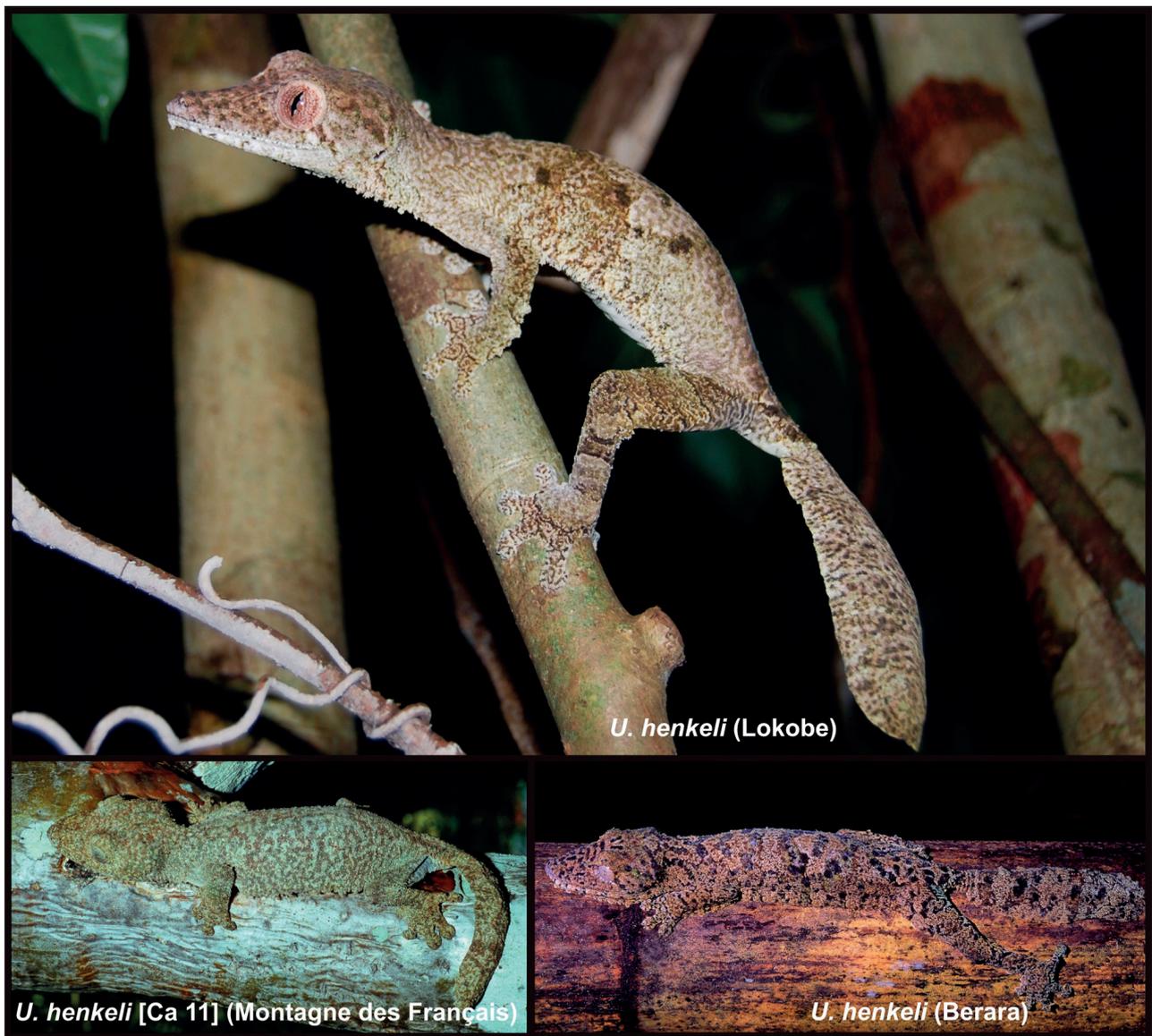


Figure 11. Photos of live specimens of *Uroplatus henkeli* and a related candidate species.

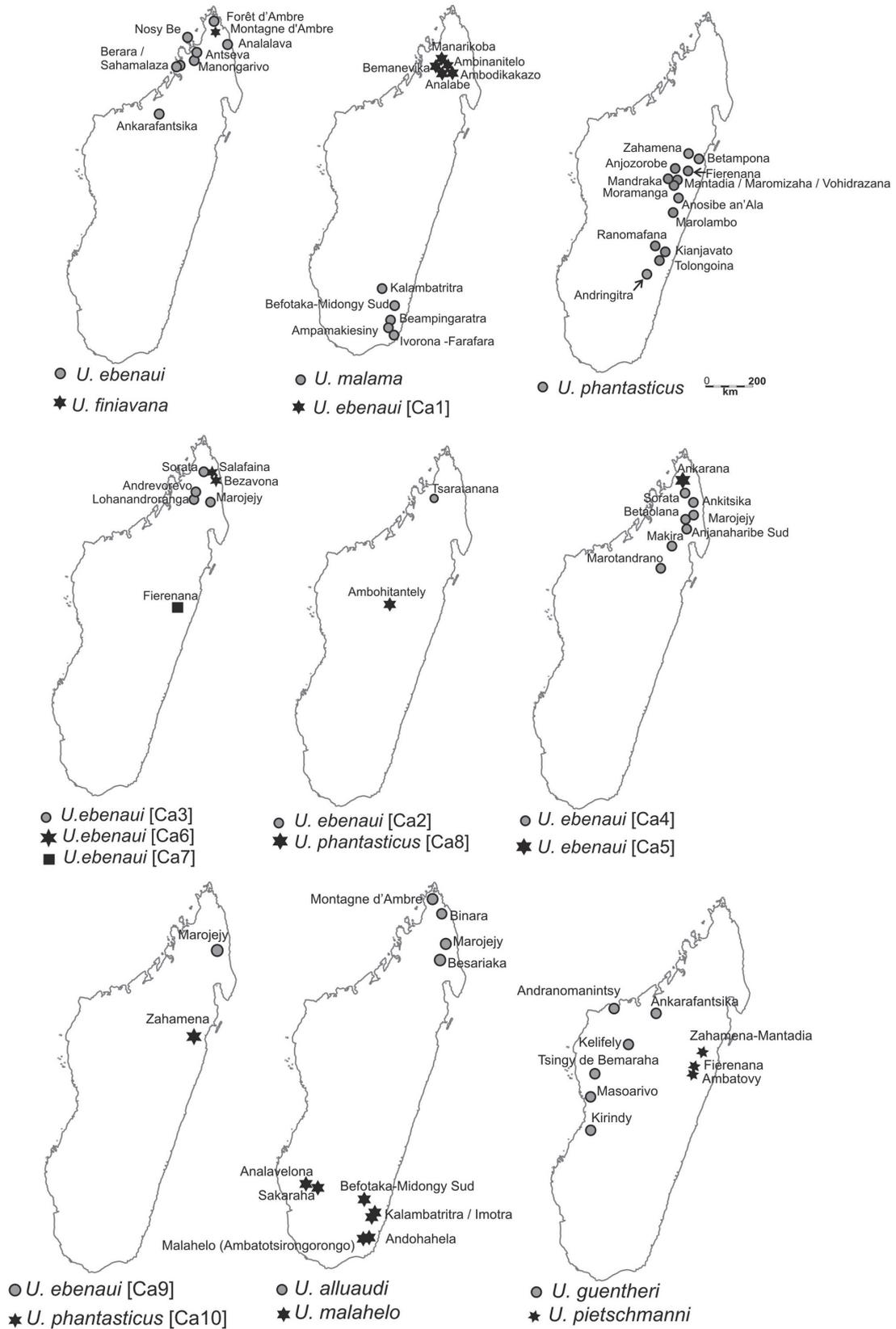


Figure 12. Geographical distribution of species and candidate species in the *Uroplatus ebenai*, *U. alluaudi*, and *U. guentheri* species groups as assessed in the present work.

sharing among localities that are at some relevant distance (> 50 km). This high degree of genetic structuring appears to be typical for all species in the genus.

Based on the revised taxonomy proposed, we will discuss geographical distribution, potential areas of endemism, and biogeographical patterns jointly for all species and candidate species of the different species groups.

Uroplatus ebenauui group

In addition to the four nominal species, we report five CCS and five UCS in this group. The highest species richness is located in the northern part of Madagascar. In mantellid frogs of Madagascar, genetic differentiation among popu-

lations was found to be inversely correlated to body size, i.e., small-sized species had a stronger genetic subdivision, probably due to a lower dispersal capacity (PABIJAN et al. 2012). In the genus *Uroplatus*, the *U. ebenauui* group, which includes the species of smallest size, also has the highest species diversity, and species such as *U. phantasticus* show strong genetic differences between populations (RATSOAVINA et al. 2012). Within the group, *U. finjavana* is the most geographically restricted form and occurs only in a small area of the Montagne d'Ambre massif. All neighbouring *U. ebenauui* group species and candidate species assessed in this work show strong genetic divergences, and in their majority also exhibit clear morphological differences

