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Two new species of the *Spinomantis bertini* species complex (Mantellidae) from south-eastern Madagascar

Carl R. Hutter[1,2], Zo F. Andriampenomanana[3], Shea M. Lambert[4], Miguel Vences[5]

1 *Biodiversity Institute and Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045–7561, USA*
2 *Museum of Natural Sciences and Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, USA*
3 *Mention Zoologie et Biodiversité Animale, Université d'Antananarivo, BP 906, Antananarivo 101, Madagascar*
4 *Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA*
5 *Zoologisches Institut, Technische Universität Braunschweig, Mendelssohnstr. 4, 38106 Braunschweig, Germany*

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Corresponding author: Carl R. Hutter (carl.hutter@gmail.com)

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Abstract

We scientifically name and describe two new species of spiny frog (Mantellidae: *Spinomantis*) from moderately high elevations in Ranomafana National Park, in south-east Madagascar. This region has been surveyed extensively and has a remarkably high anuran diversity with many undocumented species still being regularly discovered. We describe a previously identified candidate species, *S.* sp. Ca07, as *Spinomantis lavabato* **sp. nov.** and a previously undiscovered species from this region as *Spinomantis lakolosy* **sp. nov.**. The new species are morphologically cryptic within the *S. bertini* complex but can be recognized by a combination of subtle differences in coloration such as a lack or weak expression of sharp dorsolateral color border in both species. Bioacoustically, the new species are quite different from other species in the complex: *Spinomantis lakolosy* **sp. nov.** has the longest note duration with a powerful-sounding call that rings like a bell, which can be heard over the sound of rushing water in nearby streams; while *S. lavabato* **sp. nov.** differs by having the shortest note duration that is quiet and sounds like a trill. Furthermore, both species are substantially diverged in mitochondrial DNA, with pairwise distances in a fragment of the 16S rRNA marker of 7–9% to all other related species. Furthermore, we identify a lineage for future study in the complex from the nearby high-elevation site Andemaka within Ranomafana National Park that has an intermediate sounding advertisement call between the newly described species; although we cannot formally describe this lineage herein due to unavailability of voucher specimens, this lineage emphasizes the unexpectedly high diversity of sympatric species of the *S. bertini* complex in the Ranomafana area. Additionally, we identify another lineage from Ambahavala in the Anosy Chain with strong mitochondrial divergence for future study. Our findings also highlight the need for continued inventory work in high elevation rainforests of Madagascar, even in relatively well-studied regions such as Ranomafana National Park.

Key Words

Amphibia, Anura, new species, Ranomafana National Park, *Spinomantis lakolosy*, *Spinomantis lavabato*, taxonomy

Introduction

Madagascar hosts an impressively diverse and almost entirely endemic amphibian fauna, occupying a wide variety of habitats and microhabitats (Glaw and Vences 2007). Among this diversity, frogs of the genus *Spinomantis* Dubois, 1992 are both distinctive and poorly known. These frogs, classified in the family Mantellidae, are often associated with striking dermal spines and fringes on the limbs, but not all species of the genus share this trait. Fourteen species of *Spinomantis* are currently formally named, with at least ten additional candidate species awaiting formal description (Vieites et al. 2009; Perl et al. 2014; Vences et al. 2017; AmphibiaWeb 2025). Yet, unlike other Malagasy frog genera such as *Boophis*, which have seen rapid taxonomic expansion, *Spinomantis* has gained only two described species in the past decade (*S. beckei*: Vences et al. 2017; *S. mirus*: Sabino-Pinto et al. 2019), and four in the past 20 years (*S. nussbaumi* and *S. tavaratra*: Cramer et al. 2008), leaving much of its diversity undocumented.

The genus has had one of the most complex systematic histories among Malagasy amphibians. Over the past century, various *Spinomantis* species were assigned to various unrelated genera like *Boophis*, *Mantidactylus*, *Guibemantis*, *Gephyromantis*, and even the Asian genus *Rhacophorus* (Ahl 1931; Methuen and Hewitt 1913; Guibé 1947; Blommers-Schlösser 1978, 1979; Dubois 1992). This instability reflected their impressive ecomorphological diversity, with some species being morphologically more similar to distantly related frogs than to other *Spinomantis*. Molecular phylogenetic studies eventually revealed that these morphologically varied species form a monophyletic group, now recognized as *Spinomantis* (Glaw and Vences 2006; Pyron and Wiens 2011; Wollenberg et al. 2011). However, relationships between *Spinomantis* and other mantellid genera remain partially unresolved, underscoring the need for continued phylogenetic work.

