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A new large-sized species of leaf-tailed gecko (*Uroplatus*) from northern Madagascar

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Abstract. We describe a large new species of leaf-tailed gecko endemic to northern Madagascar. *Uroplatus garamaso* sp. n. is the sister species of *U. henkeli* but differs by a genetic divergence > 8% in the mitochondrial 16S rRNA gene, by the absence of haplotype sharing in four nuclear-encoded genes analyzed, a smaller body size, slightly narrower tail, a more pronounced yellowish/reddish iris colour in most individuals, and lack of black pigmentation on the tip of the tongue. The new species also appears to consistently differ from *U. henkeli* in genital morphology, with the apex of the hemipenis ending in two terminal elements consisting of 4–5 rotulae and longitudinal rows of calyces (versus an apex with irregularly distributed calyces and ending in two symmetrical structures consisting of two broader serrated fleshy elements in *U. henkeli*). We genetically confirm the occurrence of *U. henkeli* over a rather wide area, ranging from Tsingy de Bemaraha in the West to Nosy Be in the Sambirano region of northern Madagascar. Both, *U. henkeli* and the new species contain several deep mitochondrial lineages that are considered as conspecific due to extensive haplotype sharing and lack of obvious morphological differences among them.

Key words. Squamata, Gekkonidae, *Uroplatus henkeli*, *Uroplatus garamaso* sp. n., taxonomy, systematics, molecular genetics, morphology.

Introduction

Northern Madagascar, defined by BROWN et al. (2016) as the area north of a diagonal spanning from 15.5° S on the east coast to ca. 15.0° S on the west coast, is known to be an area of high regional and local endemism (VENCES et al. 2009, BROWN et al. 2014, 2016). The high elevational heterogeneity (RAXWORTHY & NUSSBAUM 1995, WOLLENBERG et al. 2008) and the mosaic of dry and humid forests, isolated volcanic mountains such as Montagne d'Ambre, as well as karstic limestone massifs such as Ankarana and Montagne des Français, have led to an astonishing degree of microendemism, where several species of organisms are known

or assumed to occupy only minute ranges (e.g., GLAW et al. 2006a, 2012, D'CRUZE et al. 2010, KÖHLER et al. 2010, MITTERMEIER et al. 2010, RUANE et al. 2016, RAKOTOARISON et al. 2017, SCHERZ 2020, VENCES et al. 2022a).

This microendemism (WILMÉ et al. 2006) characterizes numerous species of northern Madagascar's herpetofauna, for instance geckos of the genera *Blaesodactylus*, *Geckolepis* and *Paroedura* (JACKMAN et al. 2008, GLAW et al. 2014, 2018, JONO et al. 2015, SCHERZ et al. 2017) as well as *Uroplatus* (RATSOAVINA et al. 2011, 2017, 2019a, 2019b, 2020). The latter genus represents the peculiar leaf-tailed geckos of Madagascar, with a high species diversity of small-sized forms, and several large-sized species in the *U. fimbriatus*

group (GLAW et al. 2006b, GREENBAUM et al. 2007, RAXWORTHY et al. 2008, RATSOAVINA et al. 2013, GEHRING 2020), which are among the most spectacular and prominent flagship species in Madagascar's herpetofauna (WOLLENBERG et al. 2011), and are highly sought after in the reptile pet trade (UNEP-WCMC 2015, GEHRING 2020, TOROPOV 2021, CARPENTER & ANDREONE 2023).

The *U. fimbriatus* species group is currently composed of three species complexes, each consisting of large geckos with a flattened body and head, flat and broad tail, and lateral dermal fringes which allow an almost perfect camouflage when the animals roost vertically during the day with their heads pointing downwards on tree trunks (GEHRING 2020): (1) the *U. fimbriatus* complex contains *U. fimbriatus* from low-elevation rainforest in the Southern Central East and Northern Central East (geographical regions follow BOUMANS et al. 2007), as well as *U. giganteus* from the North East and North (GEHRING et al. 2018); (2) the *U. sikorae* complex contains an intriguing diversity of relatively deep genetic lineages currently classified in two species, *U. sameiti* from mainly low elevations in the Northern Central East, and the widespread *U. sikorae* from mid-elevation rainforests spanning from the extreme South East to the North (GEHRING et al. 2023); and (3) the *U. henkeli* complex, the focus of the current study, contains *U. henkeli* from the West, North West and Sambirano regions, and an undescribed candidate species *U. sp.* [Ca11] from the North.

Uroplatus henkeli was scientifically named and described by BÖHME & IBISCH (1990) in their revision of the *U. fimbriatus* group. These authors noted differences in external morphology (smaller body size, deeper axillary pits, broader lateral skin flaps, more symmetrical dorsal pattern) and hemipenial structures between specimens from the small offshore island Nosy Be in the Sambirano region, and individuals of *U. fimbriatus*, and concluded that the form from Nosy Be represents a separate species, *U. henkeli*. BÖHME & IBISCH (1990) also reported a specimen from Ankarafantsika in the North West of Madagascar which they referred to *U. henkeli* pending further confirmation. In the first comprehensive multi-gene phylogeny of the genus, GREENBAUM et al. (2007) studied four samples of the *U. henkeli* complex and found one subclade with samples from Nosy Be and Bemaraha in the West, and a second subclade with samples from Montagne des Français and Ankarana in the North, and concluded that one or more cryptic taxa may be subsumed within *U. henkeli* as then conceived. RAXWORTHY et al. (2008) found the same two subclades, extending the genetic records of *U. henkeli* to Manongarivo and Tsaratanana, and of the second subclade (called *Uroplatus sp. H*) to Analafiana. These data were aggregated and further expanded by RATSOAVINA et al. (2013), who called the northern subclade *Uroplatus henkeli* [Ca11], genetically confirmed the presence of *U. henkeli* at Ankarafantsika, and added new, genetically confirmed records of *U. henkeli* from Ambohimarina and Sahamalaza, and of *U. henkeli* [Ca11] from near Antsiranana. We here refer to this latter lineage as *U. sp.* [Ca11] to avoid confusion with *U. henkeli*.

Since its first discovery by GREENBAUM et al. (2007) the genetic lineage *U. sp.* [Ca11] has not been assessed taxonomically. Specimens assignable to this lineage have, however, already been exported from Madagascar for the pet trade, and a series of purportedly diagnostic characters in colour pattern have been reported (e.g., GEHRING 2020). In the present study, we revise the taxonomy of the *U. henkeli* species complex based on the integration of DNA sequences of mitochondrial and nuclear genes as well as external and genital morphology. We conclude that *U. sp.* [Ca11] corresponds to a distinct evolutionary lineage, and describe and name it as a species new to science.

Materials and methods

Fieldwork and sampling

Gecko specimens were collected opportunistically, mostly during the night, with the aid of headlamps and torches, and sometimes during the day by searching for roosting specimens on tree trunks. Vouchers were sacrificed using ethically approved methods such as lidocaine or ketamine overdose, fixed in 10% formalin or 98% ethanol, and preserved in 75% ethanol. Muscle tissue samples were taken from freshly killed specimens in the field and preserved in 98–100% ethanol. In other cases, small clips from the skin flaps or buccal swabs were taken from specimens in the field and preserved in 98–100% ethanol, and specimens released afterwards. Field numbers and tissue numbers refer to the collections of A. CROTTINI (ACZC, ACP), F. GLAW and M. VENCES (FGZC, FGMV), A. RAKOTOARISON (ANDO, RALC), F. M. RATSOAVINA (FRC, FRT, RATF), A. P. RASELIMANANA (APR), M. D. SCHERZ (MSTIS, MSZC); furthermore, sequences retrieved from GenBank are identified with the field numbers of R. A. NUSSBAUM (RAN) and C. J. RAXWORTHY (RAX). Museum acronyms used are UADBA (Université d'Antananarivo, Département de Biologie Animale) and ZSM (Zoologische Staatssammlung, München).

Morphology

We took morphological measurements to the nearest mm or nearest 0.1 mm: SVL (snout–vent length, defined as distance between snout tip and the proximal cloaca opening); TaL (tail length, from cloaca to tail tip); TaW (maximum tail width); ToL (total length); HL (head length, from snout tip to posterior-most margin of ear opening); HW (maximum head width); HH (maximum head height posterior to the eyes); NSD (nostril–snout tip distance, from anterior margin of nostril to snout tip); ESD (eye–snout tip distance, from anterior margin of eye to snout tip); NND (nostril–nostril distance); ED (horizontal eye diameter); EOD (horizontal ear opening diameter); EOH (vertical ear opening diameter); EED (eye–ear distance, from posterior margin of eye to anterior margin of ear opening); LAL (lower arm length, from the elbow to the tip of the

longest finger); AGD (axilla–groin distance); WFJ (maximum width of lateral fringes at lower jaws); WFF (maximum width of lateral fringes along flanks). We further performed the following scale counts: SUPL (number of supralabials); INFL (number of infralabials); L4T (scansor lamellae under fourth toe); qualitative size of rostral compared to first supralabial. Sex was determined by inspection of the tail base (presence or absence of hemipenes bulges). Tail measurements refer to original (not regenerated) tails only. Description of colour in life is based on digital photographs and colour slides.

Molecular genetics

For molecular phylogenetics, three mitochondrial gene fragments were amplified and sequenced: 12S ribosomal RNA (12S rRNA or 12S), the 3' segment of the 16S ribosomal RNA (16S rRNA or 16S), and NADH dehydrogenase subunit 4 (ND4). We used sequences compiled by RATSOAVINA et al. (2013) and complemented these with new sequences available from GenBank, or produced for this study. Because some previous molecular studies that included samples of the *U. henkeli* complex (e.g., RAXWORTHY et al. 2008, RATSOAVINA et al. 2013, PENNY et al. 2017) only sequenced either 12S, COI or ND4, and the respective tissue samples in many cases were not available to us, representatives of some regional clades in the initial dataset were present for only one gene fragment, and those of other clades for another gene fragment, thus precluding direct inference of relationships and causing phylogenetic artefacts in exploratory phylogenetic inference. New sequencing was therefore directed to generate all three gene fragments (12S, 16S and ND4) for at least one sample per major subclade.

For this purpose, we extracted total genomic DNA with a standard salt extraction protocol after proteinase K digestion (BRUFORD et al. 1992). Polymerase chain reaction with standard cycling protocols were carried out using the following primers: 12S, 12SAr-L 5'-AAACTGGGATTAGATAACCCACTAT-3' and 12SBr-H 5'-GAGGGTGACGGGCGGTGTGT-3' (PALUMBI et al. 1991); 16S, 16SAr-L 5'-CGCCTGTTTATCAAAAACAT-3' and 16SBr-H 5'-CCGGTCTGAACTCAGATCACGT-3' (PALUMBI et al. 1991); ND4, ND4 5'-CACCTATGACTACCAAAA-GCTCATGTAGAAGC-3' and LeutRNA 5'-CATTACTTT-TACTTGGATTGACC-3' (ARÉVALO et al. 1994).

In addition, we sequenced fragments of four nuclear-encoded genes: prolactin receptor (PRLR) using primers PRLR-fi 5'-GACARYGARGACCAGCAACTRATGCC-3' and PRLR-r3 5'-GACYTTGTGRACTTCYACRTAATCCAT-3' (TOWNSEND et al. 2008), oocyte maturation factor mos (CMOS) using primers CO8 5'-GCTTGTGTTCAATAGACTGG-3' and CO9 5'-TTTGGGAGCATCCAAAGTCTC-3' (HAN et al. 2004), and saccin (SACS) and leucine-rich repeat and WD repeat-containing protein (KIAA1239) following primers and the nested PCR approach described in SHEN et al. (2012).

PCR products were purified with Exonuclease I and Shrimp Alkaline Phosphatase digestion, and the purified products along with sequencing primers were shipped to LGC Genomics (Berlin) for sequencing on automated capillary sequencing instruments. We quality-checked sequences and manually trimmed poor-quality stretches in CodonCode Aligner (Codon Code Corporation). We used MEGA7 (KUMAR et al. 2016) for initial sequence alignment, exploratory phylogenetic inference, and for calculating uncorrected p-distances between sequences. Newly generated sequences were deposited in GenBank under the following accession numbers: OR081559–OR081597, OR082623–OR082742.

We curated sequences and associated metadata in a Microsoft Excel spreadsheet. The sequences of the three mitochondrial gene fragments were then exported as tab-delimited text, and used as input for Concatenator (VENCES et al. 2022b), which is part of the iTaxoTools project (VENCES et al. 2021). In this program, each gene fragment was aligned with MAFFT (KATO & STANLEY 2013) and concatenated into a Nexus-formatted file. Phylogenetic analysis of the unpartitioned concatenated alignment was performed under the Maximum Likelihood (ML) optimality criterion and with a GTR+G substitution model in RAXML (STAMATAKIS 2014) implemented in raxmlGUI 2.0 (EDLER et al. 2021), assessing node support with 1000 bootstrap replicates. Furthermore, we performed a partitioned Bayesian Inference (BI) analysis with MrBayes 3.2 (RONQUIST et al. 2012), defining three partitions (12S + 16S, with a GTR+G model; ND4 third codon positions with a GTR+G model; and ND4 first and second codon positions with a K2P+G model) and running 20 million generations, sampling every 1000 trees, and discarding the first 25% of sampled trees as burn-in.

We used the PHASE algorithm (STEPHENS et al. 2001) as implemented in the software DnaSP (Version 6.12.3; LIBRADO & ROZAS 2009) to infer alleles (haplotypes) separately for each of the nuclear DNA fragments. From each set of haplotype sequences we reconstructed a Maximum Likelihood tree using the Jukes-Cantor substitution model (chosen to avoid overparameterization) in MEGA7 (KUMAR et al. 2016) and used the resulting trees to build haplotype networks for each fragment by entering each tree with its respective alignment in the software Haploviewer, written by G. B. EWING (<http://www.cibiv.at/~greg/haploviewer>) which implements the methodological approach of SALZBURGER et al. (2011).

Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The LSID (Life Sci-

ence Identifier) for this publication is: urn:lsid:zoobank.org:pub:33939507-4292-4066-913F-8110DF20F5A7. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: salamandra-journal.com, zenodo.org.

Results

We assembled a dataset of 2225 bases of the mitochondrial DNA fragments (12S, 16S, ND4) for 47 ingroup tips. ML and BI phylogenetic trees (Fig. 1) agreed in distinguishing two main clades corresponding to *U. henkeli* (18 samples; maximum node support from bootstrap and Bayesian posterior probabilities: BS=100%; PP=1.0) and *U. sp.* [Ca11] (29 samples; BS=79%; PP=1.0). Within *U. henkeli*, three relatively shallow subclades were identified, corresponding to samples from (i) Bemaraha (BS=70%; PP=0.79), (ii) Sahamalaza (BS=91%; PP=0.99), and (iii) the remaining localities, Nosy Be (the type locality), Manongarivo, Ambohimarina, and Tsaratanana (BS=75%; PP=0.99) (Figs 1–2). Also for *U. sp.* [Ca11], three subclades were distinguished, but with distinctly deeper splits among them; one subclade included samples from Fanambana and Analafiana (BS=100%; PP=1.0), the second subclade included samples from Orangea and Ampombofofo (BS=97%; PP=1.0), and the third subclade occurred at Ankarana, Montagne des Français, Forêt d'Ambre, and the western slope of Montagne d'Ambre (BS=96%; PP=1.0). The Orangea/Ampombofofo subclade was sister to the Ankarana/Montagne des Français subclade (BS=79%; PP=1.0) and the two together formed the sister group of the Fanambana/Analafiana subclade (Figs 1–2).

Genetic distances between the main mitochondrial clades were high. In the 16S gene fragment, they amounted to 8.1–10.6% between *U. henkeli* and *U. sp.* [Ca11], 2.5–5.6% among the three subclades of *U. henkeli*, and 4.9–7.2% between the three subclades of *U. sp.* [Ca11].