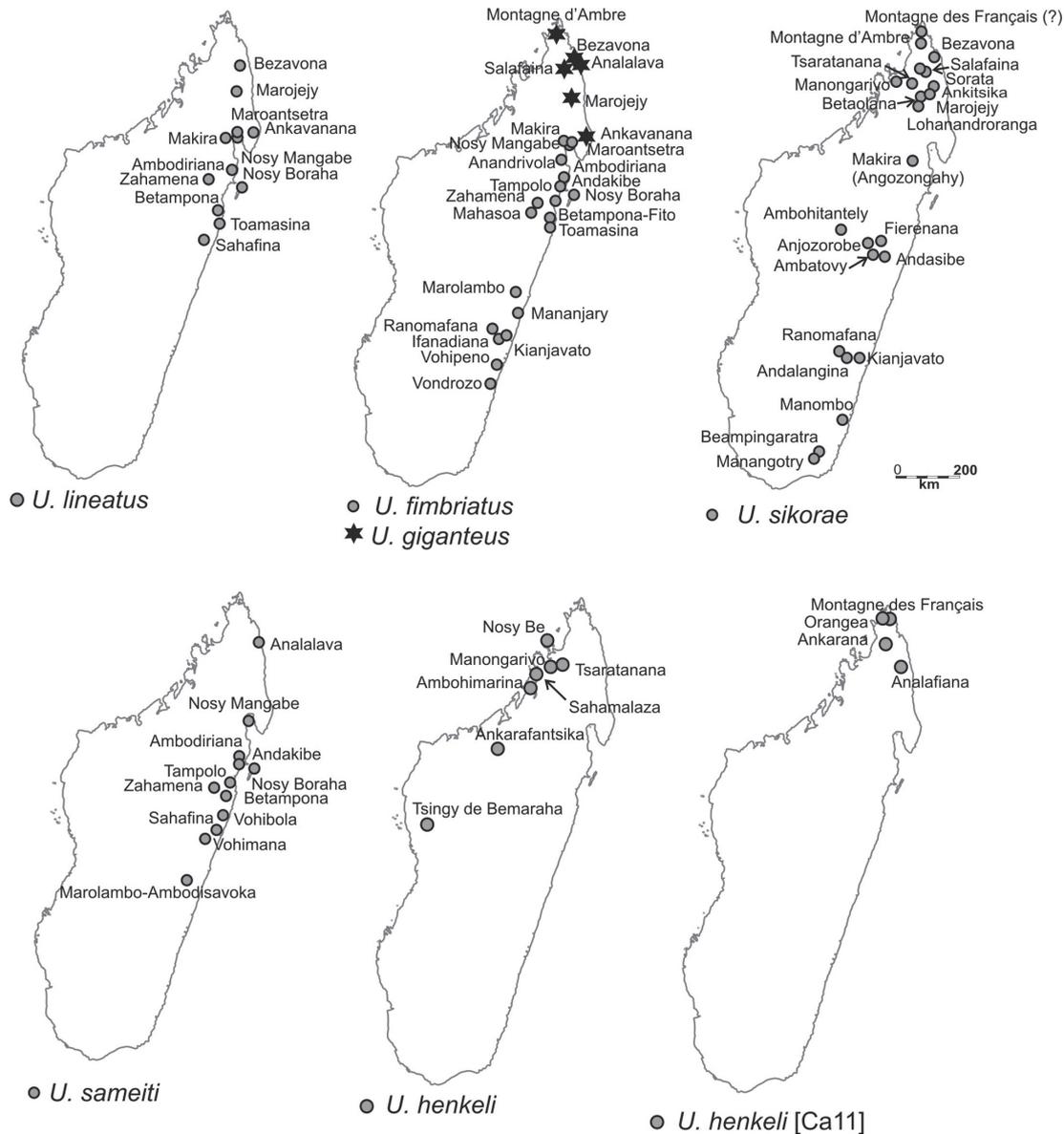


Figure 13. Geographical distribution of species and candidate species in the *Uroplatus lineatus* and *U. fimbriatus* species groups, as assessed in the present work.

as compared to *U. finivana*. We therefore hypothesize that *U. finivana* is a local endemic of the Montagne d'Ambre massif.

Among the formally named species, *U. ebenau* is the second most widespread, presumably distributed in lowland forests of the West, North West and North, although within this large distribution area, climate is rather varying, habitats are fragmented, and forests are scattered. Apart from *U. ebenau* [Ca5], this is apparently also the species of the *U. ebenau* group that is best adapted to dry conditions. Its distribution pattern supports maintaining the IUCN (International Union for Conservation of Nature) Red List assessment of this species as "Vulnerable".

The most widespread species of the group is *U. phantasticus*, but within its large range, a strong phylogeographic structure and regional genetic differentiation were observed. Detailed phylogeographic data of RATSOAVINA et al. (2012) have provided some evidence that this species expanded its distribution area in a north-south direction, and that rivers can act at least temporarily as barriers to gene flow among populations, exemplified by the rather narrow Namorona River in the Ranomafana National Park that sharply separates two mtDNA lineages of the species.

Almost all candidate species enumerated in the *U. ebenau* group in this study show morphological affinities to the nominal taxon *U. ebenau*, and almost all are restricted to the northern regions of Madagascar. In spite of high genetic divergence among *U. ebenau*-like forms and a high diversity in habitats, ranging from coastal dry forests to montane wet forests close to the tree line, there is a remarkable conservatism of morphological traits. The geography of the mountain areas that these candidate species are native to could partly shed light on the question of how species originated in this area. For instance, part of the Marojejy massif is encircled by low-altitude areas and large rivers such as the Androranga and Lokoho (CHAPERON et al. 1993), which may contribute to its isolation from the adjacent rainforests (RAXWORTHY et al. 1998). These factors may inhibit the dispersal of local endemic species, for instance in the case of *U. ebenau* [Ca9], which is only found at high-altitudes of the Marojejy massif. Connectivity between Anjanaharibe-Sud and adjacent massifs such as Tsaratanana and Marojejy exists below 1,500 m a.s.l., which explains the presence of *U. ebenau* [Ca3] in both areas. More generally, the high diversity of the *U. ebenau*-like forms in the Tsaratanana area could be related to the altitudinal differences along the mountain area and slope exposure, which might provide opportunities for adaptive divergence and specialization, in other words, sources of speciation at a small scale. For instance, *U. ebenau* [Ca2] might be restricted to a small vertical range from 2,000–2,200 m a.s.l., and *U. ebenau* [Ca1] on the western slope of the Tsaratanana massif might be restricted to altitudes below 1,200 m a.s.l. For the candidate species from the Northern Central East, *U. ebenau* [Ca7] from Fierenana, *U. ebenau* [Ca8] from Ambohitantely, and *U. phantasticus* [Ca10], we unfortunately have only limited data available

and therefore cannot provide reliable statements on their status and biogeography.

Uroplatus alluaudi group, *U. guentheri* group and *U. lineatus* group

Thanks to intensive fieldwork in the last decades (as reported in RASELIMANANA et al. 1998, BORA et al. 2010, RAKOTONDRAVONY & GOODMAN 2011), the known distribution range of *U. guentheri* now extends to Tsingy de Bemaraha whereas only Ankarafantsika and Kirindy had previously been recorded. Nevertheless, this study has revealed a significant genetic divergence between populations situated to the north and south of the Tsiribihina River. More samples will be needed to verify whether this river indeed acts as a riverine barrier like in some lemur species (PASTORINI et al. 2003, WILMÉ et al. 2006) and possibly in other reptiles (BOUMANS et al. 2007).

Uroplatus malahelo populations are separated into a western and eastern subpopulation relative to the Anosy chain, i.e., the Ambatotsirongorongo area on the eastern slope versus Analavelona and Andohahela on the western slope. In this area, rainforests are regularly interrupted by drier habitat, which might be a causal factor for the genetic divergence of these populations.

The trade in all species of these groups is limited, with zero annual export quotas for the year 2012, and they are all classified in the threatened category of the IUCN Red List, with 'Endangered' being applied to *U. guentheri*, *U. malahelo*, *U. pietschmanni* and 'Near Threatened' to *U. alluaudi*. Restricted distribution areas, low numbers of individuals encountered during field surveys, and observations that suggest decreasing populations due to habitat loss are reasons for this threat status classification. The populations of *U. lineatus* across its wide distribution area appear to be structured genetically, but the available data are insufficient for a thorough biogeographic interpretation.

Uroplatus fimbriatus group

This group of large-bodied *Uroplatus* includes the species with the largest distribution range in the genus, but also examples (such as *U. sikorae* and *U. sameiti*) of an extreme phylogeographic structure with numerous deep genetic lineages across their distribution area. The distributional data gathered thus far allow some inference on habitat specialization, such as *U. sameiti* and *U. fimbriatus* being adapted to humid lowland forests, *U. sikorae* living in mid-altitude rainforest, and *U. henkeli* ranging from Sambirano rainforest to dry deciduous forest at low altitudes. For the whole group, only one candidate species of the *U. henkeli* complex is suggested.

In the *U. sikorae* complex, the species *U. sikorae* is the most widespread, and a subdivision into various mitochondrial lineages of allopatric distribution is observed across its distribution range. One major genetic discontinuity parallels the pigmentation of the mouth, with the *U. sikorae* populations from the Southern Central East of the distribution area southwards to the surroundings of Ranomafana exhibiting an unpigmented oral mucosa.

Despite morphological differences such as this, nothing is known about a possible reproductive isolation between the different lineages within *U. sikorae*.

Biogeography of northern Madagascar

Several microendemic species of *Uroplatus* are found in northern Madagascar, which obviously is a centre of species richness and endemism for some groups (RAXWORTHY & NUSSBAUM 1995, WOLLENBERG et al. 2008, TOWNSEND et al. 2009, KÖHLER et al. 2010, RATSOAVINA et al. 2010, 2011, KAFFENBERGER et al. 2012, GLAW et al. 2012, LEMME et al. 2013).

Various hypothesis have been proposed to explain the diversification of species in this area of high endemism: (1) The mosaic of different habitats, for instance dry forest bordering rainforests on different substrates, may have triggered speciation through strict adaptation to one of these different ecological conditions, for instance in the large-sized species of *Stumpffia* (KÖHLER et al. 2010). (2) Vicariance during habitat shifts caused by climatic oscillations was proposed for *Brookesia* leaf chameleons by RAXWORTHY & NUSSBAUM (1995). (3) The possibility of ecological specialization along ecotones has been suggested by VENCES et al. (2009). For the species of the *Uroplatus ebenau* group, RATSOAVINA et al. (2011) hypothesized that, after an initial split between a southern clade composed of *U. malama* and a northern ancestral species, the latter diversified in the northern regions into *U. ebenau*-like forms with rather short tails, and other forms with longer tails of which then one (the ancestor of *U. phantasticus*) dispersed farther south and diversified further (see also RATSOAVINA et al. 2012). A genetic divergence of lineages occurring exclusively or mainly in northern Madagascar also is found in other *Uroplatus*, such as *U. giganteus* versus *U. fimbriatus*, *U. lineatus* (with a genetically divergent lineage apparently being distributed in the North East), the *U. alluaudi* group (with *U. alluaudi* being restricted to northern Madagascar), and the *U. henkeli* complex (presence of one candidate species in the northern portion of Madagascar), but this pattern is much less obvious than it is in the *U. ebenau* group.