The taxonomic complexity of *Spinomantis* stems from its exceptional ecological and morphological diversity among Malagasy genera. Arboreal ecomorphs such as *S. aglavei*, *S. fimbriatus*, and *S. phantasticus* possess prominent dermal spines and fringes, while *S. peraccae* and *S. nussbaumi* inhabit similar habitats but lack these features. Ground-dwelling ecomorphs include partly or largely saxicolous species such as the relatively large-bodied *S. elegans*, *S. guibei*, or *S. microtis*, as well as the small-sized species *S. bertini*, *S. beckei*, and *S. mirus*, referred to as the *S. bertini* complex, all without fringes or spines and associated with stream habitats. Despite this variation, all *Spinomantis* share a combination of morphological traits that distinguish the genus: intercalary elements among terminal and subterminal phalanges of their digits, subgular vocal sacs, distinct type 2 femoral glands in males, an outer metatarsal tubercle, and maxillary teeth (Glaw et al. 2000; Glaw and Vences 2006).

Herein, we describe two new *Spinomantis* species of the *S. bertini* species complex from south-eastern Madagascar and note two additional lineages of interest for future study from Andemaka and Ambahavala, discovered during recent field expeditions to Ranomafana National Park. These species are morphologically cryptic, appearing nearly identical and sharing similar habitats around streams, but they can be distinguished by their divergent advertisement calls and appear to differ in microhabitat with two species residing along fast flowing streams and one species in caves.

Materials and methods

Terminology

We follow the unified concept of species (i.e., general lineage concept), which defines a species as segments of separately evolving metapopulation lineages (Simpson 1961; Wiley 1978; de Queiroz 1998, 2005, 2007). We use multiple lines of evidence in assessing species boundaries, combining data from morphology, phylogenetics, bioacoustics, and biogeography (de Queiroz 2007; Padial et al. 2010; Vences et al. 2013). The integrated evidence is then considered and used as support for the hypothesis that a given population is an independently evolving lineage and thus a distinct species. Family and genus-level names follow the taxonomy proposed by Glaw and Vences (2006). Geographic regions for biogeographic analyses are defined according to Glaw and Vences (2007). According to this zonation, Ranomafana National Park is located within a region named the "Southern Central East" of Madagascar.

Specimen collection and morphological measurement

Specimens were collected at night through targeted searches of the new species' microhabitat along streams and within cave-like rock formations. Specimens were euthanized using tricaine methanesulfonate (MS-222), fixed in ~10% formalin (buffered with sodium phosphate to ~7.0 pH) for 24 hours and then stored in 70% ethanol for long-term preservation. Some specimens were fixed in 90% ethanol for 24 hours and then transferred to 70% ethanol. We deposited and examined alcohol-preserved specimens from the amphibian collections at the Biodiversity Institute of the University of Kansas (KU), Zoologische Staatssammlung München (ZSM), and Département de Biologie Animale, Antananarivo (UADBA). Additional collection acronyms used herein are FAZC, ZCMV, FGZC, and LR (field number series of F. Andreone, M. Vences, F. Glaw, and L. Raharivololoniaina respectively), FGMV (field number series shared between M. Vences and F. Glaw), CRH field series of Carl Richard Hutter, and ZSM (Zoologische Staatssammlung München, Germany). All photographs were taken by CRH unless otherwise noted.

Morphological measurements were taken by MV with a manual caliper with a precision of 0.1 mm. Terminology and measurements largely follow Glaw et al. (2000) and we used the following: (1) snout-vent length (SVL); (2) head width at the greatest point (HW); (3) head length (= rostrum) from snout tip to posterior edge of tympanum (HL); (4) horizontal tympanum diameter (TD); (5) horizontal eye diameter (ED); (6) eye-snout tip distance (ESD); (7) distance from eye-nostril distance (END); (8) distance from nostril-snout tip (NSD); (9) distance between nostrils (NND); (10) hand length from carpal-metacarpal articulation to tip of longest finger (HAL); (11) forelimb length from forelimb insertion to tip of longest finger (FORL); (12) tibia length from femur-tibia articulation to heel, measured along the shank (TIBL); (13) length of foot and tarsus, from tibiotarsal articulation to tip of longest toe (FOTL); (14) foot length from tarsal-metatarsal articulation to tip of longest toe (FOL); (15) hindlimb length from hindlimb insertion to tip of longest toe (HIL); (16) length of femoral gland (FGL); and (17) width of femoral gland (FGW).