The haplotype networks (Fig. 3) reconstructed from the four nuclear-encoded gene fragments were concordant with the mitochondrial tree. In networks of CMOS, PRLR and SACS, *U. henkeli* and *U. sp.* [Ca11] corresponded to fully separate clusters, while in the KIAA1239 network, one individual of *U. henkeli* was placed in the *U. sp.* [Ca11] cluster, but without haplotype sharing. In contrast, the three deep mitochondrial lineages of *U. sp.* [Ca11] were not reflected in the networks; samples from Ankarana/Montagne des Français/Montagne d'Ambre, Orangea/Ampombofofo, and Fanambana/Analafiana, showed extensive haplotype sharing, except for PRLR where the two samples from Fanambana formed a separate cluster of haplotypes (Fig. 3).

Morphological comparisons revealed a series of external morphological traits in which *U. sp.* [Ca11] differs from *U. henkeli*, even if many of them were somewhat ambiguous and not easy to recognize. In the preserved material available for examination (Table 1; Fig. 4), body size was smaller (almost without overlap), and tails narrower and

somewhat shorter in *U. sp.* [Ca11] (Figs 4–5; for detailed values, see Diagnosis section below). The body size differences agree with data presented by BÖHME & IBISCH (1990): for *U. henkeli* from the type locality Nosy Be, they reported SVLs of 130–160 mm for 12 out of 13 specimens, in agreement with our data where all adult *U. henkeli* had SVL values > 138 mm, compared to 83–139 mm in *U. sp.* [Ca11].

The examined specimens of *U. sp.* [Ca11] had hemipenes with differentiated lateral calyces, well visible in the sulcal view on the organ, better developed in the two ZSM vouchers than in the ZFMK one (Fig. 6). The holotype of *U. henkeli* from Nosy Be (Fig. 6) also has strongly developed calyces covering the truncal part of its hemipenis while those of the two ZSM vouchers from Bemaraha are indistinct. These differences might be best explained by seasonal variation – as is also known for chameleons (KLAVER & BÖHME 1986) – but may also represent geographic variation.

A difference between the hemipenes of the two species might however occur in their apical structures. In specimen ZFMK 75754 (*U. sp.* [Ca11]) the apex ends in two terminal elements consisting of 4–5 serrated semicircles (here termed rotulae, in analogy to similar structures in chameleons) grouped in a series one after another, and the calyces at the base of these clusters tend to form longitudinal rows. In contrast, the calyces of the holotype of *U. henkeli* are irregularly distributed, and the apex ends in two symmetrical structures, each of them consisting of two broader serrated fleshy elements. These differences are also apparent across the hemipenes of additional specimens examined (Fig. 6), despite differences in the expression of calyces.

The hemipenis of *U. sikorae* from a specimen collected in the Sorata Massif in northern Madagascar (Fig. 6) corresponds closely to the organ in figure 1 of BÖHME & IBISCH (1990). It differs strongly from the hemipenes of *U. henkeli* and *U. sp.* [Ca11] as well as from that of *U. fimbriatus* and *U. lineatus*, the latter of which has an additional internal sclerotized supportive element (RÖSLER & BÖHME 2006).

A further important diagnostic character between *U. henkeli* and *U. sp.* [Ca11] was observed in the pigmentation of the tongue, where specimens of *U. henkeli* (verified in individuals from the type locality Nosy Be, including the holotype, and from the Tsingy de Bemaraha) have blackish pigmentation on the bifid tongue tip (at least on the two terminal extensions, partly extending a bit further posteriorly), whereas no black pigment is present in any of the *U. sp.* [Ca11] individuals examined.

From the available photos of living specimens of *U. henkeli* and *U. sp.* [Ca11] (Figs 7–8, 10–12), a trend of more extended reddish/yellowish colour in the iris in *U. sp.* [Ca11] is apparent (Figs 10–11). Most individuals from Ankarana and Montagne des Français have a yellowish outer area of the iris, whereas especially in specimens from the western slope of Montagne d'Ambre and Tsarakibany (the latter were, however, not genetically identified; Fig. 12), there is a strongly expressed irregular network-like pattern of poorly contrasted yellow-red-brownish lines and markings on the entire iris. Although basically the same pattern also occurs

in some individuals of *U. henkeli*, it seems to be less contrasted, often giving the iris overall a greyish appearance.

The deep mitochondrial divergences, unambiguous differentiation in four nuclear-encoded markers, differences in tongue pigmentation and genital morphology, and weak but rather consistent differences in body size and tail shape

confirm that *U. sp.* [Ca11] represents an independent evolutionary lineage that should be considered as a separate species distinct from *U. henkeli* under an evolutionary and probably also under a biological species criterion. Therefore, in the following, we formally name and describe it as a species new to science.

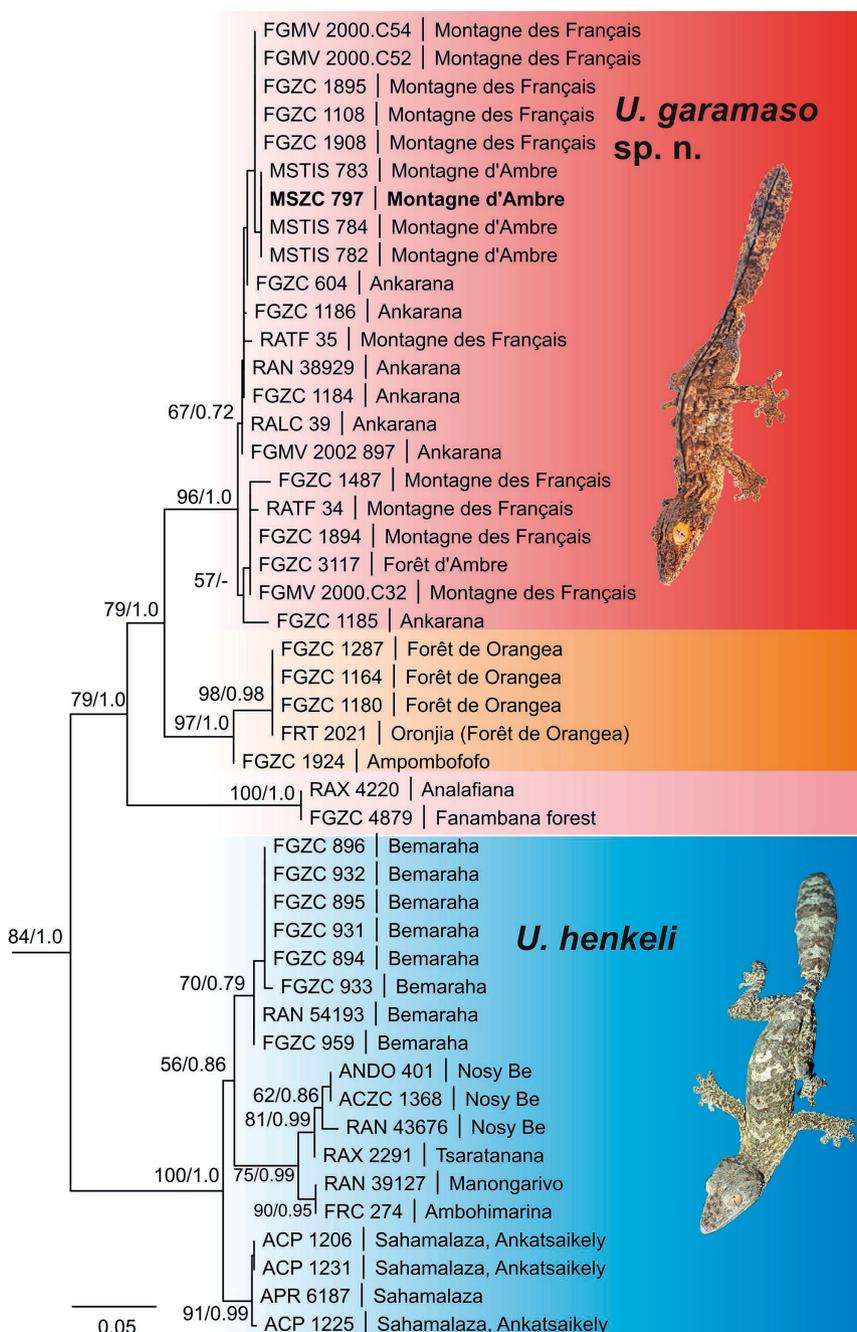


Figure 1. Phylogenetic tree of the *Uroplatus henkeli* complex based on combined sequences of fragments of the mitochondrial genes for 12S, 16S and ND4. Note that in addition to the sequences used to calculate this tree, sequences of *U. henkeli* from the locality Ankarafantsika have also been published (RAXWORTHY et al. 2008, RATSOAVINA et al. 2013). The tree was hierarchically rooted with samples of *U. fimbriatus*, *U. sameiti* and *U. sikorae* (not shown for better graphical representation of the ingroup). Inset photos show *U. garamaso* sp. n. from Montagne d'Ambre (holotype; top) and *U. henkeli* from Bemaraha (bottom). The holotype sample of *U. garamaso* sp. n. (MSZC 797 = ZSM 35/2018) is bolded.

***Uroplatus garamaso* sp. n.**

Figs 10–12

LSID: zoobank.org:act:D16E1EA5-AB6D-4BF3-87C5-01336545E161

Remarks: This species has been mentioned/listed and/or depicted by the following previous authors: BLOXAM & BARLOW (1987) – *Uroplatus fimbriatus*, record from Ankarana; HAWKINS et al. (1990) – *Uroplatus fimbriatus*, record from Ankarana; SVATEK & VAN DUIN (2002) – *Uroplatus sikorae* sp. (“Diego-*henkeli*”), account and photos with uncertain identity and without locality data, apparently from pet trade; BERGHOF (2004) – *Uroplatus* sp., record and photo from Ankarana; SCHÖNECKER & BÖHLE (2004) – “Diego”-*henkeli*; record from north Madagascar; GLAW & VENCES (2007) – *U. henkeli*, record from Ankarana; GREENBAUM et al. (2007) – *U. henkeli*, in phylogenetic tree; D’CRUZE et al. (2007) – *U. sp.*, record from Mon-

tagne des Français; PEARSON et al. (2007) – *Uroplatus* sp. A (modelled distribution map Fig. 1d; attribution uncertain); D’CRUZE et al. (2008) – *Uroplatus* sp. nov. aff. *henkeli*, record from Forêt d’Ambre Special Reserve; ARTH & BAUS (2008) – *Uroplatus henkeli*, record and photo from Montagne des Français; MÜTTERTHIES (2008) – *Uroplatus* cf. *henkeli*, records and photos from Ankarana; RAXWORTHY et al. (2008) – *Uroplatus* sp. H1 & H2, in phylogenetic tree; SCHÖNECKER (2008) – *Uroplatus* aff. *henkeli*; records and photos from Ankarana and Montagne des Français; MEGSON et al. (2009) – *Uroplatus* sp. nov. aff. *henkeli*, records from Ampombofofo; DURKIN et al. (2011) – *Uroplatus* sp. aff. *henkeli*, record from Tsarakibany; GEHRING & SCHÖNECKER (2013) – *Uroplatus* aff. *henkeli*, records and photos from Ankarana and Montagne des Français; RATSOAVINA et al. (2013) – *Uroplatus henkeli* [Ca11], in phylogenetic tree, confirmed genetic samples from Ankarana, Montagne des Français and Analafiana, photo from Montagne des Fran-

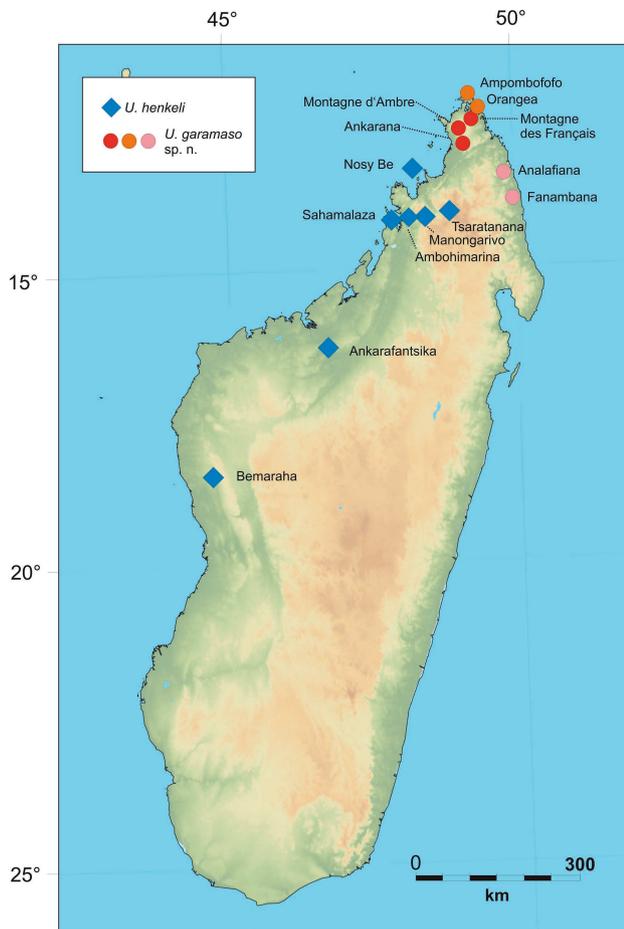


Figure 2. Map of Madagascar showing the known distribution of the species and sublineages of *Uroplatus henkeli* and *U. garamaso* sp. n.. Only localities confirmed by molecular data are shown. The locality Ankarafantsika is confirmed by DNA sequences aggregated by RATSOAVINA et al. (2013) but not included in our mitochondrial tree (Fig. 1). Map colours represent elevations; drawn with the open-source Python library matplotlib/basemap (<https://github.com/matplotlib/basemap>).

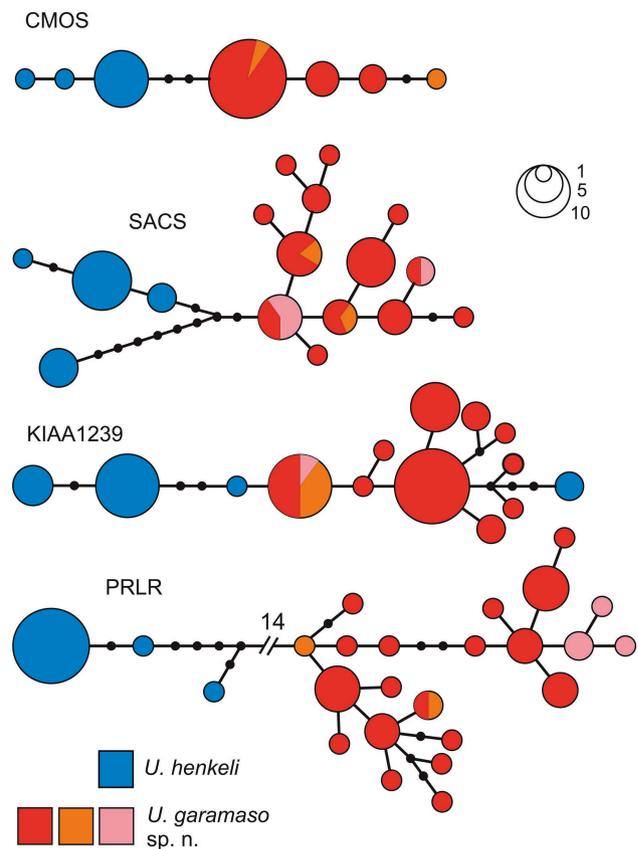


Figure 3. Haplotype networks reconstructed from phased DNA sequences of fragments of the nuclear-encoded genes CMOS (437 nucleotides for 16 specimens), PRLR (408 nt, 27 specimens), KIAA1239 (759 nt, 28 specimens), and SACS (929 nt, 24 specimens) for the *U. henkeli* complex. The PRLR network features an additional 14 mutations separating *U. henkeli* and *U. garamaso* sp. n. which are not shown to match the network graphically with the others. Note that the networks were built from phased sequences; each specimen is therefore represented by two haplotypes per network.