Conclusion

In this work, we have tried to consolidate as much information as available to us in an updated overview of species and candidate species in the genus *Uroplatus*. Based on an integrative taxonomic approach, we identified 14 nominal species and 11 taxonomically undescribed candidate species, of which the highest number is found in the *U. ebenau* group. Our data also provide some information about morphological differentiation of some of these candidate species, albeit these data are still very superficial. Taxonomic revisions are needed for almost all species groups of *Uroplatus*, but our preliminary list and distribu-

tion assessment already identifies, which species and lineages are probably geographically restricted and threatened by extinction, and the areas that harbour such lineages and thus need protection. These data will therefore be valuable for conservation prioritisation and to improve the regulation of the pet trade.

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Supplementary material

Additional information is available in the online version of this article at <http://www.salamandra-journal.com>

Supplementary Tables S1–S23: Details of localities, and Genbank accession and catalogue numbers of the underlying voucher specimens.

Supplementary Tables S24–S29: Pairwise genetic distances between *Uroplatus* specimens.

Supplementary Table S30: Table of CITES export quotas.

Online Supplementary data

FANOMEZANA M. RATSOAVINA, NOROMALALA R. RAMINOSOA, EDWARD E. LOUIS JR., ACHILLE P. RASELIMANANA, FRANK GLAW & MIGUEL VENCES: An overview of Madagascar's leaf tail geckos (genus *Uroplatus*): species boundaries, candidate species and review of geographical distribution based on molecular data. – *Salamandra*, **49**(3): 115–148.

29 Supplementary tables and Appendix

Supplementary Table S1. Localities assigned to *U. eburnai* in this and selected previous studies, and corresponding voucher specimens of the reliably assigned localities.

Locality	Coordinates and altitude	Voucher specimen	GenBank accession numbers / available sequences	References
Nosy Be – Ambatozavavy	-13.39013 48.31897 100 m	UADBA (ZCMV 13012)	ND4: ACZC 1199	This study
Nosy Be	-13.35061 48.27588 97 m	UMMZ 208442	12S and COB: RAN 43644 (EU596622, EU596703)	RAXWORTHY et al. (2008)
Manongarivo, Camp 1	-13.97700 48.42200 751 m	UADBA (FGMV 2002.2205)	12S: FGMV 2002.2205	This study
Manongarivo	Not available	ZSM 856/2003 (FGMV 2002.826)	12S and COB: FGMV 2002.826	
Manongarivo	Not available	UMMZ 208425	12S and COB: RAN 39053 (EU596623, EU596704)	RAXWORTHY et al. (2008)
Benavony near Ambanja	-13.71029 48.48611 40 m	No voucher	No genetic samples	GLAW & VENCES (1994)
Montagne des Français	-12.32966 49.36750 140 m	No voucher	No genetic samples	D'CRUZE et al. (2007)
Ampombofofo	-12.09944 49.33888 10–100 m	No voucher	No genetic samples	MEGSON et al. (2009)
Berara	-14.30000 47.90000 170–350 m	MRSN-FAZC 10631, 10632, 10633, 10634	ND4 and 12S: 2000.E37 RATF 37	ANDREONE et al. (2001) Sequences: This study
Tsingy de Bemaraha, Bendrao forest (S4)	-18.79722 44.86028 427 m	UADBA 39009	Not studied genetically; identity uncertain.	BORA et al. (2010)
Ankarafantsika	-16.25000 46.80000 100–200 m	KUZ 50724 APR 7537, APR 7538	Unpublished ND2 and 16S data by TOLLEY and RASELIMANANA	MORI et al. (2006), including photograph. Specimen from RASELIMANANA (2008) for APR acronyms.
Montagne d'Ambre (Forêt d'Ambre) near Joffreville	-12.50358 49.19028 873 m	No voucher	12S: ACZC 1426	This study
Forêt d'Ambre	-12.47533 49.21417 535 m	ZSM 2030/2008 (FGZC 3153)	12S: FGZC 3153	This study
Antseva	-13.71117833 48.569266	AMNH R152884	12S and COB: RAX 2222 (EU596621, EU596702)	RAXWORTHY et al. (2008)
Analalava	-13.622833 49.9985 ca. 235 m	AMNH R152886	12S and COB: RAX 4476 (EU596624, EU596705)	RAXWORTHY et al. (2008)
Sahamalaza and Beanka	(Sahamalaza) -14.31000 47.91500 120 m	No voucher	Unpublished ND2 and 16S data	TOLLEY & RASELIMANANA (unpublished)

Supplementary Table S2. Localities assigned to *U. finivavana* in this and selected previous studies, and corresponding voucher specimens of the reliably assigned localities.

Locality	Coordinates and altitude	Voucher specimens	Comments and references
Montagne d'Ambre (type locality)	-12.52678 48.17214 1072 m	ND4: UAMB 5.36 ND4 and 12S: FGZC 625 12S: FGZC 621, FGZC 622, FGZC 623, FGZC 624, FGZC 626, FGZC 1096 12S and COB: FGZC 619, RAN 38058,	RAXWORTHY et al. (2008) for 12S and COB RATSOAVINA et al. (2011) for morphology and ND4
Joffreville	-12.50358 49.19028 873 m	12S: ACZC 1420	RATSOAVINA et al. (2011)

Supplementary Table S3. Localities assigned to *U. phantasticus* in this and selected previous studies, and corresponding voucher specimens of the reliably assigned localities.

Locality	Coordinates and altitude	Voucher specimens and Genbank accession numbers	Comments and references
Mandraka	-19.03330 47.91670 1400 m	12S and COB : RAX 9399 (EU596668, EU596745)	RAXWORTHY et al. (2008)
Manjakandriana	48 km east of Antananarivo	unknown, MNHN?	ANGEL (1942)
Mantadia	-18.81498 48.47576 1085 m	12S and COB : RAN 37535	RAXWORTHY et al. (2008)
Fierenana	-18.48330 48.40000 940 m	ZSM 212/2002 12S and COB : RATF 38	This study
Madagascar	No precise locality	12S and COB : RAX 4013 (EU596665, EU596742) RAX 4014 (EU596666, EU596743)	RAXWORTHY et al. (2008)
Moramanga-Andasibe	-18.93330 48.41670 1005 m	12S : ZSM 1128/2003 (FGMV 2002.3103)	This study
Anosibe an'Ala	-19.32435 48.21988 881 m	ND4 and 12S : ZSM 473/2010 (FGZC 4505)	This study
Anjozorobe	-18.46294 47.93813 1297 m	ND4 and 12S : ZSM 471/2010 (FGZC 4341), UADBA (FGZC 4384), ZSM 472/2010 (FGZC 4385)	This study
Marolambo	-20.05239 48.13389 438 m	12S : RATF 28, RATF 29	This study
Vohidrazana	-18.88333 48.56667	COB : ZMA 19620 RATF 53	GREENBAUM et al. (2007)
Maromizaha	-18.97567 48.45833 980 m	ND4 : APR 8407	This study
Tolongoina	-21.35358 47.60778	ND4 : TOL 25	This study
Ranomafana	-21.25139 47.42447 921 m	ND4 and 12S : MPFC 511, MPFC 506 12S : FGMV 2002.639, FGMV 2002.640, MPFC 501, MPFC 509, MPFC 510 COB : FGMV 2002.640 RATF 46	This study
Kianjavato	-21.35983 47.84800 425 m	ND4 : KAF 191 ND4 and 12S : KAF 190 12S : KAF 179, KAF 183, KAF 194, KAF 237	This study
Ambahaka forest, Fito, Fort Carnot, Ikongo, Ankopakopaka forest	Ikongo: -21.88330 47.33330 1072 m	Only geographical record	Not genetically studied. Localities from GLAW & VENCES (2007)
Ivohibe	-22.48574 46.88795 1400 m	Only geographical record	RASELIMANANA (1999 / unpublished data). Might correspond to <i>U. malama</i> , see Table S4
Andringitra	-22.22854 46.92833 1561 m	12S and COB : RAN 44586	RAXWORTHY et al. (2008)
Betampona	-17.888271 49.225108 200 m	ND4 : BET 5.24, BET 5.19 12S and COB : RAX 8079	This study and RAXWORTHY et al. (2008)
Zahamena	Not available	12S and COB : RAN 45198	RAXWORTHY et al. (2008)

Supplementary Table S4. Localities assigned to *U. malama* in this and selected previous studies, and corresponding voucher specimens of the reliably assigned localities.

Locality	Coordinates and altitude	Voucher specimens	Comments and references
Ampamakiesiny	-24.533333 47.85000	UMMZ 196790	NUSSBAUM & RAXWORTHY (1995)
Beampingaratra (Andohahela)	-24.46325 46.70158 676 m	ND4 and 12S : MPFC 411 12S : MPFC 407, MPFC 416	This study and RATSOAVINA et al. (2011)
Befotaka-Midongy du Sud	-23.88833 46.89617 1050 m -23.83667 46.96000 1135 m	ND4 : APR 8322, APR 8267	This study (confirmed by TOLLEY and RASELIMANANA, unpublished)
Kalambatritra	-23.36593 46.49725	MRSN R2145, R2390, no genetic samples	ANDREONE & RANDRIANIRINA (2007)
Ivorona	-24.82983 46.92164 450 m	No genetic samples	IUCN Red List assessment 2011 (unpublished data)
Farafara	-24.83113 47.00555 603 m	No genetic samples	IUCN Red List assessment 2011 (unpublished data)
Pic Ivohibe	-22.48574 46.88795 1400 m	No genetic samples	RASELIMANANA (1999) [requires confirmation] – locality probably refers to <i>U. phantasticus</i> , see Table S4.

Supplementary Table S5. Localities assigned to *Uroplatus ebenau* [Ca1 JN038123] in this and selected previous studies, and corresponding voucher specimens of the reliably assigned localities.