DNA sequencing and phylogenetics

Following euthanasia, we extracted whole livers and hind limb muscles and stored the tissues in 95% ethanol. We obtained new genetic data for 11 specimens of the *S. bertini* complex and six specimens of *S. guibei* for a fragment of the mitochondrial 16S rRNA marker (16S) widely used for molecular comparisons in Mantellidae (Vieites et al. 2009). Most sequences were obtained by Sanger sequencing using methods for DNA extraction, primers, PCR amplification, and sequencing as described in Hutter et al. (2018). Additional mitochondrial data from two specimens were acquired by extracting the target markers from samples sequenced using the FrogCap Ranoidea v1 probe set (Hutter et al. 2022; available at: https://github.com/chutter/FrogCap-Sequence-Capture). Probe design, sequencing and analytical methods are described in Hutter et al. (2022) in detail. After sequencing, DNA data were manually edited for quality in Geneious Prime 2025 (Biomatters 2025) or in CodonCode Aligner (CodonCode corp.). Sequences >200 bp were deposited in GenBank (PX629884–PX629894) and the shorter *S. guibei* sequences are provided at Zenodo, https://doi.org/10.5281/zenodo.17081898.

We first aligned the new sequences with 16S sequences for all *Spinomantis* collected from GenBank to confirm the subgeneric relationship of the new species in an exploratory analysis (tree not shown). Following this tree and the evidence from the mitochondrial multigene tree of Wollenberg et al. (2011) where the *S. bertini* complex was placed in a clade with *S. guibei* that was sister to *S. microtis*, we compiled a dataset with all sequences of the *S. bertini* complex plus *S. guibei* and used one sequence of *S. microtis* as outgroup for phylogenetic inference.

DNA sequences were aligned using the G-INS-i algorithm in MAFFT (Katoh and Stanley 2013). Alignment length after trimming longer sequences was 519 bp. We used maximum-likelihood in IQ-Tree v.1.5.5 (Nguyen et al. 2015) to conduct phylogenetic tree reconstruction with default options selected. We used ModelFinder (Kalyaanamoorthy et al. 2017) to find the best-fit model of molecular evolution and assessed support using 500 full parametric bootstrap replicates.

To calculate pairwise genetic distances, we used a reduced alignment after removing several excessively short sequences (e.g., most sequences of *S. guibei* where sequences could not be resolved after a poly-C stretch in the middle of the sequence). We then calculated uncorrected pairwise distances from this alignment using MEGA7 (Kumar et al. 2016).

All alignments, treefiles, a table with genetic distances, and a table with all sequences, GenBank accession numbers and specimen metadata are available from the Zenodo repository (https://doi.org/10.5281/zenodo.17081898).

Bioacoustics

Advertisement calls were recorded in the field with an Olympus LS-10 Linear PCM Field Recorder and a Sennheiser K6-ME66 super-cardioid shotgun microphone. The calls were recorded in WAV format with a sampling rate of 44.1 kHz/s with 16 bits/sample. Representative cuts of the original sound recordings in WAV format have been deposited on Zenodo (https://doi.org/10.5281/zenodo.17081898). We measured call parameters using the software Cool Edit Pro 2.0. We obtained frequency information through Fast Fourier Transformation (FFT; width 1012 points). A Hanning window (512 bands) was used to create the spectrogram. Measures are reported as the range followed by the mean ± two standard deviations from the mean. Call-centered terminology and standards in call analyses and descriptions follows Köhler et al. (2017), with a call defined as the entire assemblage of acoustic signals emitted in sequence, and notes are subunits separated by temporally distinct segments of background noise between each note.

We chose the following relevant call variables, generally following Köhler et al. (2017): (1) number of notes per call; (2) call duration (ms); (3) call interval duration (ms); (4) note duration (ms); (5) inter-note interval duration (ms); (6) note repetition rate within call (notes/s); (7) pulse rate (/s); (8) dominant frequency (= fundamental frequency), measured at peak amplitude (Hz); and (9) approximate prevalent frequency band width (Hz).