A large new species of *Uroplatus*

Table 1. Morphometric measurements and scale counts of examined specimens of *U. henkeli*, *U. garamaso* sp. n., *U. sikorae* and *U. sameiti*. For abbreviations of measurements and counts, see Materials and methods. Other abbreviations: M, male; F, female. Ad, adult; SAD, subadult; Mat, Maturity; NM, not measured. The holotype of *U. garamaso* sp. n. is marked with an asterisk, paratypes with two asterisks.

Species / Catalogue number	Field number/ previous number	Locality	Sex	Mat	SVL	TaL	TaW	WFF	EOH	SUPL	L4T	rostral vs. 1 st SUPL
<i>U. henkeli</i>												
ZSM 195/2006**	ZFMK 49279	Nosy Be	M	Ad	144.9	90.3	27.7	3.9	2.3	56	NA	larger
ZSM 113/2006	FGZC 896	Bemaraha	M	Ad	186.0	115.5	40.8	5.5	3.8	54	11	larger
ZSM 131/2006	FGZC 933	Bemaraha	M	Ad	180.2	111.4	41.7	4.9	3.8	NM	11	larger
ZSM 112/2006	FGZC 894	Bemaraha	F	SAd	117.9	71.3	26.2	3.6	1.9	53	11	larger
ZSM 130/2006	FGZC 932	Bemaraha	F	Ad	172.0	98.0	35.8	4.9	2.1	56	11	larger
ZSM 196/2006**	ZFMK 49280	Nosy Be	F	Ad	138.2	77.9	29.5	4.2	2.2	49	11	larger
<i>U. garamaso</i> sp. n.												
ZSM 35/2018*	MSZC 797	Montagne d'Ambre, west slope	M	Ad	122.7	75.3	23.6	4.5	1.9	53	10	smaller
ZSM 525/2000**	FGMV 2000.330	Montagne des Français	M	Ad	105.0	58.5	19.5	2.4	1.8	48	9	smaller
ZSM 526/2000**	no field number	Montagne des Français	M	Ad	124.6	64.6	21.1	3.3	2.2	NM	10	larger (2×)
ZSM 2033/2008**	FGZC 1908	Montagne des Français	M	Ad	109.0	NA	NA	2.9	1.3	NM	9	smaller
ZSM 2035/2008**	FGZC 3117	Forêt d'Ambre	M	Ad	119.8	75.8	20.2	3.6	1.6	NM	9	larger (2.5–3×)
ZSM 1000/2003**	FGMV 2002-3014	Montagne des Français	F	Ad	97.7	55.0	19.0	3.3	1.5	NM	9	larger (2×)
ZSM 314/2004**	FGZC 604	Ankarana	F	Ad	125.3	73.7	18.0	4.8	1.9	NM	7	larger (2×)
ZSM 2144/2007**	FGZC 1184	Ankarana	F	Ad	139.1	76.4	23.1	4.8	2.7	NM	9	larger (2.5×)
ZSM 2145/2007**	FGZC 1186	Ankarana	F	Ad	137.7	79.5	26.2	3.7	2.7	50	9	smaller
ZSM 2032/2008**	FGZC 1894	Montagne des Français	F	Ad	133.3	74.0	25.5	3.5	2.6	45	10	larger (2×)
ZSM 889/2003**	FGMV 2002-0897	Ankarana	F	SAd	90.5	50.5	14.7	3.7	1.1	NM	9	larger
ZSM 2111/2007**	FGZC 1108	Montagne des Français	?	SAd	70.7	41.5	11.8	2.7	1.0	NM	9	smaller
<i>U. garamaso</i> sp. n. (Orangea/Ampombofofo phylogroup)												
ZSM 2034/2008	FGZC 1924	Ampombofofo	M	Ad	82.9	44.6	16.0	3.3	1.5	NM	8	smaller
ZSM 2134/2007	FGZC 1164	Orangea	M	Ad	82.8	45.3	14.9	3.6	1.3	NM	8	larger
ZSM 2192/2007	FGZC 1287	Orangea	F	Ad	96.9	56.4	14.0	3.3	1.3	NM	8	larger (2.5×)
<i>U. garamaso</i> sp. n. (Fanambana/Analafiana phylogroup)												
ZSM 1723/2012	FGZC 4879	Fanambana	M	SAd	102.8	50.8	12.5	3.7	1.7	50	8	smaller
<i>U. sikorae</i>												
ZSM 2105/2007	FGZC 1098	Montagne d'Ambre	M	Ad	100.8	50.7	17.8	4.2	1.8	49	10	larger
ZSM 1725/2012	FGZC 3616	Sorata	M	Ad	118.3	73.6	23.8	3.4	2.0	43	9	larger
ZSM 33/2018	MSZC 0492	Montagne d'Ambre	M	Ad	110.3	61.8	18.3	4.2	1.4	47	10	larger
ZSM 34/2018	MSZC 0743	Montagne d'Ambre, west slope	M	Ad	98.4	55.9	16.6	2.6	1.2	47	9	larger
ZSM 32/2018	MSZC 0458	Montagne d'Ambre	F	Ad	113.8	57.9	19.2	4.2	1.6	46	10	larger
<i>U. sameiti</i>												
ZSM 197/2006**	ZFMK 48156	Nosy Boraha	M	Ad	NM	NM	NM	NM	NM	38	NM	NM
ZSM 1577/2009	no field number	Nosy Mangabe	F	Ad	NM	NM	NM	NM	NM	44	NM	NM
ZSM 1578/2009	no field number	Nosy Mangabe	F	Ad	NM	NM	NM	NM	NM	38	NM	NM
ZSM 703/2014	DRV 5689	Mahasoa	F	Ad	NM	NM	NM	NM	NM	37	NM	NM
ZSM 192/2016	FGZC 5068	Vohimana	F	Ad	110.4	60.5	19.4	3.9	1.3	42	10	larger (2×)

çais; RASELIMANANA et al. (2018) – *Uroplatus* sp. aff. *henkeli* [Ca11] in the species lists of the protected areas of Oranjia (= Orangea), Montagne d'Ambre, Analamerana, Andrafiama-Andavakoera, and *Uroplatus* sp. in the species list of Montagne des Français, Ankarana and Loky-Manambato; GEHRING (2020) – *Uroplatus* sp. aff. *henkeli* [Ca11], short description and distribution records from Ankarana, Montagne des Français, Forêt d'Ambre, Forêt d'Orangea, Fanambana, Tsarakibany, Analafiana and Anjahakely, photos from Ankarana, Anjahakely and Montagne des Français; MEZZASALMA et al. (2022) – *Uroplatus henkeli*, karyotype from Montagne d'Ambre.

Holotype: ZSM 35/2018 (field number MSZC 797), adult male, collected by M. D. SCHERZ, J. H. RAZAFINDRAIBE, A. RAZAFIMANANTSOA and S. M. RASOLONJAVATO on the west slope of Montagne d'Ambre (-12.58199° , 49.11162° , 809 m above sea level), northern Madagascar, on 10 December 2017.

Paratypes (a total of 15 specimens): ZSM 525/2000 (FGMV 2000.330), adult male, and ZSM 526/2000 (no field number), collected by F. GLAW, K. GLAW and M. VENCES at Montagne des Français (-12.317° , 49.333°), on 15 March 2000 and 21 March 2000, respectively; ZSM 889/2003

(FGMV 2002.897), probably a subadult female, collected by F. GLAW, R. D. RANDRIANIAINA and A. RAZAFIMANANTSOA at Ankarana, on 15 February 2003; ZSM 314/2004 (FGZC 604), adult female, collected by F. GLAW, M. PUENTE and R. RANDRIANIAINA at Ankarana (near Mahamasina; -12.968° , 49.139° , ca. 100 m a.s.l.), on 25 February 2004; ZSM 2144/2007 (FGZC 1184), UADBA (FGZC 1185) and ZSM 2145/2007 (FGZC 1186), three adult females, collected by F. GLAW, P. BORA, H. ENTING, J. KÖHLER and A. KNOLL in the eastern part of Ankarana National Park (way to Petit Tsingy and Grotte des Chauves Souris, -12.9569° , 49.1183° , 90 m a.s.l.), on 28 February 2007; ZSM 1000/2003 (FGMV 2002.3014), adult female, collected by F. GLAW and R. D. RANDRIANIAINA at Montagne des Français on 20 February 2003; ZSM 2111/2007 (FGZC 1108), subadult specimen, collected by F. GLAW, P. BORA, H. ENTING, J. KÖHLER and A. KNOLL at Montagne des Français (surroundings of old fort; -12.32583° , 49.33806° , ca. 200 m a.s.l.), on 27 February 2007; UADBA (FGZC 1487), adult specimen, collected by F. GLAW, P. BORA, H. ENTING, J. KÖHLER and A. KNOLL at Montagne des Français (-12.52694° , 49.17194° , 197 m a.s.l.) on 16 April 2007; ZSM 2032/2008 (FGZC 1894), adult female, and UADBA (FGZC 1895), juvenile, collected by J. TOTOMAINTY at Montagne des Français (ca. 1.5 km [air distance] SW Andavakoera, "Frontier base camp", -12.3331° ,

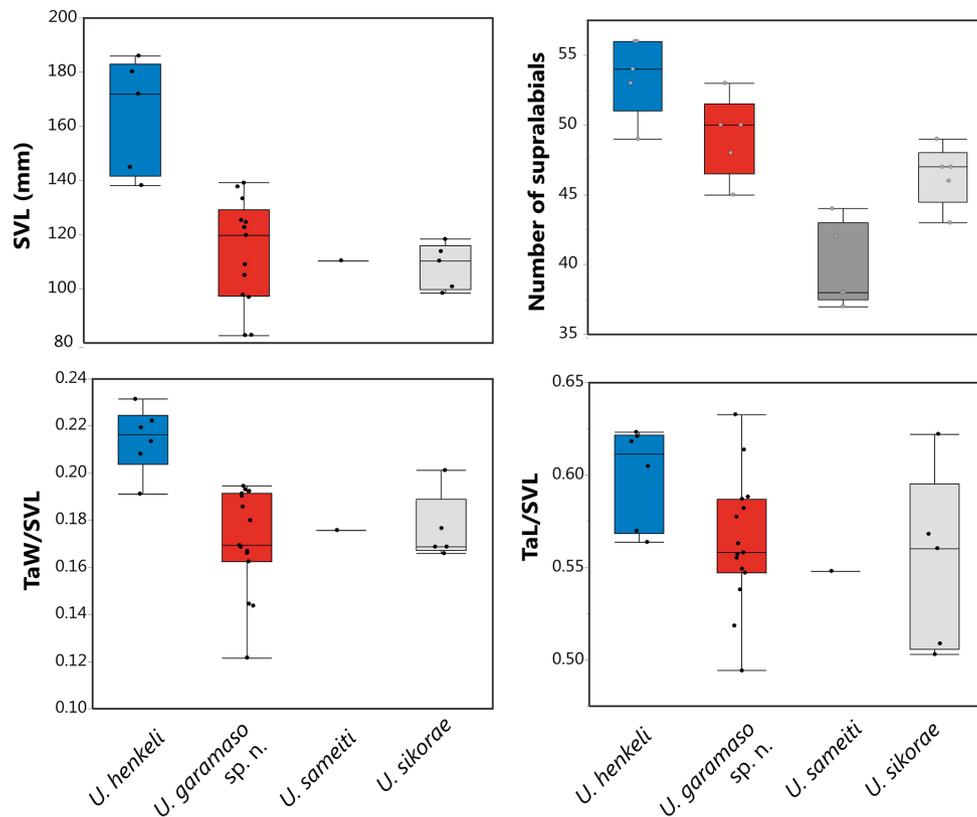


Figure 4. Morphometric variables and scale counts that are diagnostic among the four related species, *U. henkeli*, *U. garamaso* sp. n., *U. sameiti* and *U. sikorae*. The data suggest that individuals of *U. henkeli* differ from most individuals of the other three species by larger body size (SVL), larger relative tail width (TaW/SVL), a tendency of larger relative tail length (TaL/SVL), and a higher number of supralabials; while *U. sameiti* can be distinguished by a low number of supralabial scales. For original data, see Table 1.

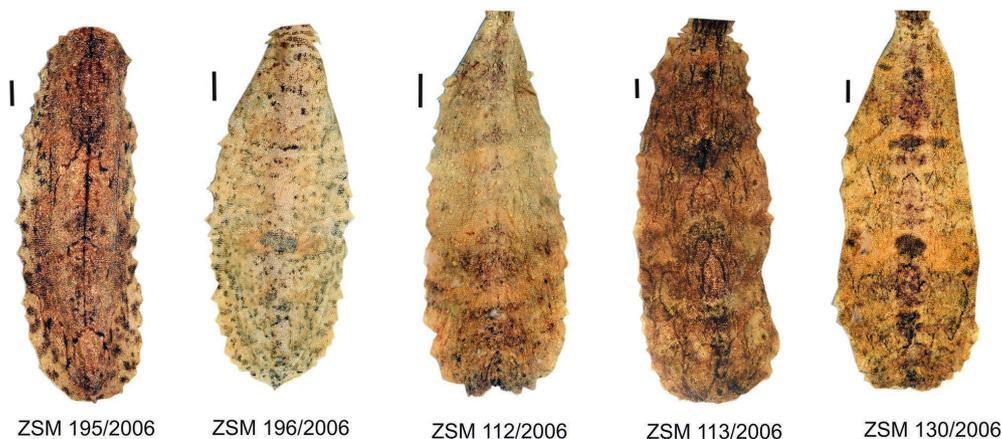
49.3557°, 140 m a.s.l.), on 01 March 2008; ZSM 2033/2008 (FGZC 1908), adult male, collected by F. GLAW and Z. T. NAGY at Montagne des Français (near old fort, -12.3259°, 49.3382°, 260 m a.s.l.), on 1 March 2008; ZSM 2035/2008 (FGZC 3117), adult specimen collected by N. D'CRUZE at Forêt d'Ambre (ca. 5 km SW Sakaramy, -12.463°, 49.220°, 479 m a.s.l.) on 19 February 2008; ZFMK 75754, adult male, collected by local collector(s) at Montagne d'Ambre, in October 2001.

Additional specimens: ZSM 2034/2008 (FGZC 1924), adult specimen, collected by S. EATON at Ampombofofo (Frontier base camp, -12.09213°, 49.32475°, 28 m a.s.l.), on 10 September 2006; ZSM 2134/2007 (FGZC 1164), subadult specimen, collected by F. GLAW, P. BORA, H. ENTING, J. KÖHLER and A. KNOLL at Forêt d'Orangea (East of Ramena), in March 2007; ZSM 2192/2007 (FGZC 1287), subadult specimen, collected by J. KÖHLER, F. GLAW and H. ENTING at Forêt d'Orangea (East of Ramena), on 14 March 2007; ZSM 1723/2012 (FGZC 4879), adult male, collected by F. GLAW, O. HAWLITSCHKEK, T. RAJOAFIARISON, A. RAKOTOARISON,

F. M. RATSOAVINA and A. RAZAFIMANANTSOA at Fanambana (dry forest, -13.615°, 49.995°, 53–67 m a.s.l.), on 6–7 December 2012. These specimens from the Orangea/Ampombofofo and Fanambana/Analafiana lineages are not included in the paratype series because of their high genetic divergence, which requires further taxonomic revision in the future.

Diagnosis: Assigned to the genus *Uroplatus* and within the genus to the *U. fimbriatus* group based on molecular phylogenetic relationships and typical general appearance: a large Malagasy gecko with flat tail and lateral dermal fringes along head and body. It differs from *U. fimbriatus* and *U. giganteus* by smaller body size (SVL of adults < 140 mm vs. ≥ 150 mm) and a different iris colouration without a pattern of vertical lines. It can be distinguished from most populations of *U. sikorae*, including the ones from northern Madagascar, by absence of black colour on the oral mucosa (vs. presence), from *U. sameiti* by a larger number of supralabials (45–53 vs. 37–44, according to counts reported herein; Table 1), and from both these species by hab-

Uroplatus henkeli



Uroplatus garamaso sp. n.