Locality	Coordinates and altitude	Voucher specimens and Genbank accession numbers	Comments and references
Bemanevika	-14.43061 48.60179 1466 m	ND4 and 12S : DRV 6409; ZCMV 12503 12S : DRV 6418;	This study
Analabe	-14.50478 48.87597 1361 m	ND4 : ZCMV 12280; ND4 and 12S : ZCMV 12275, 12S : ZCMV 12276, ZCMV 12277	This study
Ambodikakazo	-14.20975 48.89814 1411 m	ND4 and 12S : MPFC 562 MPFC 564; 12S : MPFC 556, DRV 6324, DRV 6325, DRV 6326	This study
Ambinanitelo	-14.20975 48.97022 1280 m	12S : DRV 6263	This study
Manarikoba	-14.04154 48.78389 1176 m	12S and COB : 2001.F10	This study
Tsaratanana	No precise locality	12S : RAX 3263 (EU596632)	RAXWORTHY et al. (2008)

Supplementary Table S6. Localities assigned to *Uroplatus ebenau* [Ca2 JN038124] in this and selected previous studies, and corresponding voucher specimens and Genbank accession numbers for at least one specimen of the reliably assigned localities.

Locality	Coordinates and altitude	Voucher specimens and Genbank accession numbers	Comments and references
Tsaratanana (Matsaborimaiky)	-14.15253 48.95729 2040 m	ND4 and 12S : ZCMV 12388, ZCMV 12389; 12S : DRV 6192, DRV 6248 12S and COB : RAX 5461 (EU596640, EU596718), RAN 43228 (EU596639, EU596717)	This study and RAXWORTHY et al. (2008)

Supplementary Table S7. Localities assigned to *U. ebenau* [Ca3 JN038126] in this and selected previous studies, and corresponding voucher specimens of the reliably assigned localities.

Locality	Coordinates and altitude	Voucher specimens and Genbank accession numbers	Comments and references
Marojejy	-14.440833 49.739917 1576 m	12S and COB : ZSM 79/2005 (ZCMV 2030)	This study
Sorata	-13.68568 49.44185 1300 m	12S and COB : RAX 5176 (EU596637, EU596716)	RAXWORTHY et al. (2008)
Andrevorevo	-14.34644 49.10028 1717 m	ND4 and 12S : DRV 6280, DRV 6281	RATSOAVINA et al. (2011)
Lohanandroranga	-14.41650 49.147583 1400–1800 m	12S : RAX 6740 (EU596638)	RAXWORTHY et al. (2008)

Supplementary Table S8. Localities assigned to *U. ebenau* [Ca4] in this and selected previous studies, and corresponding voucher specimens of the reliably assigned localities.

Locality	Coordinates and altitude	Voucher specimens and Genbank accession numbers	Comments and references
Anjanaharibe-Sud	-14.74500 49.46167 1400 m	ND4: JAR 3.1 and JAR 3.2	RATSOAVINA et al. (2011)
Marojejy Tsararano	Not available -14.90667 49.68667 850 m	COB and 12S: RAN 42092 (EU596708, EU596628) No genetic samples, only geographical records (tentatively assigned to this candidate species)	RAXWORTHY et al. (2008) ANDREONE et al. (2000)
Betaolana	-14.40550 49.38030 1260 m	COB and 12S: RAX 3515 (EU596707, EU596627), RAX 3449 (EU596625, EU596706) 12S: RAX 3487 (EU596626)	RAXWORTHY et al. (2008)
Sorata	-13.68568 49.44185 1300 m	12S and COB: RAX 5012 (EU596631, EU596711), RAX 4877 (EU596630, EU596710)	RAXWORTHY et al. (2008)
Makira western slope	-15.46675 49.12889 1067 m	12S: ZCMV 11308, ZCMV 11309	This study
Ankitsika	-13.87239 49.78408 830 m	12S and COB: RAX 4706 (EU596629, EU596709)	RAXWORTHY et al. (2008)
Marotandrano	-16.28000 48.80167 1000 m	ND4: APR 5859	This study

Supplementary Table S9. Localities assigned to *Uroplatus ebenau* [Ca5] in this and selected previous studies, and corresponding voucher specimens and Genbank accession numbers for at least one specimen of the reliably assigned localities.

Locality	Coordinates and altitude	Voucher specimens	Comments and references
Ankarana	-12.96833 49.13916 100 m	ZSM 288/2004 (FGZC 552) 12S: FGZC 552	This study

Supplementary Table S10. Localities assigned to *U. ebenau* [Ca6] in this and selected previous studies, and corresponding voucher specimens of the reliably assigned localities.

Locality	Coordinates and altitude	Voucher specimens and Genbank accession numbers	Comments and references
Salafaina	-13.44590 49.71238 521 m	12S and COB: RAX 4433 (EU596636, EU596715)	RAXWORTHY et al. (2008)
Bezavona	-13.53333 49.86666 574 m	12S and COB: RAX 4029 (EU596635, EU596714)	RAXWORTHY et al. (2008)

Supplementary Table S11. Localities assigned to *U. ebenauai* [Ca7 JX205405] in this and selected previous studies, and corresponding voucher specimens of the reliably assigned localities.

Locality	Coordinates and altitude	Voucher and Genbank accession numbers	Comments and references
Fierenana	-18.54333 48.44888 948 m	ZSM 212/2002 (MV 2001-1402) COI: JX205405 12S: RATF 39	GREENBAUM et al. (2007)
Madagascar	No precise locality	12S: RAX 4012 (EU596633)	RAXWORTHY et al. (2008)

Supplementary Table S12. Localities assigned to *U. alluaudi* in this and selected previous studies, and corresponding voucher specimens of the reliably assigned localities.

Locality	Coordinates and altitude	Voucher specimens and Genbank accession numbers	Comments and references
Binara (Daraina)	-13.26330 49.60330 725 m	No genetic data	RAKOTONDRAVONY et al. (2006)
Besariaka	-14.84667 49.59500 918 m	MRSN R1630 (not studied genetically)	ANDREONE & APREA (2006)
Marojejy	No precise locality	No genetic data	RAKOTOMALALA & RASELIMANANA (2003)
Montagne d'Ambre	-12.48333 49.31666 800 m	ZSM 251/2004 (FGZC 490) ND4: RATF 81, RATF 15 12S: ZSM 2104/2007 (FGZC 1097), ZSM 2031/2008 (FGZC 1861) 12S and COB: RAN 38128 (EU596620, EU596701) COB: FGZC 490	This study except RAN acronyms which are from RAXWORTHY et al. (2008)

Supplementary Table S13. Localities assigned to *U. pietschmanni* in this and selected previous studies, and corresponding voucher specimens of the reliably assigned localities.

Locality	Coordinates and altitude	Voucher specimens and Genbank accession numbers	Comments and references
Fierenana	-18.46833 48.38500 1041 m		
Corridor Zahamena-Mantadia	-17.66666 48.83333 400–1500 m	ND4: ZAH 219	This study
Madagascar	No precise locality	COB: RAX 7152 12S and COB: RAX 7153 (EU596687, EU596763)	RAXWORTHY et al. (2008)
Not available	No precise locality	ND4: HDZ 13267, HDZ 17199	Samples from captive-bred specimens
Ambatovy	-18.47360 48.20089 1076 m	No genetic data	RASELIMANANA (2010)

Supplementary Table S14. Localities assigned to *U. guentheri* in this and selected previous studies, and corresponding voucher specimens of the reliably assigned localities.

Locality	Coordinates and altitude	Voucher specimens and Genbank accession numbers	Comments and references
Ankarafantsika	-16.22149 46.93113 160 m	ND4: RATF 40, 12S: ZSM 476/2001	RUSSELL & BAUER (1987)
Tsaramandroso	Not available	12S and COB: RAX 9808 (EU596689, EU596765)	RAXWORTHY et al. (2008)
Madagascar	no precise locality	12S and COB: RAX 7157 (EU596688, EU596764)	RAXWORTHY et al. (2008)
Kirindy, Morondava	-20.78333 44.16666 77 m	ND4: RATF 4, APR 7208	This study
Andranomanintsy	-16.52000 44.76833 35 m	Only geographical records	GOODMAN et al. (2008)
Ambalimby-Masoarivo	-19.61500 44.76833 110 m	Only geographical records	RASELIMANANA et al. (2008)
Ankilogo (Tsingy de Bemaraha)	-19.13111 44.70889 57 m	specimens: UADBA 28031, UADBA 28045	BORA et al. (2010)
Tsingy de Bemaraha	-18.69275 44.77227 50–400 m	Only geographical records	BORA et al. (2010)
Kelifely	-17.31500 46.00333 290 m	Only geographical records	RAKOTONDRAVONY & GOODMAN (2011)

Supplementary Table S15. Localities assigned to *U. malahelo* in this and selected previous studies, and corresponding voucher specimens of the reliably assigned localities.

Locality	Coordinates and altitude	Voucher specimens and Genbank accession numbers	Comments and references
Ambatotsirongorongo Mountain, Malahelo	-25.07917 46.78333 350 m	12S and COB: RAN 40559 (EU596661, EU596738)	RAXWORTHY et al. (2008)
Kalambatritra, Imotra and Sakaraha	Imotra: -23.73985 46.41173 1200 m	No genetic samples	PEARSON et al. (2007)
Befotaka-Midongy du Sud	-23.739167 44.026667 875 m	No genetic samples	TOLLEY & RASELIMANANA (unpublished data)
Analavelona	-22.75000 44.16670 600 m	12S and COB: RAN 51170 (EU596662, EU596739)	RAXWORTHY et al. (2008)
Andohahela (Manangotry)	-24.76339 46.86264 279 m	ND4: ZCSH 172, AND 17 12S: RAN 52578 (EU596663)	This study and RAXWORTHY et al. (2008) for RAN specimens

Supplementary Table S16. Localities assigned to *U. lineatus* in this and selected previous studies, and corresponding voucher specimens and GenBank accession numbers for at least one specimen of the reliably assigned localities.