Finally, we evaluated the amount of bioacoustic differences between species following Köhler et al. (2017). We considered differences in general call structure (e.g., pulsed/tonal notes, consistent note arrangements, amplitude envelope shape; Ryan and Rand 1990) and such temporal variables that are putatively less influenced by temperature, body size, and behavior (e.g., note duration, pulse rate; Gerhardt et al. 2000; Köhler et al. 2017) to be important traits for distinguishing species.

Results

The Maximum Likelihood phylogenetic tree inferred from the 16S data (alignment length 519 bp; 34 ingroup samples included; Fig. 1) supported all species and candidate species included as reciprocally monophyletic, which high bootstrap support values of BS = 94–100%. The *S. bertini* complex was resolved as a monophyletic group (BS = 95%), sister to *S. guibei*. The two sympatric species, *S. bertini* and *S. beckei* from Andohahela in the South East were resolved as sister taxa (BS = 75%) and, together with one newly sequenced genetic lineage from Ambahavala in the Anosy Massif, formed the sister group of *S. mirus*. The two focal lineages from Ranomafana were sister to each other (BS = 87%) and together the sister group of all other species of the *S. bertini* complex (BS = 60%).

The two focal lineages from Ranomafana differed from other lineages of the *S. bertini* complex by an un-

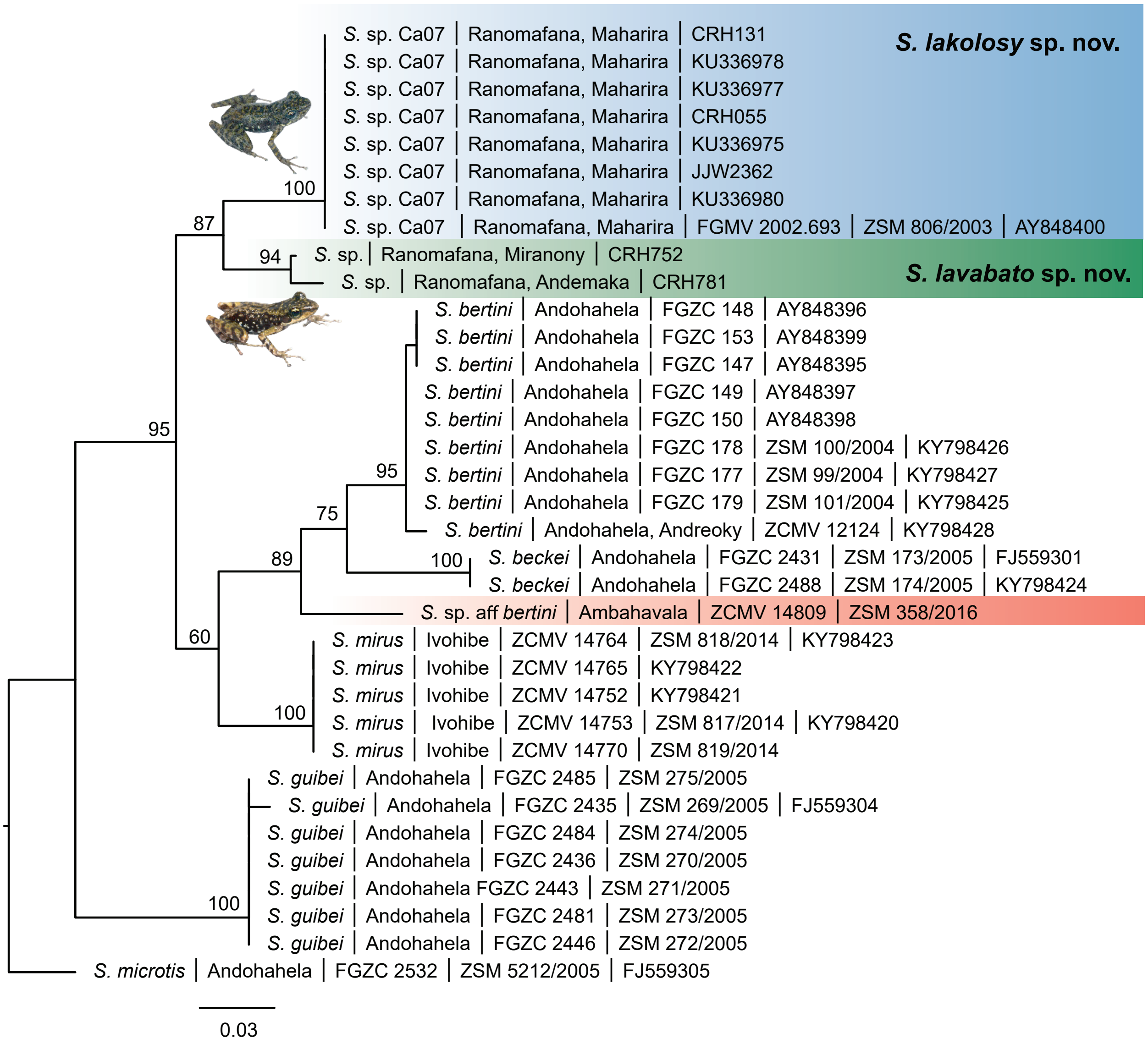

Figure 1. Maximum likelihood tree inferred from a 519 bp alignment of DNA sequences of the mitochondrial 16S rRNA gene in the *Spinomantis bertini* complex and the related *S. guibei*. Colors mark the two new species described herein and the new candidate species from Ambahavala. Numbers at nodes are bootstrap values in percent (500 replicates), not shown for most shallow nodes. The tree was rooted with *S. microtis*.