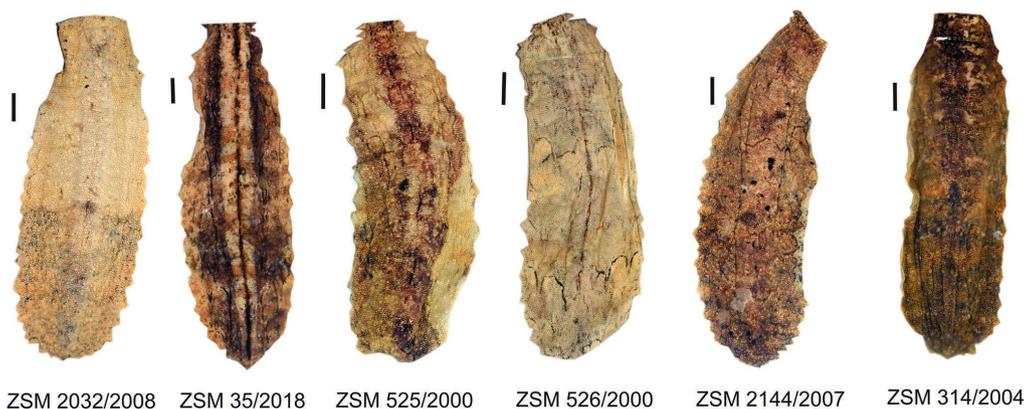


Figure 5. Tails of preserved specimens of *Uroplatus henkeli* and *U. garamaso* sp. n. in dorsal view. Note the tendency of *U. henkeli* tails of being relatively broader. Scale bars represent 5 mm.

itat (dry or transitional forest vs. humid rainforest). The new species is most similar to, and phylogenetically the sister species of, *U. henkeli* (Figs 7–9), from which it differs mainly by smaller adult body size (SVL 83–139 mm vs. 138–186 mm), a smaller relative tail width (TaW/SVL 0.12–0.19 vs. 0.19–0.23), an unpigmented tip of the tongue (vs. black tip in *U. henkeli*), more extended yellow-reddish colour in the iris of most individuals, and apical serrated rotulae (vs. symmetrical fleshy apical structures with serrated elements) on hemipenes. Furthermore, the new species is genetically highly distinct from all other *Uroplatus* in the mitochondrial and nuclear-encoded genes studied, with numerous diagnostic substitutions in all pairwise comparisons and > 8% pairwise distance in the 16S gene fragment. The karyotype of the new species, based on a specimen from Montagne d'Ambre genotyped using a 16S sequence, was $2n = 36$, with loci of NORs in a peritelomeric position on the 6th chromosome pair (MEZZASALMA et al. 2022).

Description of the holotype: Adult male (ZSM 35/2018), in good condition (Fig. 14), with partly everted hemipenes.

Head large, triangular and distinctly depressed. Head, body, limbs, and tail covered with small, irregular-sized, juxtaposed, flat scales. Largest scales (with a maximum diameter of less than 1 mm) are scattered irregularly on dorsal surface, conical. Distinct membranous, serrated fringes of 1.0–5.2 mm width along flanks, inner and outer sides of lower arms, outer sides of upper and lower legs, and along lower jaws, but almost entirely absent along inner sides of upper and lower limbs. Distinct, partly serrated dermal fringes on dorsal and posterior margins of the eyes. Outline of tail elongated, with only slight traces of irregular indentations, tail tip pointed. Axillar indentations posterior to forelimb insertion, weakly developed. Venter and ventral parts of the legs and tail with fine, rather homogeneous, granular scalation, with slightly enlarged scalation on chest and belly. One pointed tubercle of ca. 1.5 mm length on each side, lateral of the cloaca. Throat with many small granular scales, mental scalation consisting of very small scales, mental scale not clearly recognizable, no enlarged mental and postmental scales. Paired, lateral postcranial endolymphatic sacs not recognizable. Limbs slender. Web-

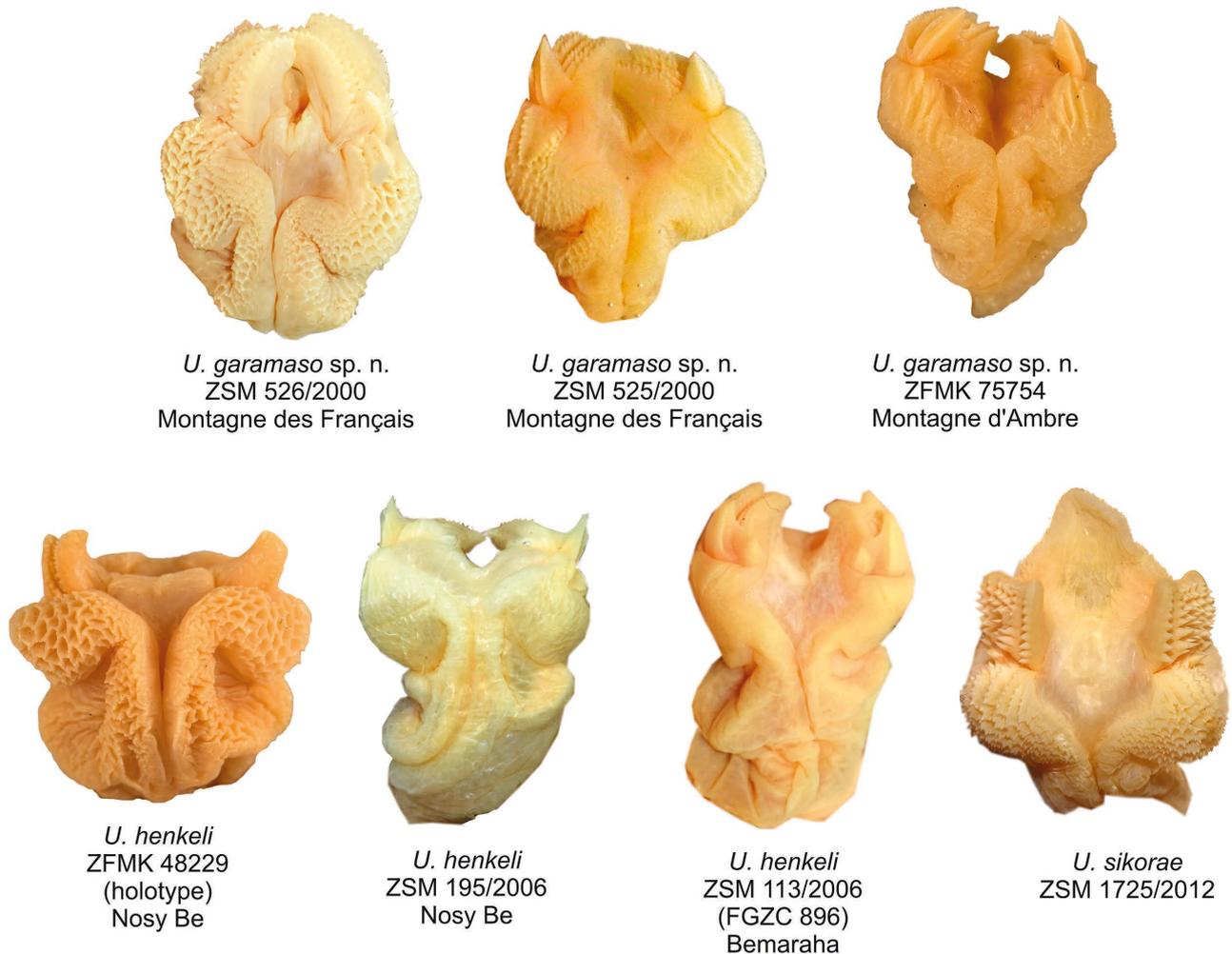


Figure 6. Photographs of everted hemipenes in preservative of *U. henkeli*, *U. garamaso* sp. n. and *U. sikorae* in sulcal view. Not to scale.

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bing-like skin with very fine scalation between toes I and II, and II and III, reaching level of more than half the toe length; between toes III and IV, and IV and V distinctly less than half of toe length. Webbing-like skin between all fingers at least half the finger length. Nine adhesive subdigital lamellae on each side below fourth toe. Rostral scale, slightly damaged, undivided, barely enlarged compared to neighboring supralabials, slightly wider (1.3 mm) than tall (1.1 mm). Eyes large, pupil vertical, with crenate borders, nares directed dorsolaterally, separated from each other by ca. 10 small granular scales, separated from first supralabial scale by 2 scales, and from rostral scale by 4 scales.

Measurements (in mm) and scale counts: SVL 122.7; TaL 75.3; TaW 23.6; ToL 198.0; HL 37.5; HW 26.7; HH 12.6; NSD 3.6; ESD 18.5; NND 5.5; ED 6.8; EOD 1.5; EOH 1.9; EED 12.6; LAL 33.8; AGD 59.5; WFJ 2.7; WFF 4.5; SUPL 53; INFL 48; L4T 10.

After fixation and preservation in ethanol for more than 5 years, dorsal ground colour beige, with brown and dark brown bark-like marbling and different brown markings. Dorsum with a narrow brown vertebral stripe, running from the neck to the tail tip, with few interruptions on proximal parts of the tail. Brown, V-shaped marking on snout tip, continuing as two parallel brown lines across interorbital region,

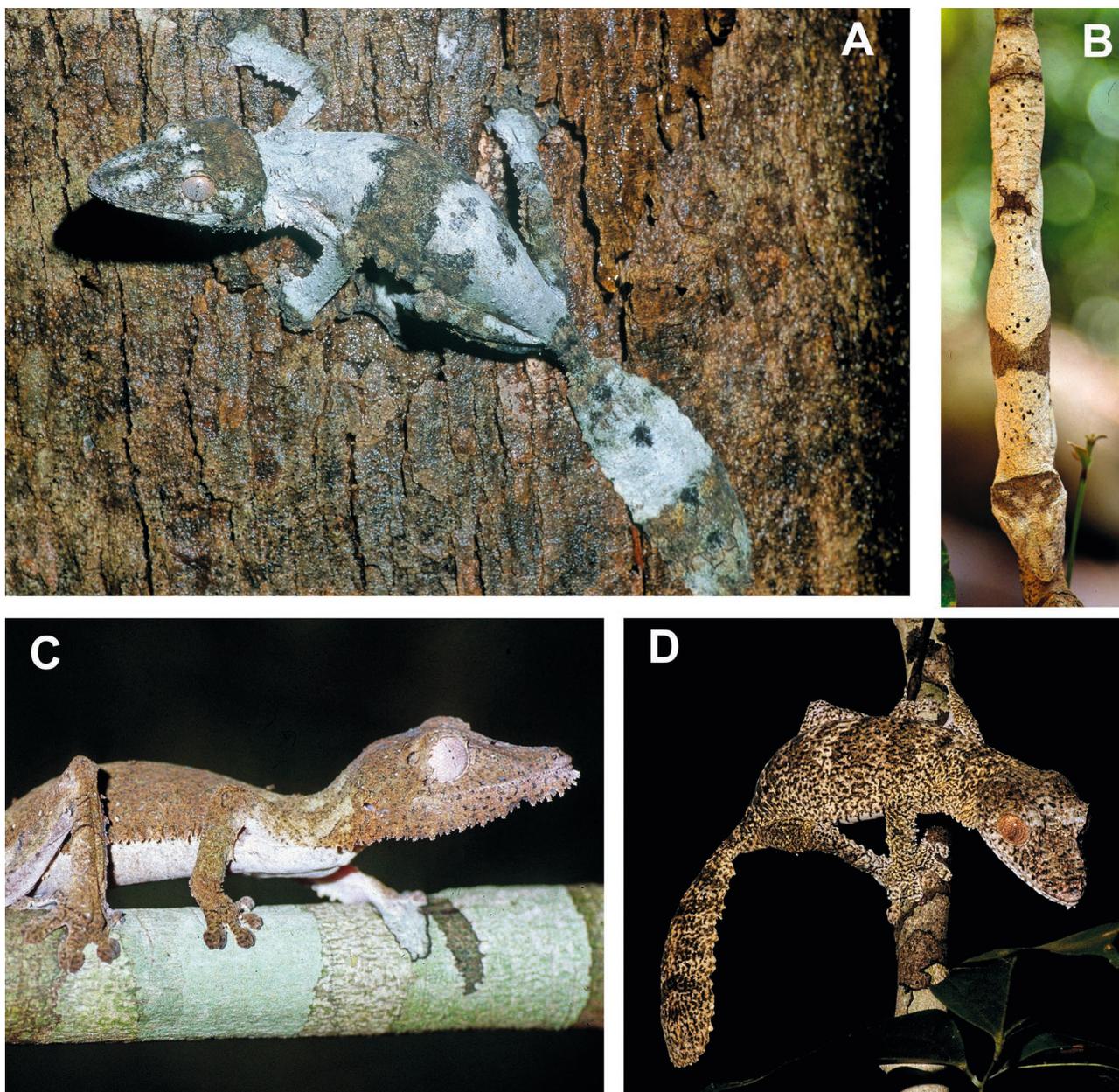


Figure 7. *Uroplatus henkeli* in life: (A) individual from Berara (Sahamalaza), photographed in 2000 (not reliably assignable to a voucher specimen); (B–D) individuals from Nosy Be, the type locality of *U. henkeli*, photographed in 1992 (B, D) and 1994 (C), not collected.

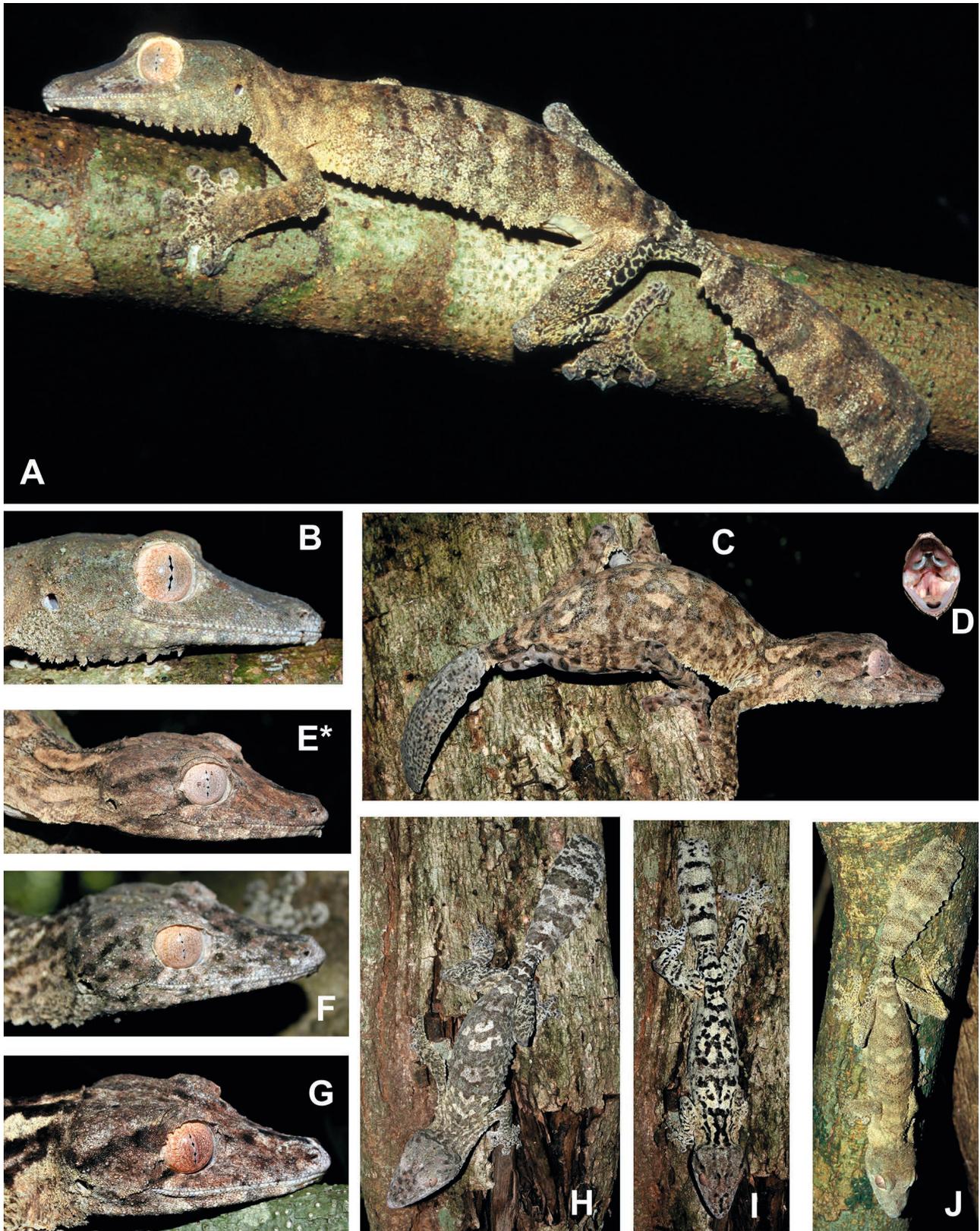


Figure 8. *Uroplatus henkeli* in life, individuals from the Tsingy de Bemaraha (all photographed in 2006, not unambiguously assignable to available voucher specimens, although corresponding to the samples included in our molecular analysis): (A, H, J) three different females; (G, I) specimen of unknown sex; (C, E) probable male specimen. * Photo has been mirrored.

posteriorly to the neck. Thin brown line running from posterior margin of the eye, reaching region above the ear opening. Dorsal surfaces of thighs brown, those of shanks and feet brown, marbled with grey. Posterior surfaces of thighs proximally with a contrasting cream and black marbled pattern. Pointed tubercles lateral of the cloaca white. Dorsal surfaces of arms cream, with diffuse brown marbling. Throat, chest, abdomen and ventral surfaces of forelimbs and hindlimbs creamy white. Ventral surface of tail cream with greyish brown marbling, ventral surfaces of feet and knees brown. Ventral surfaces of proximal parts of fingers grey. Inner mouth and tongue uniform cream (unpigmented).