Locality	Coordinates and altitude	Voucher and GenBank accession numbers	Comments and references
Northern Central Eastern populations			
Toamasina	No precise locality	12S and COB : RAX 4011 (EU596660, EU596737), RAX 4010 (EU596659, EU596736)	RAXWORTHY et al. (2008)
Zahamena	-17.66666 48.83333 400 – 1500 m	Voucher specimen at UADBA, no genetic samples	
Betampona	-17.88827 49.22510 200 m	ND4 : BET 5.20, BET 5.25	This study
Sahafina	-18.81060 48.98030 96 m	ND4 : RATF 12, RATF 10	GEHRING et al. (2010)
Nosy Boraha (Sainte Marie)	-16.91842 49.88692 102 m	No genetic samples	
Ambodiriana	-16.64911 49.67275 200 m	No genetic samples	ADEFA (personal communication)
Northeastern population			
Makira	-15.20569 49.62027 329 m	No genetic samples	GEHRING et al. (2010)
Marojejy	-14.43667 49.77500 495 m	12S and COB : RAN 42243 (EU596657, EU596734)	RAXWORTHY et al. (2008)
Ankavanana	-15.308333 50.233333	12S and COB : RAN 42559 (EU596658, EU596735)	RAXWORTHY et al. (2008)
Bezavona	-13.53333 49.86667 574 m	12S and COB : RAX 3867 (EU596656, EU596733)	RAXWORTHY et al. (2008)
Maroantsetra	-15.42698 49.74147 8 m	No genetic samples	GLAW & VENCES (2007)
Nosy Mangabe	-15.49324 49.76776 229 m	No genetic samples	ANGEL (1942), BAUER & RUSSELL (1989), GLAW & VENCES (2007)

Supplementary Table S17. Localities assigned to *U. fimbriatus* in this and selected previous studies, and corresponding voucher specimens and GenBank accession numbers for at least one specimen of the reliably assigned localities.

Locality	Coordinates and altitude	Voucher and GenBank accession numbers	Comments and references
Anandrivola, Maroantsetra, Nosy Mangabe, Tampolo, Fito, Zahamena, Mananjary, Vohipeno, Ifanadiana, Vondrozo, Ranomafana, Mahasoia	(Anandrivola: -15.81644 49.68924, 76 m) (Mahasoia: -17.29769 48.70199 753 m)	No molecular data available	GLAW & VENCES (2007) (some localities not included) (own data)
Betampona	-17.88827 49.22510 200 m	12S: RAX 7458	RAXWORTHY et al. (2008)
Andakibe	-16.78098 49.73447	12S and COB: RAX 9112 (EU596645, EU596722)	RAXWORTHY et al. (2008)
Toamasina	-18.1667 49.3833 20 m	12S: RAX 4007 (EU596649)	RAXWORTHY et al. (2008)
Nosy Boraha (Sainte Marie)	16.91772 49.87547 107 m	ND4: FRC 534	This study
Marolambo	-20.05239 48.13389 438 m	ND4: RATF 30	This study
Kianjavato-Vatovavy	-21.35983 47.84800 425 m	ND4: VVAT 16, KAF 147, KAF 249	This study

Supplementary Table S18. Localities assigned to *U. giganteus* in this and selected previous studies, and corresponding voucher specimens and Genbank the reliably assigned localities.

Locality	Coordinates and altitude	Voucher specimens and GenBank accession numbers	Comments and references
Montagne d'Ambre	-12.48333 49.31666 800 m	12S and COB: RAN 38460 COB: ZSM 267/2004 FGZC 514	RAXWORTHY et al. (2008), GLAW et al. (2006)
Marojejy	-14.43333 49.76167 828 m	ZSM55-2005 COB: ZCMV 864 RATF 66 12S: RAN 42239 (EU596647)	GREENBAUM et al. (2007) and RAXWORTHY et al. (2008)
Salafaina	-13.44590 49.71238 242 m	12S and COB: RAX 4327 (EU596642, EU596720)	RAXWORTHY et al. (2008)
Ankavanana	-15.308333 50.233333	12S and COB: RAN 42560 (EU596648, EU596725)	RAXWORTHY et al. (2008)
Bezavona	-13.53333 49.86666 585 m	12S and COB: RAX 3830 (EU596641, EU596719)	RAXWORTHY et al. (2008)
Analalava	-13.59993 49.98273 235 m	12S and COB: RAX 4470 (EU596643, EU596721)	RAXWORTHY et al. (2008)

Supplementary Table S19. Localities assigned to *U. sikorae* in this and selected previous studies, and corresponding voucher specimens of the reliably assigned localities.

Locality	Oral mucosa colouration	Coordinates and altitude	Voucher specimens and GenBank accession numbers	Comments and genetic sample references
Populations around type locality				
near Andrangoloaka	Black	–	SMF 9632 no genetic data	Type locality
Andasibe	Black	-18.9333 48.4167 1099 m	ND4: FGMV 2002.951 RATF51, ND4 and COB: ZSM 920/2003 RATF 52	This study
Ambatovy	Black	-18.47360 48.20089 1076 m	ND4: PSG 2523, PSG 2524	This study
Anjozorobe	Black	-18.46294 47.93813 1298 m	ND4: FGZC 4351	This study
Fierenana	Black	-18.4833 48.4000 940 m	ND4: FGMV 2002.223 RATF 57	This study
Ambohitantely	Black	-18.17167 47.28167 1550 m	ND4: APR 7636	This study
North, North East and Samibrano regions				
Montagne d'Ambre	Black	-12.48333 49.31666 800 m	ND4: FGZC 511 RATF 85, FGZC 510 RATF 84 12S and COB: RAN 38129 COB: FGZC 508 RATF 82	This study and from RAXWORTHY et al. (2008) for samples with acronym RAN
Makira Massif (Angozongahy)	Black	-15.43703 49.11861 1005 m	ND4: DRV 5716, ZCMV 11310 (RATF 75)	This study
Manongarivo	Black	-13.97556 48.42667 307 m	ND4 and COB: FGMV 2002.783 (RATF 48)	This study
Tsararano	Not available	-14.90667 49.68667 849 m		
Manarikoba (Tsaratana)	Black	-14.04000 48.78389 1042 m	ND4: 2001-G48 RATF 43	
Tsaratana and Antsahamanara	Black	-14.04500 48.78528 1042 m	12S and COB: RAX 3262 (EU596673, EU596750), RAX 2941 (EU596672, EU596749)	Records and samples are from RAXWORTHY et al. (2008), Antsahamanara locality can be associated because it is part of the Tsaratana massifs
Lohanandroranga	Not available	-14.41650 49.14758 1400–1800 m	12S: RAX 6704 (EU596681)	
Anjanaharibe-Sud	Not available	-14.75500 49.50500 832 m	No genetic samples	
Montagne des Français	Black	-12.32967 49.36750 84 m	ND4: FGMV 2002-3010, RATF 64	This study (identity needs confirmation)

Locality	Oral mucosa colouration	Coordinates and altitude	Voucher specimens and GenBank accession numbers	Comments and genetic sample references
North, North East and Samibrano regions				
Marojejy	Black	-14.43333 49.76167 945 m	ND4 :ZCMV 2037 12S and COB : RAN 39721 (EU596680, EU596757)	This study and RAXWORTHY et al. (2008) for samples with acronym RAN
Betaolana	Not available	-14.40550 49.38030 1260 m	12S and COB : RAX 3644 (EU596679, EU596756)	
Sorata	Not available	-13.68568 49.44185 1300 m	12S and COB : RAX 5260 (EU596677, EU596754)	RAXWORTHY et al. (2008)
Salafaina	Not available	-13.44590 49.71238 600 m	12S and COB :RAX 4434 (EU596676, EU596753)	RAXWORTHY et al. (2008)
Bezavona	Not available	-13.53333 49.86666 574 m	12S and COB : RAX 3937 (EU596675, EU596752)	RAXWORTHY et al. (2008)
Ankitsika	Not available	-13.87239 49.78408 830 m	12S and COB : RAX 4483 (EU596682, EU596758)	RAXWORTHY et al. (2008)
Southern Central East and South East regions				
Kianjavato	pink	-21.35983 47.84800 425 m	ND4 : KAF 125, KAF 137, KAF 338, KAF 154	This study
Andalangina	pink	-21.29722 47.60305 494 m	ND4 : KAF 340	This study
Manangotry	pink	-24.76339 46.86264 279 m	ND4 : AND 51, AND 8, AND 48	This study
Beampingaratra	pink	-24.46347 46.88014 677 m	ND4 : MPFC 420	This study
Ranomafana	pink	-21.25139 47.42447 921 m	ND4 :MPFC 502, URANO 4.45, MPFC 505 COB : ZSM 690-2003 RATF 4	This study
Manombo	pink	-24.00850 46.74166 960 m	ND4 :M 106B	This study
Midongy-Befotaka	Not available	-23.739167 44.026667 875 m		RASELIMANANA unpublished data
Ifanadiana, Ivohibe, Manantantely, Sainte Luce, Malahelo, Eminiminy	pink	Manantantely -24.98300 46.91700 155 m	No genetic samples:	GLAW & VENCES (2007)

Supplementary Table S20. Localities assigned to *U. sameiti* in this and selected previous studies, and corresponding voucher specimens and of the reliably assigned localities.

Locality	Coordinates and altitude	Voucher specimens and GenBank accession numbers	Comments and references
Nosy Boraha (Sainte Marie)	-16.91734 49.87399 68 m	ND4: FRC 532, FRC 533	This study
Tampolo	-17.28866 49.41155 4 m	ND4: RATF 14	This study
Vohibola	-18.60580 49.21383 19 m	ND4: RATF 5, RATF 6	This study
Ambodiriana	-16.67455 49.70277 53 m	ND4: RATF 21, RATF 17 12S: RAX 8954 (EU596684)	This study
Tsararano	-14.90667 49.68667 849 m	No genetic samples	ANDREONE et al. (2000)
Nosy Mangabe	-15.50000 49.76666 153 m	ND4: RATF 2, RATF 3	This study
Vohimana	-18.92077 48.51583 774 m	ND4: MPFC 122	This study
Marolambo and Ambodisavoka	-20.05711 48.18066 667 m	ND4: RATF 24, RATF 148	This study
Sahafina	-18.81063 48.98033 56 m	ND4: RATF 9	This study
Andakibe	-16.78098 49.73447	12S: RAX 9089 (EU596685)	RAXWORTHY et al. (2008)

Supplementary Table S21. Localities assigned to *U. sameiti* (deviating mitochondrial lineages) in this and selected previous studies, and corresponding voucher specimens and Genbank accession numbers for at least one specimen of the reliably assigned localities.