corrected pairwise 16S distances of 7.0–11.3%, and from each other by 5.4–6.2%. The newly sequenced Ambahavala lineage differed from *S. bertini* and *S. beckei* by 6.4–6.8% while the two sympatric species *S. beckei* and *S. bertini* differed from each other by 6.0–6.4% and from *S. mirus* by 8.0–9.3%. Within one of the focal lineages from Ranomafana, the two specimens from Miranony and Andemaka (Fig. 2) differed by 1.4%.

The genetic divergence of the focal lineages from Ranomafana to all other nominal species in the *S. bertini* complex of at least 7% is much higher than the reference value of 3% used by Vieites et al. (2009) to define candidate species of Malagasy frogs, and the same is true for the distance between the two Ranomafana lineages which differ by a minimum of 5.4%. The concordance of high mitochondrial divergences, subtle morphological differences and substantial bioacoustic differences in sympatry (detailed in the Diagnosis sections below), provides convincing evidence that the two focal lineages are distinct species both under evolutionary and biological species criteria. We therefore proceed to formally name and describe these two lineages as new species and discuss possible further taxonomic divergence within one of them and flag the genetically divergent lineages from Ambahavala and Andemaka as lineages of interest for future study.

Spinomantis lakolosy sp. nov.

https://zoobank.org/FA47F621-2FF5-4244-888A-4184CC3D9CED

Figs 3, 4; Table 1

Common English name: Bell Ringing Madagascar Frog.

Common Malagasy name: Ny sahona maneno lakolosy.

Available names. There are no junior synonyms available in the *S. bertini* complex that could represent earlier available names for the new species.