In life, general colour pattern was identical to that in preservative described above, but the specimen had a darker appearance in general (Fig. 10), with the ventral ground colour having been brown, instead of cream. Most likely, *U. garamaso* sp. n., like all species of the *U. fimbriatus* species group, is also capable of a distinct colour and pattern change when the animals are stressed (GEHRING 2020). Outer iris golden-yellowish, particularly in posterior region; inner iris beige, with diffuse fine vertical brown lines.

Variation: *Uroplatus garamaso* sp. n. shows a high variation both in genetics (three deep mitochondrial lineages currently assigned to the species; see above) and morphology. Especially in colour pattern, it is highly variable, similar to other species of the *U. fimbriatus* group (GEHRING et al. 2018, 2023). According to colour photos herein, specimens can dorsally have a fine pattern of blackish reticulations on a grey (Ankarana; Fig. 11) or light brown (Fanambana; Fig. 13) base colour, a dark vertebral stripe (holotype, Fig. 10), large areas of uniformly light grey colour on head and anterior body, posterior body, and tail (Montagne des Français; Fig. 10), or a grey ground colour with irregular longitudinal dark stripes, dorsolaterally and laterally behind the eye (Forêt d'Orangea; Fig. 13). The iris can be greyish or more brownish with irregular, often very fine darker brownish reticulations, but usually the outer iris area is distinctly yellowish to orange. Morphological variation is shown in Table 1 and in Figs 4–6. Body size (SVL) is 105–123 mm in adult males and 98–139 mm in supposedly adult females (whose maturity is however more difficult to ascertain), in the Ankarana/Montagne d'Ambre/Montagne des

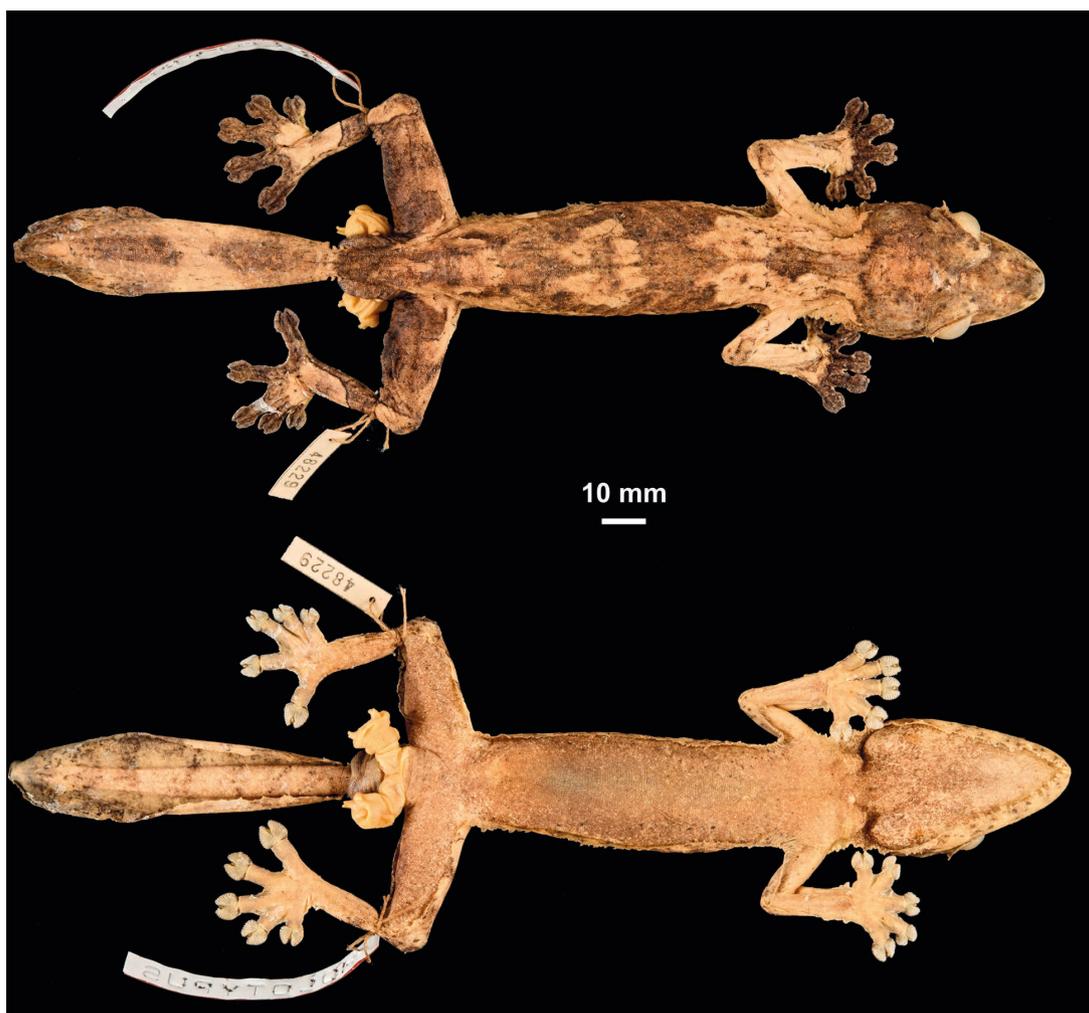


Figure 9. Preserved holotype of *Uroplatus henkeli* (ZFMK 48229; adult male from Nosy Be) in dorsal and ventral views.

Français lineage, while specimens from Forêt d'Orangea (males 83 mm, female 97 mm) may be smaller.

Etymology: The species epithet is a Malagasy term containing the Malagasy word *maso* (= eye) and is used in Madagascar to refer to someone with bright, shiny eyes. The name refers to the often characteristic eye colouration of the new species, and is used as a noun in apposition to the genus name.

Natural history: We observed numerous individuals of the new species in the deciduous dry forests of Montagne des Français, Forêt d'Orangea, Analamerana and Ankarana, as well as in the transitional forests of Forêt d'Ambre and the lower-elevation rainforests of Montagne d'Ambre in the rainy seasons between 2000 and 2022. Almost all individuals were encountered at night on trees whilst active, either on branches or on tree trunks ca. 1–4 m above the ground. Individuals were encountered in dense pristine forest, de-

graded forests with more isolated trees and at the edge of forests in the vicinity of plantations. Two gravid females were captured on 28 February 2007 (ZSM 2144/2007 and UADBA [FGZC 1185]), the former of which laid the whitish eggs after capture.

In 2004, individuals of *U. garamaso* sp. n. were found on the west side of the Ankarana Special Reserve near the Andrafiabe campsite, where they were active on solitary larger trees at night. It was quite common at the Anilotra campsite. It is noteworthy that this was not a closed forest area, but rather a savannah-like landscape in which individual trees were relatively isolated from each other in a loose community with sparse undergrowth of different shrubs.

In December 2017, specimens of *U. garamaso* sp. n. on Montagne d'Ambre were encountered primarily in the dry deciduous forest on the west slope of the mountain, sympatrically with *U. ebenauui*, *U. giganteus*, *U. sikorae*, and *U. alluaudi*, and at lower elevation than *U. finiavana*. Individuals were all encountered actively hunting at night on

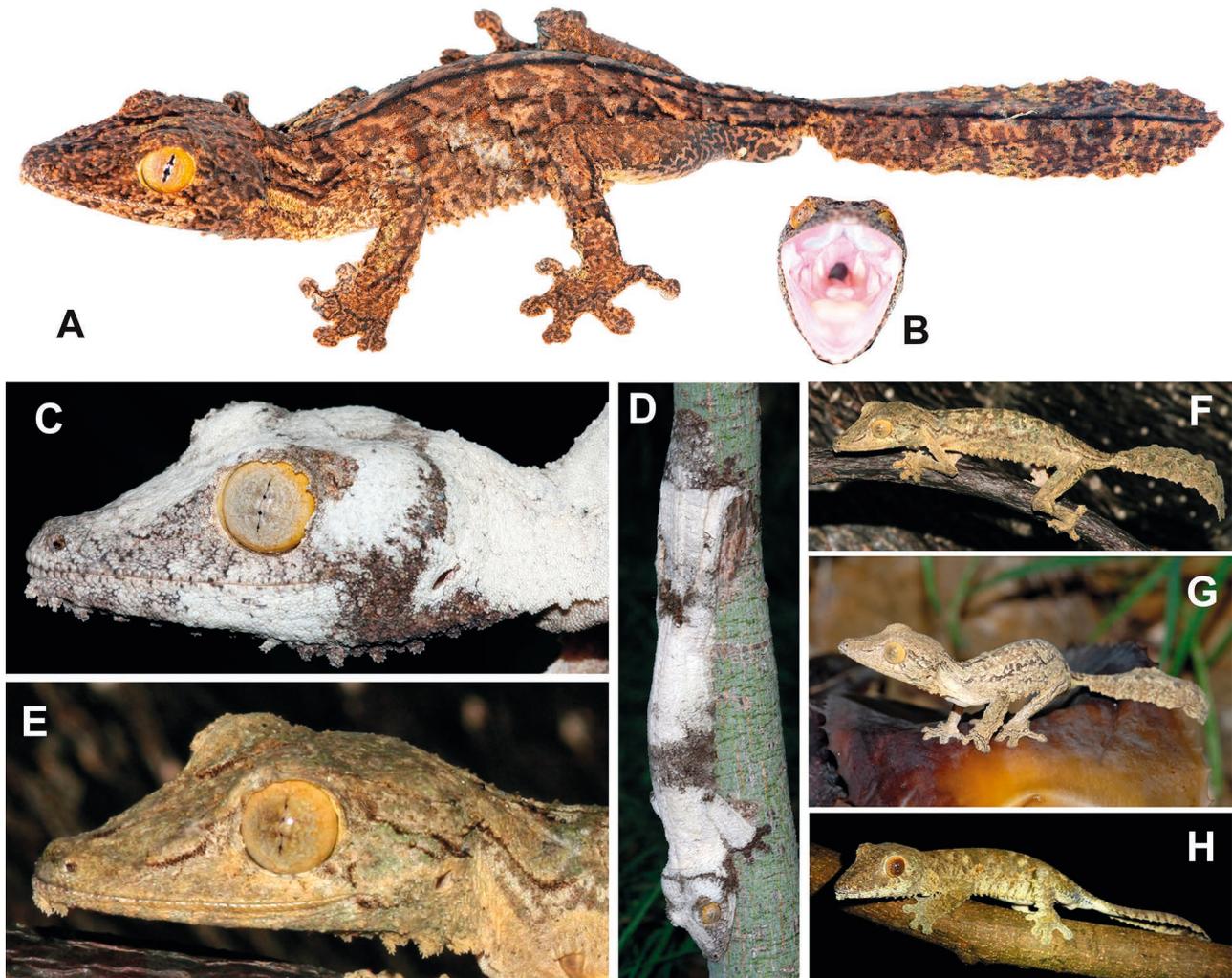


Figure 10. *Uroplatus garamaso* sp. n. in life: (A, B) adult male holotype ZSM 35/2018 from Montagne d'Ambre National Park, western slope; (C–H) specimens from Montagne des Français; (G) corresponding to specimen ZSM 2111/2007.

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trees, in horizontal or in vertical positions. Numerous individuals probably assignable to this species were also encountered in the Antsolipa forest and nearby fragments, near Tsarakibany (south of Montagne d'Ambre) in August 2009 by MDS (see also the reports by LABANOWSKI & LOWIN 2011 and DURKIN et al. 2011). All but one of the in-

dividuals were found active at night, and all in dry deciduous forest. Two specimens were found on the ground, one actively crawling on tree stumps at night and one found on the ground in the middle of the research camp during the day. No other *Uroplatus* species was encountered in this area.

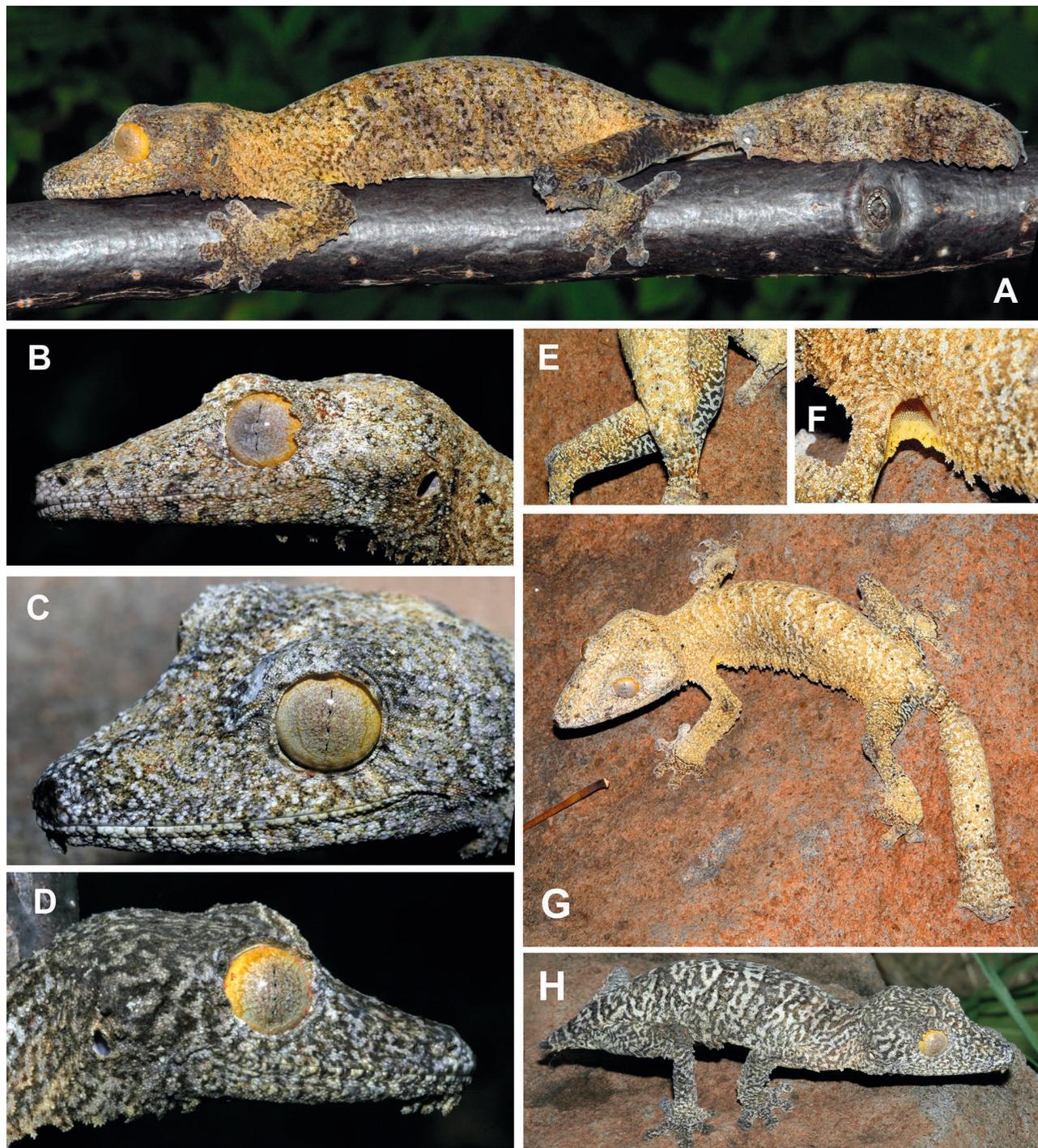


Figure 11. *Uroplatus garamaso* sp. n. in life, individuals from Ankarana National Park: (A) female specimen ZSM 2145/2007; (B, C) specimens of unknown sex, not unambiguously assignable to available voucher specimens; (D, H), female specimen not unambiguously assignable to a voucher specimen; (E, F, G) female specimen ZSM 2144/2007.