Locality	Coordinates and altitude	Voucher specimens and GenBank accession numbers	Comments and references
Zahamena	-17.66666 48.83333 400–1500 m	ND4: ZAH 94, ZAH 95, ZAH 117, ZAH 119 12S and COB: RAN 45197 (EU596686, EU596761)	This study and RAXWORTHY et al. (2008) for RAN acronym
Analalava	-13.622833 49.9985	12S and COB: RAX 4483 (EU596682, EU596758)	RAXWORTHY et al. (2008)
Betampona	-17.888271 49.225108 200 m	12S and COB: RAX 7700	RAXWORTHY et al. (2008)

Supplementary Table S22. Localities assigned to *U. henkei* in this and selected previous studies, and corresponding voucher specimens and Genbank accession numbers for at least one specimen of the reliably assigned localities.

Locality	Coordinates and altitude	Voucher specimens and GenBank accession numbers	Comments and references
Nosy Be	-13.41137 48.33304 113 m	12S and COB : RAN 43676 (EU596651, EU596728)	RAXWORTHY et al. (2008)
Ankarafantsika	-16.19107 47.10499 275 m	ND4 : APR 7508 COB : FGMV 2000. C1 RATF 40	This study
Tsaratana		12S and COB : RAX 2291 (EU596650, EU596727)	RAXWORTHY et al. (2008)
Tsingy de Bemaraha	-18.69275 44.77227 335 m	12S : FGZC 894 12S and COB : RAN 38460 COB : FGZC 896 RATF 105	This study and RAXWORTHY et al. (2008) for RAN acronym
Manongarivo	-13.96167 48.43333 219 m	12S and COB : RAN 39127 (EU596652, EU596729)	RAXWORTHY et al. (2008)
Ambohimarina (ca. 20 km west of Maromandia)	-14.22111 48.14211 115 m	ND4 : FRC 274	This study
Kelifely	-17.31500 46.00333 290 m	No genetic samples	RAKOTONDRAVONY & GOODMAN (2011)
Ankara	-17.24333 46.10166 258 m	No genetic samples	RAKOTONDRAVONY & GOODMAN (2011)
Sahamalaza	-14.31000 47.91500 120 m	ND4 : APR 6187	This study

Supplementary Table S23. Localities assigned to *U. henkeli* [Ca11] in this and selected previous studies, and corresponding voucher specimens for at least one specimen of the reliably assigned localities.

Locality	Coordinates and altitude	Voucher specimens and GenBank accession numbers	Comments and references
Ankarana	-12.93360 49.12688 124 m	ND4: FGZC 1186 RATF 124, FGZC 604 RATF 93, RALC 139, FGZC 1185 RATF 123, FGZC 1410 RATF 129 ND4 and COB: FGMV 2002.897 RATF 50, 12S and COB: RAN 38929 (EU596655, EU596732)	This study and RAXWORTHY et al. (2008) for samples with RAN acronym
Tsarakibany	-12.77211 49.16763 379–435 m	Not genetically studied	DURKIN et al. (2011)
Montagne des Français	-12.40550 49.36640 240 m	ND4: RATF 34, FGZC 1894, RATF 133, COB: FGMV 2000.312	This study
Analafiana	-13.46637 49.83329 101 m	12S and COB: RAX 4220 (EU596654, EU596731)	RAXWORTHY et al. (2008)
Foret d'Orangea (Ramena)	-12.27333 49.39250 11 m	ND4: FGZC 1287 RATF 125 ZSM 2192/2007	This study

Supplementary Table S24. Summary of the average, minimum and maximum values in % of uncorrected pairwise distances among nominal species of *Uroplatus* in three mitochondrial genes.

	ND4	COB	12S
Average	28.4	27.2	18.1
Maximal	37.8 (<i>U. pietschmanni</i> - <i>U. finivavana</i>)	33.0 (<i>U. guentheri</i> - <i>U. lineatus</i>)	23.2 (<i>U. lineatus</i> - <i>U. ebenau</i>)
Minimal	8.4 (<i>U. giganteus</i> - <i>U. henkeli</i>)	8.6 (<i>U. sikorae</i> - <i>U. sameiti</i>)	6.3 (<i>U. fimbriatus</i> - <i>U. giganteus</i>)

Supplementary Table S25. Uncorrected pairwise distances in % for the mitochondrial cytochrome *b* (COB) gene.

Described species	1	2	3	4	5	6	7	8	9	10	11	12	
<i>U. ebenau</i> (Nosy Be)	1												
<i>U. phantasticus</i> (Mandraka)	2	0.327											
<i>U. finiavana</i>	3	0.284	0.252										
<i>U. alluaudi</i>	4	0.281	0.307	0.301									
<i>U. malahelo</i>	5	0.291	0.268	0.284	0.235								
<i>U. guentheri</i>	6	0.294	0.291	0.278	0.258	0.216							
<i>U. pietschmanni</i>	7	0.297	0.307	0.288	0.206	0.258	0.284						
<i>U. lineatus</i>	8	0.294	0.327	0.320	0.255	0.314	0.330	0.275					
<i>U. fimbriatus</i>	9	0.326	0.272	0.286	0.276	0.252	0.272	0.259	0.252				
<i>U. giganteus</i>	10	0.310	0.291	0.297	0.235	0.261	0.291	0.248	0.301	0.169			
<i>U. henkeli</i>	11	0.300	0.290	0.261	0.293	0.265	0.272	0.251	0.307	0.247	0.272		
<i>U. sikorae</i> (Andasibe)	12	0.305	0.315	0.291	0.285	0.292	0.279	0.295	0.308	0.247	0.243	0.277	
<i>U. sameiti</i> (Ranomafana)	13	0.304	0.327	0.252	0.291	0.294	0.278	0.281	0.320	0.249	0.252	0.265	0.082

Supplementary Table S26. Uncorrected pairwise distances in % for the mitochondrial ND4 gene. Specimens included are representative of specific populations, representing type localities where possible. Bold number represents the highest distance value between taxa.

Described species	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>U. alluaudi</i> RATF 115 Montagne d'Ambre	1												
<i>U. guentheri</i> RAFT 40 Ankarafantsika	2	0.282											
<i>U. malahelo</i> ZCSH 172 Manangotry	3	0.268	0.260										
<i>U. pietschmanni</i> ZAH 219 Zahamena	4	0.255	0.287	0.301									
<i>U. lineatus</i> BET 5.25 Betampona	5	0.286	0.311	0.323	0.329								
<i>U. fimbriatus</i> FRC 534 Nosy Boraha	6	0.275	0.290	0.314	0.312	0.334							
<i>U. giganteus</i> APR 07508 Montagne d'Ambre	7	0.298	0.292	0.315	0.321	0.319	0.290						
<i>U. sikorae</i> RATF 51 Andasibe	8	0.280	0.295	0.322	0.268	0.313	0.253	0.204					
<i>U. sameiti</i> FRC 532 Nosy Boraha	9	0.275	0.309	0.309	0.327	0.321	0.256	0.238	0.125				
<i>U. phantasticus</i> FGZC 4384 Anjozorobe	10	0.302	0.279	0.277	0.291	0.313	0.312	0.311	0.299	0.321			
<i>U. ebenau</i> ACZC1199 Nosy Be	11	0.289	0.304	0.349	0.323	0.343	0.333	0.354	0.339	0.323	0.297		
<i>U. finiavana</i> UAMB5.36 Montagne d'Ambre	12	0.335	0.342	0.342	0.378	0.333	0.303	0.357	0.331	0.342	0.294	0.352	
<i>U. malama</i> APR08322	13	0.273	0.292	0.277	0.319	0.313	0.325	0.303	0.282	0.285	0.279	0.319	0.357
<i>U. henkeli</i> FRC 274 Ambohimarina	14	0.286	0.287	0.319	0.307	0.313	0.275	0.084	0.194	0.240	0.315	0.360	0.321

Supplementary Table S27. Uncorrected pairwise distances in % for the mitochondrial 12S gene. Specimens included are representative of specific populations, representing type localities where possible. Bold numbers represent the lowest and the highest distance value between taxa.