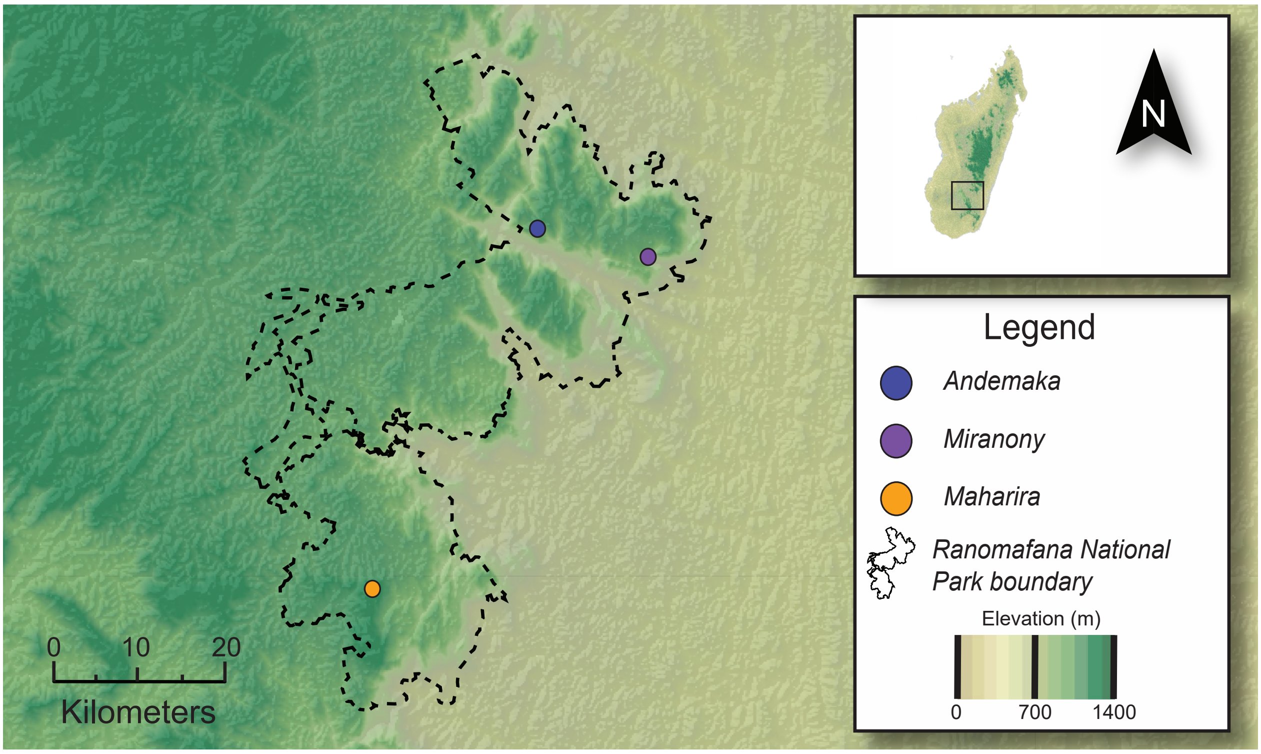

Figure 2. The distribution of the three species in the *Spinomantis bertini* species complex in within Ranomafana National Park (Southern Central East of Madagascar). *Spinomantis lakolosy* occurs at Miranony, *Spinomantis lavabato* is found at Maharira, and a divergent population here assigned provisionally to *S. lavabato* is found at Andemaka.

Figure 3. *Ex-situ* dorsal-lateral, dorsal, and ventral photographs of (**A**) female *Spinomantis lakolosy* (paratype: KU340867, CRH 751; ventral side CRH 678) and (**B**) male specimen KU340884 (CRH 781) from the divergent population here provisionally assigned to *S. lakolosy*.

Table 1. Morphometric measurements (in mm) of the two new species. See Materials and Methods for abbreviations.

Species	***S. lavabato* sp. nov.**				***S. lakolosy* sp. nov.**	
Voucher	KU336975	KU336977	KU336978	ZSM 806/2003	KU340852	KU340867
Field Number	JJW2336	JJW2352	CRH 118	FGMV 2002.693	CRH 726	CRH 751
Locality	Ranomafana, Maharira	Ranomafana, Maharira	Ranomafana, Maharira	Ranomafana, Maharira	Ranomafana, Miranony	Ranomafana, Miranony
Status	Holotype	Paratype	Paratype	Paratype	Holotype	Paratype
Sex	Male	Male	Female	Male	Female?	Female
SVL	24.4	24.2	26.7	23.3	21.8	25.5
HW	8.0	8.0	7.9	7.7	6.5	7.4
HL	9.2	9.2	10.0	9.3	8.1	9.3
TD	2.4	1.7	2.0	2.1	1.8	2.2
ED	3.9	3.5	3.9	2.9	3.2	3.2
END	1.7	2.1	1.8	2.1	1.7	1.8
NSD	1.6	1.6	1.5	1.5	1.2	1.1
NND	2.4	2.5	2.7	2.5	2.3	2.3
FORL	17.0	18.8	18.9	15.7	15.4	16.7
HAL	7.8	7.3	8.1	7.7	6.6	6.8
HIL	39.5	39.1	45.0	38.3	36.7	41.3
FOTL	17.7	17.6	20.3	16.3	16.0	18.8
FOL	10.7	10.7	11.8	10.2	10.4	11.5
TIL	12.8	12.8	14.3	12.1	11.9	13.7
FGL	4.7	4.2	NA	4.4	NA	NA
FGW	2.2	2.0	NA	1.4	NA	NA

Etymology. The specific epithet *lakolosy* is a Malagasy word meaning "bell". The name was chosen to describe the advertisement call of this species, which sounds like a ringing bell. The name is to be treated as an invariable noun in apposition.

Remarks. Previously undocumented species.

Type material. *Holotype*. KU340852 (CRH 726), sex unknown, possibly subadult female. Collected by Carl R. Hutter, Zo F. Andriampenomanana, Solo Justin, and Richard E. Glor on February 2nd, 2015, at Miranony Forest (21.1468°S, 47.5447°E; ca. 1100 m a.s.l) in mid-altitude rainforest within Ranomafana National Park in the Southern Central East of Madagascar, Fianarantsoa province (Fig. 4).