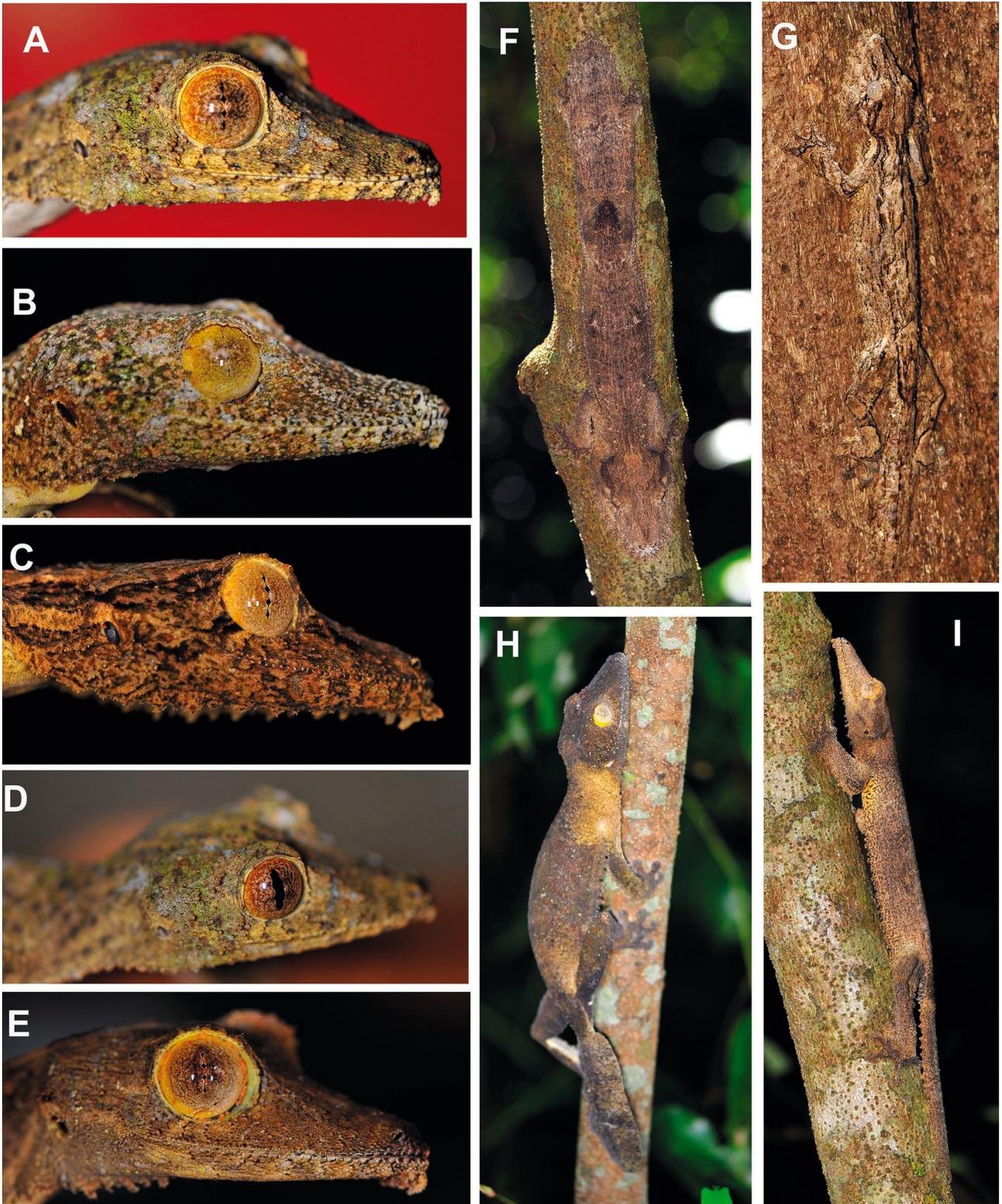


Figure 12. Individuals probably assignable to *Uroplatus garamaso* sp. n. from Antsolipa forest fragment near Tsarakibany (located between Montagne d'Ambre and Ankarana) in life (vouchers not collected and no genetic data available from this locality).

Regarding the captive breeding of *U. garamaso* sp. n., little information has been published so far. SVATEK & VAN DUIN (2002), most likely referring to this species, report that females deposit up to eight clutches per season at intervals of approximately four weeks, each consisting of one or two spherical eggs (diameter 14–16 mm). At varying incubation temperatures of 22–27°C juveniles hatched after 91–103 days, whereas at a constant temperature of 26°C they already hatched 70–75 days after egg deposition (SVATEK & VAN DUIN 2002). According to MARUSHCHAK (pers. comm. to PSG) the incubation conditions hardly differ from *U. henkeli*: The eggs are deposited under leaves or beneath logs on the ground and are usually rolled in substrate. At incubation temperature of 26°C, hatchlings will emerge after 107–133 days. At cooler temperatures (20–24°C), incubation can be prolonged to up to 174 days (MARUSHCHAK et al. 2022). It is unknown if the different incubation periods at 26°C (70–75 versus 107–133 days) refer to non-constant incubation temperatures in the longer period (e.g., with lower night temperatures) or have other causes.

Distribution: The new species is reliably known, based on genotyped samples, from the following localities: (1) the type locality, on the western slope of Montagne d'Ambre; (2) Ankarana National Park, (3) Montagne des Français, and (4) Forêt d'Ambre, corresponding to the low elevation forest on the northeastern slopes of Montagne d'Ambre National Park. Additional observations probably corre-

sponding to this species are from (5) Antsolipa, near Tsarakibany (located at -12.76883°, 049.15633°). Specimens probably referring to this species, although belonging to divergent mitochondrial lineages have been collected at (6) Forêt d'Orangea (including Oronjia protected area), (7) Ampombofofo, (8) Fanambana forest, and (9) Analafiana. Additional records from (10) Analamerana, (11) Andrafiarana-Andavakoera and (12) Loky-Manambato need further studies to confirm their identity.

Discussion

By providing evidence for distinctness at the species level, and formal scientific naming of *Uroplatus garamaso*, this study adds to the species diversity of one of the most fascinating genera of Malagasy squamates, and further affirms the high degree of regional endemism in northern Madagascar. Taking into account the most recent descriptions (see UETZ et al. 2022) and the new species described herein, there are currently 22 *Uroplatus* species, whereas only six species were recognized in the revision of BAUER & RUSSELL (1989). From the genetic lineages already identified, there are still at least two that require taxonomic scrutiny and that have a high probability to represent distinct species, interestingly both from Zahamena National Park in the Central East of Madagascar. Here, one genetically highly divergent lineage of the *U. ebenaui* group oc-

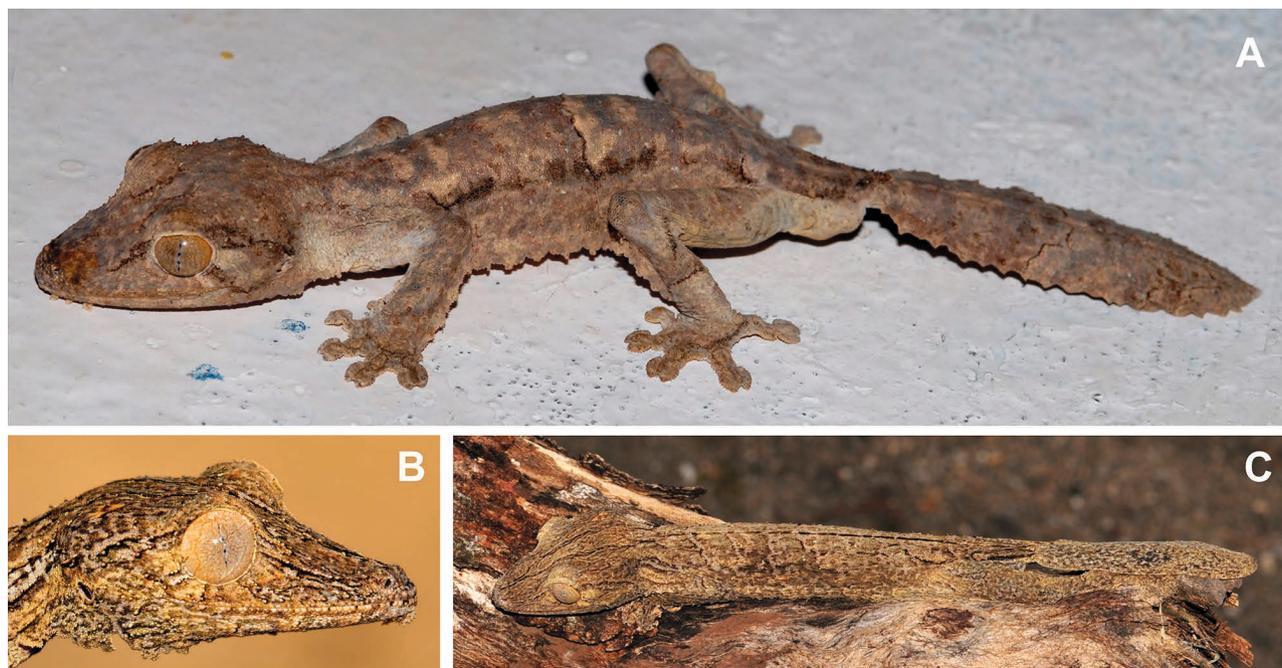


Figure 13. Individuals of genetically divergent mitochondrial phylogroups, tentatively assigned to *Uroplatus garamaso* sp. n., in life: (A) individual from Forêt d'Orangea (ZSM 2134/2007); (B, C) individual from Fanambana forest (not unambiguously assignable to a voucher specimen).

curs (RATSOAVINA et al. 2013, 2020), along with a further such lineage of the *U. fimbriatus* group, possibly related to *U. sameiti* (GEHRING et al. 2023). It is certainly possible that additional species of leaf-tailed geckos will be discovered in previously unsurveyed forest fragments in Madagascar, or that some of the other mitochondrial lineages within widespread species such as *U. ebenauai*, *U. giganteus*, *U. phantasticus*, or *U. sikorae* (RATSOAVINA et al. 2012, 2013, GEHRING et al. 2018, 2023) will turn out to be differentiated at the species level, once thorough population genomic and hybrid zone analyses are carried out. For the time being, we can conclude that most of the cryptic diversity of leaf-tailed geckos discovered by the initial genetic screenings of GREENBAUM et al. (2007), RAXWORTHY et al. (2008) and RATSOAVINA et al. (2013) has now been taxonomically assessed and classified.

The recognition of *U. garamaso* at species level further increases the number and proportion of species of squamates – especially geckos – microendemic to, or with a small distribution range in, northern Madagascar. The occurrence of the same mitochondrial subclade of *U. garamaso* both in Montagne des Français and in Ankarana is remarkable. These sites are karstic massifs with dry/transitional forest, but many northern Malagasy endemics are known to occur in only one or the other of them. Among geckos, this applies for instance to *Blaesodactylus microtuberculatus*, *Geckolepis megalepis*, *Lygodactylus expectatus*,

L. rarus, *Paroedura homalorhina*, *Phelsuma roesleri*, and *Uroplatus fetsy* that have only been found in Ankarana, whereas *Paroedura hordiesi* and *P. lohatsara* appear to be microendemic to Montagne des Français (GLAW et al. 2010, 2014, 2018, JONO et al. 2015, SCHERZ et al. 2017, VENCES et al. 2022a). It is likely that *U. garamaso* is primarily an inhabitant of dry and transitional forest, and much less specialized to the karstic limestone than many of the other species, especially the *Paroedura* species and *Lygodactylus expectatus*. Therefore, *U. garamaso* may have been able to disperse, and maintain gene flow, via forest corridors on other substrate types, as might have been the case in the other more widespread species.

Oral mucosa colour is a very valuable taxonomic character in the small-sized species of the *U. ebenauai* group, where some species have an unpigmented mucosa while others have variable but species-specific degrees of black or red pigment (RATSOAVINA et al. 2019a, 2019b, 2020). In a recent revision of the *Uroplatus sikorae* complex (GEHRING et al. 2023), extreme morphological similarity between lineages, despite their rather substantial genetic divergences, was reported. The only distinguishing character partly consistent with lineage assignment was the colour of the oral mucosa, with distinctly black pigmentation in the northern lineages of *U. sikorae*, but unpigmented oral mucosa in both *U. sameiti* and southern *U. sikorae* lineages. Here, we add another example of species-specific differences in

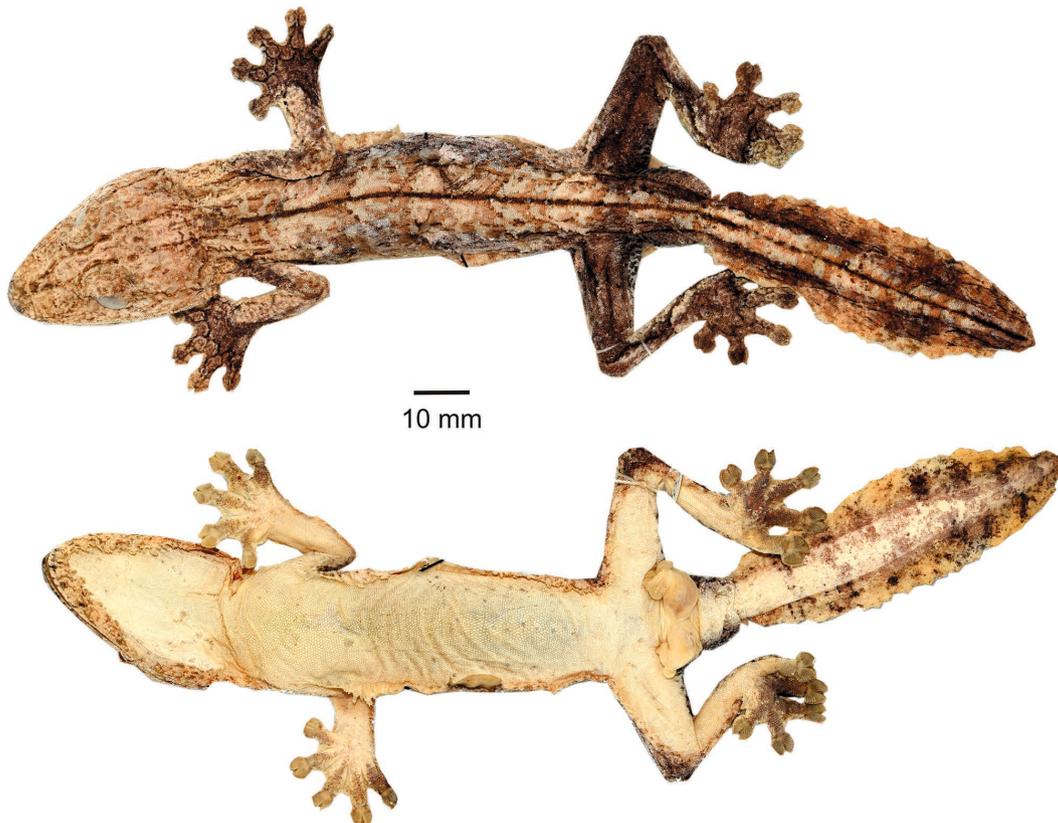


Figure 14. Preserved male holotype (ZSM 35/2018) of *Uroplatus garamaso* sp. n. in dorsal and ventral views.

internal oral pigmentation by reporting on the apparently species-specific black tip of the tongue in *U. henkeli*, which is missing in *U. garamaso*. The biological function of internal oral pigmentation in these animals remains unknown; as mentioned by RATSOAVINA et al. (2015), the pattern becomes visible when threatened specimens open their mouth in aggressive behaviour, but it is unknown whether these geckos also display such behaviour in interactions with conspecifics. The many examples now available for species-specific tongue or mucosa pigmentation support the hypothesis of a function in intraspecific communication, clearly warranting behavioural research on this topic.