Species and candidate species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	
<i>U. alluaudi</i> RATF 115 Montagne d'Ambre	1																														
<i>U. guentheri</i> RAX 9808 Tsaramandroso	2	0.221																													
<i>U. pietschmanni</i> RAX 7153	3	0.143	0.204																												
<i>U. malahelo</i> RAN 40559 Ambatotsirongorongo	4	0.209	0.180	0.201																											
<i>U. lineatus</i> RAX 4011 Toamasina	5	0.164	0.244	0.184	0.206																										
<i>U. henkeli</i> RAN 43676 Nosy Be	6	0.199	0.234	0.143	0.222	0.170																									
<i>U. fimbriatus</i> RAX 9112 Andakibe	7	0.161	0.219	0.159	0.171	0.171	0.133																								
<i>U. giganteus</i> RAN 38460 Montagne d'Ambre	8	0.184	0.216	0.140	0.188	0.165	0.142	0.063																							
<i>U. giganteus</i> RAN 42560 Ankavanana	9	0.177	0.232	0.153	0.175	0.174	0.133	0.054	0.060																						
<i>U. sameiti</i> RAX 8954 Ambodiriana	10	0.149	0.216	0.137	0.210	0.158	0.101	0.108	0.124	0.117																					
<i>U. henkeli</i> [Ca11] RAN 38929 Ankarana	11	0.177	0.244	0.162	0.222	0.177	0.091	0.136	0.149	0.149	0.079																				
<i>U. sameiti</i> RAN 45197 Zahamena	12	0.161	0.218	0.140	0.171	0.151	0.107	0.092	0.114	0.108	0.054	0.104																			
<i>U. sikorae</i> RAX 2941 Tsaratanana	13	0.161	0.241	0.156	0.206	0.161	0.123	0.098	0.130	0.127	0.060	0.098	0.063																		
<i>U. sameiti</i> RAX 7700 Betampona	14	0.155	0.225	0.143	0.194	0.139	0.111	0.095	0.105	0.105	0.041	0.092	0.044	0.057																	
<i>U. phantasticus</i> [Ca10] RAN 45198 Zahamena	15	0.179	0.224	0.206	0.215	0.223	0.204	0.204	0.208	0.205	0.183	0.198	0.192	0.198	0.176																
<i>U. ebenau</i> [Ca9] RAN 42274 Marojejy	16	0.206	0.222	0.201	0.220	0.235	0.222	0.201	0.220	0.223	0.203	0.222	0.206	0.216	0.203	0.158															
<i>U. ebenau</i> [Ca7] RATF 39 Fierenana	17	0.189	0.232	0.197	0.197	0.218	0.219	0.187	0.207	0.190	0.193	0.203	0.196	0.206	0.197	0.142	0.173														
<i>U. ebenau</i> [Ca6] RAX 4029 Bezavona	18	0.198	0.230	0.197	0.203	0.230	0.224	0.196	0.212	0.190	0.190	0.205	0.202	0.199	0.199	0.121	0.146	0.130													
<i>U. ebenau</i> [Ca5] RATF 92 Ankarana	19	0.220	0.261	0.223	0.225	0.252	0.228	0.219	0.226	0.219	0.225	0.225	0.225	0.212	0.232	0.205	0.231	0.228	0.201												
<i>U. ebenau</i> [Ca4] RATF 73 Makira West	20	0.204	0.231	0.203	0.232	0.240	0.231	0.219	0.232	0.222	0.203	0.208	0.221	0.221	0.212	0.148	0.163	0.143	0.087	0.237											
<i>U. ebenau</i> [Ca3] DRV 6280 Andrevorevo	21	0.179	0.199	0.178	0.212	0.217	0.199	0.196	0.203	0.193	0.174	0.205	0.183	0.199	0.180	0.140	0.149	0.156	0.103	0.228	0.097										
<i>U. ebenau</i> [Ca2] ZCMV 12389 Tsaratanana	22	0.188	0.212	0.169	0.216	0.232	0.215	0.199	0.226	0.216	0.193	0.219	0.202	0.209	0.206	0.160	0.152	0.125	0.110	0.243	0.097	0.120									
<i>U. ebenau</i> [Ca1] DRV 6324 Ambodikakazo	23	0.215	0.238	0.201	0.207	0.234	0.235	0.204	0.226	0.201	0.204	0.238	0.200	0.222	0.201	0.170	0.175	0.107	0.129	0.235	0.153	0.155	0.148								
<i>U. ebenau</i> ACZC 1199 Nosy Be	24	0.216	0.220	0.224	0.196	0.232	0.232	0.185	0.191	0.201	0.223	0.213	0.204	0.213	0.204	0.203	0.223	0.217	0.191	0.257	0.212	0.204	0.217	0.214							
<i>U. finjavana</i> ACZC 1420 Joffreville	25	0.209	0.229	0.220	0.207	0.225	0.219	0.178	0.194	0.194	0.203	0.222	0.210	0.210	0.203	0.154	0.181	0.154	0.139	0.235	0.124	0.142	0.121	0.171	0.192						
<i>U. malama</i> MPFC 411 Beampingaratra	26	0.158	0.196	0.156	0.181	0.151	0.180	0.171	0.162	0.181	0.143	0.174	0.158	0.158	0.143	0.182	0.203	0.205	0.198	0.219	0.195	0.182	0.197	0.211	0.201	0.174					
<i>U. phantasticus</i> RAX 9399 Mandraka	27	0.185	0.236	0.206	0.221	0.229	0.224	0.211	0.208	0.212	0.196	0.208	0.201	0.204	0.183	0.029	0.170	0.151	0.130	0.207	0.151	0.140	0.166	0.169	0.190	0.150	0.182				
<i>U. phantasticus</i> FGZC 4341 Anjozorobe	28	0.191	0.233	0.218	0.218	0.232	0.220	0.210	0.214	0.211	0.195	0.201	0.204	0.204	0.182	0.019	0.173	0.148	0.124	0.217	0.151	0.143	0.169	0.169	0.192	0.150	0.191	0.022			
<i>U. phantasticus</i> RATF 45 Ranomafana	29	0.178	0.227	0.212	0.208	0.225	0.223	0.207	0.204	0.208	0.195	0.213	0.201	0.201	0.179	0.025	0.167	0.148	0.121	0.207	0.141	0.137	0.163	0.166	0.192	0.147	0.178	0.013	0.022		
<i>U. phantasticus</i> KAF 183 Kianjavato	30	0.175	0.226	0.205	0.211	0.219	0.210	0.201	0.198	0.201	0.188	0.207	0.194	0.194	0.173	0.032	0.166	0.148	0.117	0.207	0.141	0.139	0.159	0.162	0.189	0.150	0.175	0.025	0.028	0.013	
<i>U. phantasticus</i> RATF 38 Fierenana	31	0.191	0.230	0.218	0.215	0.232	0.220	0.210	0.214	0.211	0.195	0.201	0.204	0.204	0.182	0.022	0.173	0.148	0.124	0.214	0.151	0.143	0.169	0.169	0.186	0.150	0.191	0.025	0.009	0.025	0.032

Supplementary Table S28. Uncorrected pairwise distances in % for the mitochondrial COB gene. Specimens included are representative of specific populations, representing type localities where possible. Two voucher numbers are given for some specimens,, usually referring to museum (ZSM) and field or lab numbers (RATF). Bold numbers represent the lowest and the highest distance value between taxa.

Species and Candidate species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	
<i>U. alluaudi</i> RATF 81 Montagne d'Ambre	1																										
<i>U. malahelo</i> RAN 40559 Ambatotsirongorongo	2	0.235																									
<i>U. guentheri</i> ZSM 476/2001 Ankarafantsika	3	0.258	0.216																								
<i>U. pietschmanni</i> ZCMV 2482	4	0.206	0.258	0.284																							
<i>U. lineatus</i> ZCMV 2486 / RATF72	5	0.255	0.314	0.330	0.275																						
<i>U. fimbriatus</i> RAX 9112 Andakibe	6	0.276	0.252	0.272	0.259	0.252																					
<i>U. giganteus</i> ZSM 267/2004 / FGZC 514 Montagne d'Ambre	7	0.235	0.261	0.291	0.248	0.301	0.169																				
<i>U. henkeli</i> RAN 43676 Nosy Be	8	0.293	0.265	0.272	0.251	0.307	0.247	0.272																			
<i>U. phantasticus</i> RAX 8079 Betampona	9	0.324	0.294	0.307	0.297	0.324	0.272	0.304	0.290																		
<i>U. phantasticus</i> RATF 38 / ZSM 212/2002 Fierenana	10	0.297	0.284	0.310	0.281	0.304	0.276	0.297	0.279	0.075																	
<i>U. phantasticus</i> RAN 44586 Andringitra	11	0.307	0.271	0.294	0.294	0.310	0.276	0.307	0.276	0.144	0.124																
<i>U. phantasticus</i> FGMV 2002.640 / RATF 46 Ranomfana	12	0.307	0.278	0.297	0.291	0.317	0.276	0.310	0.283	0.121	0.108	0.029															
<i>U. phantasticus</i> RAX 9399 Mandraka	13	0.307	0.268	0.291	0.307	0.327	0.272	0.291	0.290	0.108	0.092	0.118	0.101														
<i>U. sikorae</i> ZSM 690/2003 FGMV 2002.311 RATF 44 Ranomafana	14	0.291	0.294	0.278	0.281	0.320	0.249	0.252	0.265	0.317	0.320	0.317	0.324	0.327													
<i>U. sikorae</i> ZSM 920/2003 FGMV 2002.951 / RATF 52 Andasibe	15	0.285	0.292	0.279	0.295	0.308	0.247	0.243	0.277	0.341	0.311	0.305	0.311	0.315	0.082												
<i>U. finiavana</i> ZSM322/2004 FGZC 619 / RATF 95	16	0.301	0.284	0.278	0.288	0.320	0.286	0.297	0.261	0.271	0.268	0.261	0.268	0.252	0.291	0.275											
<i>U. ebenau</i> i ZSM 856/2003 / FGMV 2002.826 Manongarivo	17	0.281	0.291	0.294	0.297	0.297	0.326	0.310	0.300	0.307	0.314	0.314	0.307	0.327	0.304	0.305	0.284										
<i>U. ebenau</i> i [Ca1] FGMV 2001.F10 / RATF42 Manarikoba	18	0.333	0.320	0.301	0.297	0.366	0.346	0.337	0.325	0.271	0.271	0.291	0.278	0.278	0.330	0.348	0.248	0.317									
<i>U. ebenau</i> i [Ca2] RAN 43228 Tsaratanana	19	0.297	0.281	0.271	0.278	0.317	0.292	0.297	0.283	0.235	0.239	0.258	0.245	0.239	0.288	0.295	0.216	0.271	0.255								
<i>U. ebenau</i> i [Ca3] ZSM 79/2005 ZCMV 2030 / RATF 67 Marojejy	20	0.333	0.284	0.288	0.281	0.317	0.279	0.281	0.279	0.232	0.252	0.245	0.239	0.232	0.327	0.318	0.186	0.275	0.245	0.206							
<i>U. ebenau</i> i [Ca4] RAX 3449 Betaolana	21	0.320	0.281	0.265	0.275	0.314	0.276	0.268	0.283	0.209	0.229	0.248	0.255	0.242	0.310	0.308	0.193	0.275	0.278	0.206	0.131						
<i>U. ebenau</i> i [Ca6] RAX 4433 Salafaina	22	0.310	0.284	0.284	0.275	0.320	0.272	0.255	0.272	0.235	0.245	0.245	0.239	0.229	0.284	0.295	0.154	0.281	0.229	0.196	0.141	0.183					
<i>U. ebenau</i> i [Ca9] RAN 42274 Marojejy	23	0.297	0.271	0.284	0.275	0.310	0.299	0.291	0.311	0.275	0.284	0.265	0.261	0.271	0.337	0.341	0.261	0.304	0.265	0.275	0.252	0.252	0.255				
<i>U. phantasticus</i> [Ca10] RAN 45198 Zahamena	24	0.320	0.284	0.301	0.301	0.324	0.266	0.304	0.293	0.026	0.056	0.127	0.111	0.101	0.317	0.325	0.275	0.320	0.278	0.232	0.242	0.212	0.239	0.281			
<i>U. sameiti</i> RAN 45197 Zahamena	25	0.284	0.297	0.281	0.278	0.307	0.233	0.245	0.258	0.333	0.317	0.320	0.327	0.320	0.167	0.151	0.281	0.307	0.353	0.301	0.297	0.307	0.297	0.337	0.330		
<i>U. sameiti</i> RAX 7700 Betampona	26	0.289	0.258	0.252	0.275	0.302	0.227	0.248	0.238	0.332	0.326	0.326	0.319	0.329	0.151	0.148	0.252	0.295	0.322	0.285	0.292	0.302	0.279	0.319	0.336	0.174	
<i>U. henkeli</i> [Ca11] ZSM 889/2003 / RATF 50 Ankarana	27	0.278	0.235	0.258	0.261	0.301	0.213	0.229	0.152	0.284	0.281	0.275	0.275	0.278	0.235	0.216	0.268	0.317	0.314	0.275	0.258	0.248	0.245	0.294	0.278	0.222	0.208