The populations here assigned in a preliminary way to *U. garamaso* belong to three divergent mitochondrial lineages differing by as much as 7.2% pairwise distances in a fragment of the 16S gene that has been frequently used for DNA barcoding Madagascar's herpetofauna. For instance, VIEITES et al. (2009) for Malagasy amphibians applied a 3% 16S distance threshold to define candidate species, but emphasized that additional evidence is needed to ascertain these really represent independent evolutionary units that should be formally recognized as species (see also discussion in VENCES et al. 2022a). It is striking that the deep mitochondrial lineages within *U. garamaso* show widespread haplotype sharing in the nuclear-encoded genes studied herein, a pattern that could be due to incomplete lineage sorting or gene flow over recent evolutionary time. As incomplete lineage sorting is favoured by large effective population sizes without population bottlenecks, which is unlikely for large-sized forest geckos in the mosaic landscape of northern Madagascar, we hypothesize that cessation of gene flow among these lineages may not yet have occurred and a certain amount of genetic admixture among them may still be taking place. In this context, it is important to emphasize that many geckos apparently are characterized by higher mitochondrial distances than other squamates (NAGY et al. 2012, VENCES et al. 2022a), a phenomenon that merits further investigation. In the case of *U. garamaso*, for the time being, we suggest that the mitochondrial divergence alone – in the absence of nuclear gene or morphological differentiation – is insufficient for an additional taxonomic split, and the genetic variation is best addressed as representing deep conspecific lineages. More extensive phylogenomic data, preferably on the lineages' hybrid zones, are needed for their in-depth taxonomic assessment.

Despite its occurrence in several protected areas, populations of *U. garamaso* are heavily threatened. All known sites are at relatively low elevations and several of them have been and continue being under strong human pressure, with cattle grazing and slash-and-burn agriculture taking place even within the protected areas (GEZON 2000, D'CRUZE et al. 2007, 2008, CARDIFF & BEFOURROUACK 2008, MEGSON et al. 2009, SABEL et al. 2009, GOODMAN et al. 2018). Although *U. henkeli* has been observed in shade-grown coffee plantations (BLUMGART et al. 2017, EVANS 2019), the former authors suggested that it may be unlikely to persist in large coffee plantations without interspersed areas of forest. We observed leaf-tailed geckos possibly as-

signable to *U. garamaso* being quite common in disturbed forest at Analamerana Special Reserve (APR, pers. obs.). However, in general, species of the *U. fimbriatus* group do not appear to tolerate extensive forest degradation. Hence, the high genetic variation found in these geckos at small spatial scales calls for increased efforts to preserve intact primary forests throughout their distribution range. Furthermore, our new taxonomy will also allow for the collection and export of *U. garamaso* for the pet trade to be monitored more closely. This species has been in the pet trade since at least 2001 (paratype ZFMK 75754; see also SVATEK & VAN DUIN 2002), and possibly considerably longer, under various names, including 'Henkeli "Diego"', 'Diego Suarez Henkeli', and '*Uroplatus* aff. *henkeli*'. L. WIEDEMANN established the species in captivity in the USA in 2010 (pers. comm. to MDS), and they also continued to be imported after that date as *Uroplatus henkeli*, but always in very low numbers (3–5 per year to the USA, according to L. WIEDEMANN). It has also been present in low numbers in the German pet trade.

However, due to the fact that *U. garamaso* was exported (albeit in small numbers) for the pet trade without being recognized and declared as a taxon of its own, it cannot be ruled out that interbreeding and hybridization between *U. henkeli* and *U. garamaso* occurred during the selection of breeding groups. CAPEZZONE (1995) reported hybridization between the more distantly related *U. fimbriatus* and *U. henkeli*, so it can be assumed that the two sister taxa *U. henkeli* and *U. garamaso* may also interbreed and produce viable hybrids. To keep the populations of *U. garamaso* in captivity as species-pure as possible, breeders should pay special attention to the exact identification of the species to avoid crossbreeding. Inspection of the mouth, as has long been practiced for *U. sikorae* vs. *U. sameiti* (though now known to be problematic, as mentioned above), and members of the *U. ebenaui* group, serve a quick and seemingly reliable way to achieve that identification.

It is striking that only very little information is available, in general, on the ecology of animals as prominent as the large-sized leaf-tailed geckos of the *U. fimbriatus* group. Long-term field population studies are largely missing (for an exception, see INGADY 2011 on *U. giganteus*), and much of the information on their reproduction is based on captive data from hobbyists (summarized in GEHRING 2020), as is the case for *U. garamaso*. With the extended information on genetic lineages now at hand for all species of the *U. fimbriatus* group (GEHRING et al. 2018, 2023, and this study), it is now time to initiate a long-term field study program on selected populations. At the same time, however, it is important to keep allowing a small number of individuals to be exported under the Malagasy CITES quota system (RAXWORTHY & VENCES 2010, UNEP-WCMC 2015), giving hobbyists the opportunity to contribute to the understanding of life history and behaviour of these fascinating geckos. It is important that hobbyists keep publishing their experiences with keeping and breeding these geckos, including failures, as such data will be crucial in case conservation breeding programs need to be established in the future.

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References

- ARÉVALO, E., S. K. DAVIS & J. W. SITES JR. (1994): Mitochondrial DNA-sequence divergence and phylogenetic relationships among eight chromosomate races of the *Sceloporus grammicus* complex (Phrynosomatidae) in Central Mexico. – *Systematic Biology*, **43**: 387–418.
- ARTH, S. & S. BAUS (2008): Herpetologische Reiseindrücke aus dem Kalkmassiv der Montagne des Français in Nord-Madagaskar. – *Terraria*, **12**: 23–29.
- BAUER, A. M. & A. P. RUSSELL (1989): A systematic review of the genus *Uroplatus* (Reptilia: Gekkonidae) with comments on its biology. – *Journal of Natural History*, **23**: 169–203.
- BERGHOF, H.-P. (2004): Unterwegs im "Reserve Speciale" von Ankarana. – *Draco*, **19**: 44–49.
- BLOXAM, Q. M. C. & S. C. BARLOW (1987): A summary of the reptile field survey in the Ankarana massif, Madagascar. – *Dodo*, **24**: 61–67.
- BLUMGART, D., J. DOLHEM & C. J. RAXWORTHY (2017): Herpetological diversity across intact and modified habitats of Nosy Komba Island, Madagascar. – *Journal of Natural History*, **51**: 626–642.
- BÖHME, W. & P. IBISCH (1990): Studien an *Uroplatus*. I. Der *Uroplatus-fimbriatus*-Komplex. – *Salamandra*, **26**: 246–259.
- BOUMANS, L., D. R. VIEITES, F. GLAW & M. VENCES (2007): Geographical patterns of deep mitochondrial differentiation in widespread Malagasy reptiles. – *Molecular Phylogenetics and Evolution*, **45**: 822–839.
- BROWN, J. L., A. CAMERON, A. D. YODER & M. VENCES (2014): A necessarily complex model to explain the biogeography of the amphibians and reptiles of Madagascar. – *Nature Communications*, **5**: e5046.
- BROWN J. L., N. SILLERO, F. GLAW, P. BORA, D. R. VIEITES & M. VENCES (2016): Spatial biodiversity patterns of Madagascar's amphibians and reptiles. – *PloS One*, **11**: e0144076.
- BRUFORD, M. W., O. HANOTTE, J. F. Y. BROOKFIELD & T. BURKE (1992): Single-locus and multilocus DNA fingerprint. In: HOELZEL, A. R. (ed.): *Molecular Genetic Analysis of Populations: A Practical Approach*. – IRL Press, Oxford, 225–270.
- CAPEZZONE, F. (1995): A note on hybridisation between *Uroplatus fimbriatus* and *Uroplatus henkeli*. – *Herpetile: Journal of the International Herpetological Society*, **20**: 45.
- CARDIFF, S. G. & J. BEFOURROUACK (2008): La Réserve spéciale de l'Ankarana. – pp. 571–584 in GOODMAN, S. M. (ed.): *Paysages Naturels et Biodiversité de Madagascar*. – Muséum national d'Histoire naturelle, WWF, Paris.
- CARPENTER, A. I. & F. ANDREONE (2023): Valorisation of Madagascar's Wildlife Trade and Wildlife Tourism; What are the Conservation Benefits? – *Preprints.org* **2023**, 2023060946.
- D'CRUZE, N., J. KÖHLER, M. FRANZEN & F. GLAW (2008): A conservation assessment of the amphibians and reptiles of the Forêt d'Ambre Special Reserve, north Madagascar. – *Madagascar Conservation and Development*, **3**: 44–54.
- D'CRUZE, N., J. KÖHLER, M. VENCES & F. GLAW (2010): A new fat fossorial frog (Microhylidae: Cophylinae: *Rhombophryne*) from the rainforest of the Forêt d'Ambre Special Reserve, northern Madagascar. – *Herpetologica*, **66**: 182–191.
- D'CRUZE, N., J. SABEL, K. GREEN, J. DAWSON, C. GARDNER, J. ROBINSON, G. STARKIE, M. VENCES & F. GLAW (2007): The first comprehensive survey of amphibians and reptiles at Montagne des Français, Madagascar. – *Herpetological Conservation and Biology*, **2**: 87–99.
- DURKIN, L., M. D. STEER & E. M. S. BELLE (2011): Herpetological surveys of forest fragments between Montagne d'Ambre National Park and Ankarana Special Reserve, Northern Madagascar. – *Herpetological Conservation and Biology*, **6**: 114–126.
- EDLER, D., J. KLEIN, A. ANTONELLI & D. SILVESTRO (2021): raxml-GUI 2.0: a graphical interface and toolkit for phylogenetic analyses using RAXML. – *Methods in Ecology and Evolution*, **12**: 373–377.
- EVANS, B. (2019): Quantifying the conservation value of plantation forests for a Madagascan herpetofauna. – *Herpetological Conservation and Biology*, **14**: 269–287.
- GEHRING, P.-S. (2020): Leaf-tailed Geckos – the complete *Uroplatus*. – Chimaira, Frankfurt am Main.
- GEHRING, P.-S., M. D. SCHERZ, C. A. BAILEY, E. E. LOUIS, F. M. RATSOAVINA, F. GLAW, M. VENCES (2023): High diversity of deep mitochondrial lineages meets low morphological distinctiveness – insights into the complex phylogeography of the Malagasy leaf-tailed geckos *Uroplatus sikorae* and *U. sameiti*. – *Salamandra*, **59**: 158–178.
- GEHRING, P.-S. & P. SCHÖNECKER (2013): Auf der Suche nach Plattschwanzgeckos in Madagaskar. – *Draco*, **13**: 18–33.
- GEHRING, P.-S., S. SIARABI, M. D. SCHERZ, F. M. RATSOAVINA, A. RAKOTOARISON, F. GLAW & M. VENCES (2018): Genetic differentiation and species status of the large-bodied leaf-tailed geckos *Uroplatus fimbriatus* and *U. giganteus*. – *Salamandra*, **54**: 132–146.
- GEZON, L. L. (2000): Political ecology and conflict in Ankarana, Madagascar. – *Ethnology*, **36**: 85–100.
- GLAW, F., P.-S. GEHRING, J. KÖHLER, M. FRANZEN & M. VENCES (2010): A new dwarf species of day gecko, genus *Phelsuma*, from the Ankarana pinnacle karst in northern Madagascar. – *Salamandra*, **46**: 83–92.