Supplementary Table S29. Uncorrected pairwise distances in % for the ND4 mitochondrial gene fragment. Specimens included are representative of specific populations, representing type localities where possible. Note that the low divergence of *U. henkeli* from Ambohimarina to several other taxa is due to the small overlap of DNA fragments. Bold numbers represent the lowest and the highest distance value between taxa.

Species and Candidate species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
<i>U. alluaudi</i> RATF 115 Montagne d'Ambre	1																													
<i>U. guentheri</i> RAFT 40 Ankarafantsika	2	0.282																												
<i>U. malahelo</i> ZCSH 172 Manangotry	3	0.268	0.260																											
<i>U. pietschmanni</i> ZAH 219 Zahamena	4	0.255	0.287	0.301																										
<i>U. lineatus</i> BET 5.25 Betampona	5	0.286	0.311	0.323	0.329																									
<i>U. fimbriatus</i> FRC 534 Sainte Marie	6	0.275	0.290	0.314	0.312	0.334																								
<i>U. henkeli</i> APR 07508 Ankarafantsika	7	0.298	0.292	0.315	0.321	0.319	0.290																							
<i>U. sikorae</i> PSG 2523 Ambatovy	8	0.253	0.299	0.321	0.281	0.321	0.259	0.239																						
<i>U. sameiti</i> KAF 125 Kianjavato	9	0.282	0.282	0.321	0.285	0.307	0.262	0.234	0.112																					
<i>U. sameiti</i> AND 51 Manangotry	10	0.257	0.304	0.329	0.279	0.299	0.253	0.230	0.094	0.100																				
<i>U. sameiti</i> URANO 4.45 Ranomafana	11	0.277	0.309	0.345	0.279	0.311	0.264	0.238	0.118	0.092	0.084																			
<i>U. sikorae</i> RATF 51 Andasibe	12	0.280	0.295	0.322	0.268	0.313	0.253	0.204	0.024	0.085	0.095	0.092																		
<i>U. sameiti</i> FRC 532 Nosy Boraha	13	0.275	0.309	0.309	0.327	0.321	0.256	0.238	0.150	0.188	0.177	0.188	0.125																	
<i>U. sameiti</i> MPFC 0122 Vohimana	14	0.277	0.290	0.314	0.305	0.323	0.269	0.243	0.141	0.174	0.181	0.178	0.122	0.087																
<i>U. phantasticus</i> FGZC 4384 Anjozorobe	15	0.302	0.279	0.277	0.291	0.313	0.312	0.311	0.299	0.295	0.293	0.313	0.299	0.321	0.320															
<i>U. phantasticus</i> MPFC 511 Ranomafana	16	0.314	0.297	0.283	0.303	0.311	0.319	0.307	0.295	0.297	0.283	0.307	0.301	0.312	0.308	0.086														
<i>U. phantasticus</i> BET 5.19 Betampona	17	0.307	0.292	0.289	0.293	0.307	0.310	0.315	0.308	0.305	0.303	0.321	0.303	0.314	0.320	0.038	0.086													
<i>U. henkeli</i> [Ca11] RATF 50 Ankarana	18	0.294	0.301	0.322	0.294	0.313	0.271	0.148	0.191	0.210	0.203	0.217	0.201	0.212	0.225	0.289	0.284	0.289												
<i>U. sameiti</i> ZAH117 Zahamena	19	0.268	0.289	0.289	0.271	0.299	0.255	0.208	0.152	0.140	0.152	0.160	0.118	0.157	0.174	0.269	0.273	0.273	0.193											
<i>U. phantasticus</i> [Ca10] ZAH257 Zahamena	20	0.282	0.265	0.295	0.303	0.329	0.332	0.347	0.330	0.323	0.323	0.327	0.308	0.359	0.327	0.242	0.242	0.244	0.317	0.311										
<i>U. ebenauui</i> [Ca8] APR 07667 Ambohitantately	21	0.300	0.282	0.289	0.301	0.315	0.301	0.335	0.297	0.291	0.299	0.311	0.308	0.323	0.314	0.227	0.237	0.231	0.325	0.301	0.259									
<i>U. ebenauui</i> APR 05859 Marotrandrano	22	0.309	0.292	0.315	0.309	0.325	0.332	0.343	0.371	0.333	0.329	0.329	0.339	0.359	0.348	0.255	0.267	0.259	0.327	0.325	0.279	0.273								
<i>U. ebenauui</i> [Ca4] JAR3.2 Anjanaharibe	23	0.300	0.304	0.297	0.303	0.349	0.332	0.343	0.359	0.325	0.337	0.333	0.334	0.352	0.351	0.255	0.261	0.267	0.334	0.317	0.277	0.275	0.080							
<i>U. ebenauui</i> [Ca3] DRV 6280 Andrevorevo	24	0.280	0.292	0.305	0.313	0.311	0.319	0.317	0.344	0.317	0.323	0.337	0.306	0.350	0.342	0.248	0.261	0.255	0.305	0.289	0.275	0.271	0.174	0.176						
<i>U. ebenauui</i> [Ca2] ZCMV 12389 Tsaratanana	25	0.295	0.289	0.301	0.319	0.317	0.349	0.309	0.319	0.315	0.305	0.325	0.310	0.330	0.327	0.253	0.271	0.265	0.327	0.293	0.269	0.281	0.259	0.251	0.246					
<i>U. ebenauui</i> [Ca1] MPFC 562 Ambodikakazo	26	0.311	0.297	0.279	0.313	0.325	0.323	0.323	0.290	0.311	0.305	0.313	0.299	0.327	0.325	0.244	0.242	0.250	0.296	0.307	0.253	0.187	0.287	0.285	0.293	0.295				
<i>U. ebenauui</i> ACZC 1199 Nosy Be	27	0.289	0.304	0.349	0.323	0.343	0.333	0.354	0.306	0.328	0.330	0.345	0.339	0.323	0.320	0.297	0.306	0.295	0.348	0.323	0.343	0.297	0.325	0.315	0.330	0.323	0.334			
<i>U. finiavana</i> UAMB5.36 Montagne d'Ambre	28	0.335	0.342	0.342	0.378	0.333	0.303	0.357	0.339	0.345	0.303	0.348	0.331	0.342	0.357	0.294	0.312	0.300	0.363	0.336	0.321	0.297	0.255	0.267	0.240	0.285	0.315	0.352		
<i>U. malama</i> APR08322	29	0.273	0.292	0.277	0.319	0.313	0.325	0.303	0.295	0.297	0.291	0.295	0.282	0.285	0.275	0.279	0.295	0.281	0.298	0.277	0.305	0.313	0.299	0.301	0.307	0.297	0.321	0.319	0.357	
<i>U. henkeli</i> FRC 274 Ambohimarina	30	0.286	0.287	0.319	0.307	0.313	0.275	0.084	0.223	0.230	0.232	0.236	0.194	0.240	0.247	0.315	0.313	0.309	0.138	0.214	0.339	0.341	0.329	0.331	0.303	0.317	0.309	0.360	0.315	0.321

Supplementary Table S30. Table of CITES export quota for *Uroplatus* species. Species in bold face are commercialized following the quotas 2012.

Species	IUCN status (Version 2013.1)	CITES annual quota							
		2012	2011	2010	2009	2008	2007	2006	2005
<i>Uroplatus alluaudi</i>	Near threatened	0	0	0	0	0	0	0	0
<i>Uroplatus eburnai</i>	Vulnerable	83	250	250	2000	2000	2000	2000	2000
<i>Uroplatus finiavana</i>	Not evaluated	0	0	0	0	0	0	0	0
<i>Uroplatus fimbriatus</i>	Least Concern	487	312	312	2000	2000	2000	2000	2000
<i>Uroplatus giganteus</i>	Vulnerable	0	0	0	0	0	0	0	0
<i>Uroplatus guentheri</i>	Endangered	0	125	125	100	100	100	100	100
<i>Uroplatus henkeli</i>	Vulnerable	35	125	125	200	200	200	200	200
<i>Uroplatus lineatus</i>	Least Concern	227	63	63	1000	1000	1000	1000	1000
<i>Uroplatus malahelo</i>	Endangered	0	0	0	0	0	0	0	0
<i>Uroplatus malama</i>	Vulnerable	0	0	0	100	100	100	100	100
<i>Uroplatus phantasticus</i>	Least Concern	70	0	0	2000	2000	2000	2000	2000
<i>Uroplatus pietschmanni</i>	Endangered	0	0	0	500	500	500	500	500
<i>Uroplatus sameiti</i>	Least Concern	0	0	0	0	0	0	0	0
<i>Uroplatus sikorae</i>	Least Concern	867	2 000	2000	2000	2000	2000	2000	2000