- GLAW, F., S. HOEGG & M. VENCES (2006a): Discovery of a new basal relic lineage of Madagascan frogs and its implications for mantellid evolution. – *Zootaxa*, **1334**: 27–43.
- GLAW, F., J. KÖHLER, T. M. TOWNSEND & M. VENCES (2012): Rivaling the world's smallest reptiles: Discovery of miniaturized and microendemic new species of leaf chameleons (*Brookesia*) from northern Madagascar – *PLoS One*, **7**: e31314.
- GLAW, F., J. KÖHLER & M. VENCES (2018): Three new species of nocturnal geckos of the *Paroedura oviceps* clade from xeric environments of Madagascar (Squamata: Gekkonidae). – *Zootaxa*, **4433**: 305–324.
- GLAW, F., J. KOSUCH, F. W. HENKEL, P. SOUND & W. BÖHME (2006b): Genetic and morphological variation of the leaf-tailed gecko *Uroplatus fimbriatus* from Madagascar, with description of a new giant species. – *Salamandra*, **42**: 129–144.
- GLAW, F., H. RÖSLER, I. INEICH, P.-S. GEHRING, J. KÖHLER & M. VENCES (2014): A new species of nocturnal gecko (*Paroedura*) from karstic limestone in northern Madagascar. – *Zoosystematics and Evolution*, **90**: 249–259.
- GLAW, F. & M. VENCES (2007): A Field Guide to the Amphibians and Reptiles of Madagascar, 3rd ed. – Vences and Glaw Verlag, Cologne.
- GOODMAN, S. M., M. J. RAHERILALAO & S. WOHLHAUSER (2018, Eds): Les Aires Protégées Terrestres de Madagascar: leur Histoire, Description et Biota. – Association Vahatra, Antananarivo.
- GREENBAUM, E., A. M. BAUER, T. R. JACKMAN, M. VENCES & F. GLAW (2007): A phylogeny of the enigmatic Madagascan geckos of the genus *Uroplatus* (Squamata: Gekkonidae). – *Zootaxa*, **1493**: 41–51.
- HAN, D., K. ZHOU & A. M. BAUER (2004): Phylogenetic relationships among gekkotan lizards inferred from c-mos nuclear DNA sequences and a new classification of the Gekkota. – *Biological Journal of the Linnean Society*, **83**: 353–368.
- HAWKINS, A. F. A., P. CHAPMAN, J. U. GANZHORN, Q. M. C. BLOXAM, S. C. BARLOW & S. J. TONGE (1990): Vertebrate conservation in Ankarana special reserve, Northern Madagascar. – *Biological Conservation*, **54**: 83–110.
- INGADY, M. Z. L. (2011): Habitat préférentiel d'*Uroplatus giganteus* (Reptilia, Gekkonidae), dans le complexe de la Montagne d'Ambre, Nord de Madagascar. – *Malagasy Nature*, **5**: 89–103.
- JACKMAN, T. R., A. M. BAUER, E. GREENBAUM, F. GLAW & M. VENCES (2008): Molecular phylogenetic relationships among species of the Malagasy-Comoran gecko genus *Paroedura* (Squamata: Gekkonidae). – *Molecular Phylogenetics and Evolution*, **46**: 74–81.
- JONO, T., A. M. BAUER, I. BRENNAN & A. MORI (2015): New species of *Blaesodactylus* (Squamata: Gekkonidae) from Tsingy karstic outcrops in Ankarana National Park, northern Madagascar. – *Zootaxa*, **3980**: 406–416.
- KATO, K. & D. M. STANDLEY (2013): MAFFT multiple sequence alignment software version 7: improvements in performance and usability. – *Molecular Biology and Evolution*, **30**: 772–780.
- KLAVER, C. & W. BÖHME (1986): Phylogeny and classification of the Chamaeleonidae (Sauria) with special reference to hemipenis morphology. – *Bonner Zoologische Monographien*, **22**: 1–64.
- KÖHLER, J., M. VENCES, N. D'CRUZE & F. GLAW (2010): Giant dwarfs: discovery of a radiation of large-bodied 'stump-toed frogs' from karstic cave environments of northern Madagascar. – *Journal of Zoology*, **282**: 21–38.
- KUMAR, S., G. STECHER & K. TAMURA (2016): MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. – *Molecular Biology and Evolution*, **33**: 1870–1874.
- LABANOWSKI, R. J. & A. J. LOWIN (2011): A reptile survey in a dry deciduous forest fragment in northern Madagascar showing new records for the little-known snake *Pararhadinaea melanogaster* and a range extension for the skink *Amphiglossus tanysona*. – *Herpetology Notes*, **4**: 113–121.
- LIBRADO, P. & J. ROZAS (2009): DnaSP v5: A software for comprehensive analysis of DNA polymorphism data. – *Bioinformatics*, **25**: 1451–1452.
- MARUSHCHAK, O., A. MARUSHCHAK, D. TKACHEV, G. GHIVORA & O. NEKRASOVA (2022): Data on the reproductive biology and temperature-dependent patterns of Henkel's Leaf-tailed Gecko, *Uroplatus henkeli*, at the BION Terrarium Center. – *Herpetological Review*, **53**: 610–616.
- MEGSON, S., P. MITCHELL, J. KÖHLER, C. MARSH, M. FRANZEN, F. GLAW & N. D'CRUZE (2009): A comprehensive survey of amphibians and reptiles in the extreme north of Madagascar. – *Herpetology Notes*, **2**: 31–44.
- MEZZASALMA, M., E. BRUNELLI, G. ODIERNA & F. M. GUARINO (2022): First insights on the karyotype diversification of the endemic Malagasy leaf-toed geckos (Squamata: Gekkonidae: *Uroplatus*). – *Animals*, **12**: 2054.
- MITTERMEIER, R. A., E. E. LOUIS JR., M. RICHARDSON, C. SCHWITZER, O. LANGRAND, A. B. RYLANDS, F. HAWKINS, S. RAJAABELINA, J. RATSIMBAZAFY, R. RASOLOARISON, C. ROOS, P. M. KAPPELER & J. MACKINNON (2010): Lemurs of Madagascar (3rd ed.). – Conservation International, Arlington, USA.
- MÜTTERTHIES, C. (2008): Biologie, Haltung und Zucht von Henkels Plattschwanzgecko, *Uroplatus henkeli*. – *Terraria*, **14**: 63–71.
- NAGY, Z. T., G. SONET, F. GLAW & M. VENCES (2012): First large-scale DNA barcoding assessment of reptiles in the biodiversity hotspot of Madagascar, based on newly designed COI primers. – *PLoS One*, **7**: e34506.
- PALUMBI, S. R., A. MARTIN, S. ROMANO, W. O. McMILLAN, L. STICE & G. GRABOWSKI (1991): The Simple Fool's Guide to PCR, Version 2.0. – Privately published document compiled by S. Palumbi, Dept. Zoology, Univ. Hawaii, Honolulu
- PEARSON, R. G., C. J. RAXWORTHY, M. NAKAMURA & A. T. PETERSON (2007): Predicting species distribution from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. – *Journal of Biogeography*, **34**: 102–117.
- PENNY, S. G., A. CROTTINI, F. ANDREONE, A. BELLATI, L. M. S. RAKOTOZAFY, M. W. HOLDERIED, C. SCHWITZER & G. M. ROSA (2017): Combining old and new evidence to increase the known biodiversity value of the Sahamalaza Peninsula, Northwest Madagascar. – *Contributions to Zoology*, **86**: 273–296.
- RAKOTOARISON, A., M. D. SCHERZ, F. GLAW, J. KÖHLER, F. ANDREONE, M. FRANZEN, J. GLOS, O. HAWLITSCHKEK, T. JONO, A. MORI, S. H. NDRIANTSOA, N. RASOAMAMPIONONA RAMINOSOA, J. C. RIEMANN, M. O. RÖDEL, G. M. ROSA, D. R. VIEITES, A. CROTTINI & M. VENCES (2017): Describing the smaller majority: integrative taxonomy reveals twenty-six new species of tiny microhylid frogs (genus *Stumpffia*) from Madagascar. – *Vertebrate Zoology*, **67**: 271–398.
- RASELIMANANA, A. P., F. GLAW & M. VENCES (2018): Liste des reptiles connus dans 98 aires protégées terrestres de Madagascar.

- car / List of the known reptiles in 98 protected areas of Madagascar. – in: GOODMAN, S. M., M. J. RAHERILALAO & S. WOHLHAUSER (eds): Les aires protégées terrestres de Madagascar : Leur histoire, description et biote / The terrestrial protected areas of Madagascar: Their history, description, and biota. – Association Vahatra, Antananarivo.
- RATSOAVINA, F. M., P.-S. GEHRING, M. D. SCHERZ, D. R. VIEITES, F. GLAW & M. VENCES (2017): Two new species of leaf-tailed geckos (*Uroplatus*) from the Tsaratanana mountain massif in northern Madagascar. – *Zootaxa*, **4347**: 446–464.
- RATSOAVINA, F. M., F. GLAW, A. P. RASELIMANANA, A. RAKOTOARISON, D. R. VIEITES, O. HAWLITSCHKE, M. VENCES & M. D. SCHERZ (2020): Towards completion of the species inventory of small-sized leaf-tailed geckos: two new species of *Uroplatus* from northern Madagascar. – *Zootaxa*, **4895**: 251–271.
- RATSOAVINA, F. M., E. E. LOUIS JR., A. CROTTINI, R. D. RANDRIANIAINA, F. GLAW & M. VENCES (2011): A new leaf tailed gecko species from northern Madagascar with a preliminary assessment of molecular and morphological variability in the *Uroplatus ebenau* group. – *Zootaxa*, **3022**: 39–57.
- RATSOAVINA, F. M., N. R. RAMINOSOA, E. E. LOUIS JR., A. P. RASELIMANANA, F. GLAW & M. VENCES (2013): An overview of Madagascar's leaf tailed geckos (genus *Uroplatus*): species boundaries, candidate species and review of geographical distribution based on molecular data. – *Salamandra*, **49**: 115–148.
- RATSOAVINA, F. M., F. A. RANJANAHARISOA, F. GLAW, A. P. RASELIMANANA, A. MIRALLES & M. VENCES (2015): A new leaf-tailed gecko of the *Uroplatus ebenau* group (Squamata: Gekkonidae) from Madagascar's central eastern rainforests. – *Zootaxa*, **4006**: 143–160.
- RATSOAVINA, F. M., A. P. RASELIMANANA, M. D. SCHERZ, A. RAKOTOARISON, J. H. RAZAFINDRAIBE, F. GLAW & M. VENCES (2019a): Finaritra! A splendid new leaf-tailed gecko (*Uroplatus*) species from Marojejy National Park in north-eastern Madagascar. – *Zootaxa*, **4545**: 563–577.
- RATSOAVINA, F. M., M. D. SCHERZ, K. A. TOLLEY, A. P. RASELIMANANA, F. GLAW & M. VENCES (2019b): A new species of *Uroplatus* (Gekkonidae) from Ankarana National Park, Madagascar, of remarkably high genetic divergence. – *Zootaxa*, **4683**: 84–96.
- RATSOAVINA, F. M., M. VENCES & E. E. LOUIS JR. (2012): Phylogeny and phylogeography of the Malagasy leaf-tailed geckos in the *Uroplatus ebenau* group. – *African Journal of Herpetology*, **61**: 143–158.
- RAXWORTHY, C. J. & R. A. NUSSBAUM (1995): Systematics, speciation and biogeography of the dwarf chameleons (*Brookesia*; Reptilia, Squamata, Chamaeleontidae) of northern Madagascar. – *Journal of Zoology*, **235**: 525–558.
- RAXWORTHY, C. J., R. G. PEARSON, B. M. ZIMKUS, S. REDDY, A. J. DEO, R. A. NUSSBAUM & C. M. INGRAM (2008): Continental speciation in the tropics: contrasting biogeographic patterns of divergence in the *Uroplatus* leaf-tailed gecko radiation of Madagascar. – *Journal of Zoology*, **275**: 423–440.
- RAXWORTHY, C. J. & M. VENCES (2010): *Uroplatus henkeli*. – The IUCN Red List of Threatened Species. Version 2015.2. – <http://www.iucnredlist.org>, accessed 22 December 2022.
- RÖSLER, H. & W. BÖHME (2006): Peculiarities of the hemipenes of the gekkonid lizard genera *Aristelliger* Cope, 1891 and *Uroplatus* Duméril, 1806. – pp. 121–124 in: VENCES, M., J. KÖHLER, T. ZIEGLER & W. BÖHME (eds): *Herpetologia Bonnensis II*, Bonn.
- RONQUIST, F., M. TESLENKO, P. VAN DER MARK, D. L. AYRES, A. DARLING, S. HÖHNA, B. LARGET, L. LIU, M. A. SUCHARD & J. P. HUELSENBECK (2012): MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. – *Systematic Biology*, **61**: 539–542.
- RUANE, S., F. T. BURBRINK, B. RANDRIAMAHATANTSOA & C. J. RAXWORTHY (2016): The cat-eyed snakes of Madagascar: phylogeny and description of a new species of *Madagascarophis* (Serpentes: Lamprophiidae) from the Tsingy of Ankarana. – *Copeia*, **104**: 712–721.
- SABEL, J., K. GREEN, J. DAWSON, J. ROBINSON, C. GARDNER, G. STARKIE & N. D'CRUZE (2009): The conservation status of mammals and avifauna in the Montagne des Français massif, Madagascar. – *Madagascar Conservation & Development*, **4**: 44–51.
- SALZBURGER, W., G. B. EWING & A. VON HAESELER (2011): The performance of phylogenetic algorithms in estimating haplotype genealogies with migration. – *Molecular Ecology*, **20**: 1952–1963.
- SCHERZ, M. D. (2020): Diamond frogs forever: a new species of *Rhombophryne* Boettger, 1880 (Microhylidae, Cophylinae) from Montagne d'Ambre National Park, northern Madagascar. – *Zoosystematics and Evolution*, **96**: 313–323.
- SCHERZ, M. D., J. D. DAZA, J. KÖHLER, M. VENCES & F. GLAW (2017): Off the scale: a new species of fish-scale gecko (Squamata: Gekkonidae: *Gekkelepis*) with exceptionally large scales. – *PeerJ*, **5**: e2955.
- SCHÖNECKER, P. (2008): Geckos of Madagascar, the Seychelles, Comoros and Mascarene Islands. – Edition Chimaira, Terralog, **12**: 1–144.
- SCHÖNECKER, P. & A. BÖHLE (2004): Die Geckogattungen Madagaskars. – *Draco*, **19**: 56–67.
- SHEN, X. X., D. LIANG & P. ZHANG (2012): The development of three long universal nuclear protein-coding locus markers and their application to osteichthyan phylogenetics with nested PCR. – *PLoS One*, **7**: e39256.
- STAMATAKIS, A. (2014): RAXML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. – *Bioinformatics*, **30**: 1312–1313.
- STEPHENS, M., N. J. SMITH & P. DONNELLY (2001): A new statistical method for haplotype reconstruction from population data. – *American Journal of Human Genetics*, **68**: 978–989.
- SVATEK, S. & S. VAN DUIN (2002): Plattschwanzgeckos. Die Gattung *Uroplatus*. – Brähler Verlag.
- TOROPOV, P. (2021): Reptile traffickers trawl scientific literature, target newly described species. – *Reptiles & Amphibians*, **28**: 367–370.
- TOWNSEND, T. M., E. R. ALEGRE, S. T. KELLEY, J. J. WIENS & T. W. REEDER (2008): Rapid development of multiple nuclear loci for phylogenetic analysis using genomic resources: an example from squamate reptiles. – *Molecular Phylogenetics and Evolution*, **47**: 129–142.
- UETZ, P., P. FREED, R. AGUILAR & J. HOŠEK (2022, eds.): The Reptile Database. – <http://www.reptile-database.org>, accessed 03 October 2022.
- UNEP-WCMC (2015): Review of selected species subject to long-standing import suspensions. Part I: Africa. – UNEP-WCMC, Cambridge.
- VENCES, M., A. MIRALLES, S. BROUILLET, J. DUCASSE, A. FEDOSOV, V. KHARCHEV, I. KOSTADINOV, S. KUMARI, S. PATMANIDIS,

- M. D. SCHERZ, N. PULLANDRE & S. S. RENNER (2021): iTaxo-Tools 0.1: Kickstarting a specimen-based software toolkit for taxonomists. – *Megataxa*, **6**: 77–92.
- VENCES, M., M. MULTZSCH, S. GIPPNER, A. MIRALLES, A. CROTTINI, P.-S. GEHRING, A. RAKOTOARISON, F. M. RATSOAVINA, F. GLAW & M. D. SCHERZ (2022a): Integrative revision of the *Lygodactylus madagascariensis* group reveals an unexpected diversity of little brown geckos in Madagascar’s rainforest. – *Zootaxa*, **5179**: 1–61.
- VENCES, M., S. PATMANIDIS, V. KHARCHEV & S. S. RENNER (2022b): Concatenator, a user-friendly program to concatenate DNA sequences, implementing graphical user interfaces for MAFFT and FastTree. – *Bioinformatics Advances*, **2**: vbac50.
- VENCES, M., K. C. WOLLENBERG, D. R. VIEITES & D. C. LEES (2009): Madagascar as a model region of species diversification. – *Trends in Ecology and Evolution*, **24**: 456–465.
- VIEITES, D. R., K. C. WOLLENBERG, F. ANDREONE, J. KÖHLER, F. GLAW & M. VENCES (2009): Vast underestimation of Madagascar’s biodiversity evidenced by an integrative amphibian inventory. – *Proceedings of the National Academy of Sciences of the U.S.A.*, **106**: 8267–8272.
- WILMÉ, L., S. M. GOODMAN & J. U. GANZHORN (2006): Biogeographic evolution of Madagascar’s microendemic biota. – *Science*, **312**: 1063–1065.
- WOLLENBERG, K. C., R. K. B. JENKINS, R. RANDRIANAVELONA, R. RAMPILAMANANA, M. RALISATA, A. RAMANANDRAIBE, O. R. RAVOAHANGIMALALA & M. VENCES (2011): On the shoulders of lemurs: pinpointing the ecotouristic potential of Madagascar’s unique herpetofauna. – *Journal of Ecotourism*, **10**: 101–117.
- WOLLENBERG, K. C., D. R. VIEITES, A. VAN DER MEIJDEN, F. GLAW, D. C. CANNATELLA & M. VENCES (2008): Patterns of endemism and species richness in Malagasy cophyline frogs support a key role of mountainous areas for speciation. – *Evolution*, **62**: 1890–1907.