***Paratypes*.** KU340867 (CRH 751), adult female. KU340868 (CRH 752) adult male. Collected on February 2nd, 2015, with all other collection data the same as the holotype.

Diagnosis. *Spinomantis lakolosy* is placed in the family Mantellidae, subfamily Mantellinae as diagnosed by Glaw and Vences (2006). Phylogenetic evidence assigns the new species to the genus *Spinomantis* with phylogenetic affinities to *S. bertini*. The new species can be diagnosed to the genus *Spinomantis* morphologically by presence of intercalary elements between ultimate and penultimate phalanges of fingers and toes, presence of distinct femoral glands of type 1 (Glaw et al. 2000) in males, outer metatarsal tubercle present, maxillary teeth present, and adults living along streams in rainforests.

The new species is distinguished by a combination of the following characters within *Spinomantis*: (1) a dorsal color pattern of dark brown with golden-olive mottling and whitish dots; (2) a dark flank coloration with mottling of irregular white spots which rather diffusely transitions towards the dorsal coloration without sharp, regular color border; (3) light brown and dark bands on the ventral surface of the legs; (4) thick frenal stripe; (5) absence of dermal fringes or spines; and (6) advertisement calls with notes arranged in a series with a combination of a long note duration, long inter-note interval, and low dominant frequency.

Spinomantis lakolosy sp. nov. can easily be distinguished from other *Spinomantis* species not in the *S. bertini* species complex by many morphological characters. The new species differs from the arboreal species *S. aglavei*, *S. fimbriatus*, *S. massi*, *S. nussbaumi*, *S. peraccae*, *S. phantasticus*, and *S. tavaratra* by having terrestrial habits and smaller body size (female SVL 25 mm versus male and female SVL range of 31–56 mm). The new species differs from *S. aglavei*, *S. fimbriatus*, *S. massi*, *S. phantasticus*, and *S. tavaratra* by smooth skin and an absence of dermal spines or fringes; from *S. elegans* by a lack of a clearly delimited ocellated dorsal pattern and smaller body size (female SVL 25 mm versus male and female SVL range of 50–60 mm); from *S. guibei* by a smaller body size (female SVL 25 mm versus male and female SVL range of 29–40 mm) and a brown-yellow-gold color pattern versus green; from *S. microtis* by a smaller body size (female SVL 25 mm versus male and female SVL range of 30–48 mm), smaller terminal discs on fingers and toes, and smooth skin; and from *S. brunae* by a smaller size (female SVL 25 mm versus male and female SVL range of 32–35 mm) and absence of gold and black mottling on the dorsum.

When comparing *Spinomantis lakolosy* sp. nov. to other species in the *S. bertini* complex, the following differences are apparent: (1) *S. bertini*: has more white coloration on ventral side and a more distinct frenal stripe that extends farther to the tip of the snout and is more yellow in coloration, a dorsal-lateral line with yellow borders (versus absence of line), dorsal coloration that is more uniform (versus mottled in the new species); (2) *S. beckei*:

Figure 4. Preserved holotypes of (**A**) *Spinomantis lakolosy* sp. nov., KU340852 (CRH 726) and (**B**) *S. lavabato* sp. nov., KU336975 (field number JJW 2336) in dorsal and ventral views.

has a distinct dorsal-lateral line and much smaller brown spotting, a thinner frenal stripe that extends past the arm but does not extend to the snout, whitish coloration on the hind limbs and less distinct bands, and more brown rather than yellow in coloration; and (3) *S. mirus*: has more yellow-brown background dorsal coloration while the new species has more brown mottling and some reddish coloration on the flanks and hind limbs, the new species has dark brown flanks versus yellow in *S. mirus*. Also, in all these species in most individuals, the transition between dorsal and flank color occurs along a sharp, regular and distinguishable color border which is less distinctly expressed in the new species.

Bioacoustically, *Spinomantis lakolosy* sp. nov. differs from other species in the *S. bertini* complex by: (1) *S. bertini*: a much shorter note duration (20–26 ms versus 67–105 ms); and (2) *S. beckei*: a much shorter note duration (20–26 ms versus 67–105 ms) and frequency modulation with a terminal end note. Additionally, despite having a similar body size, *S. lakolosy* sp. nov. has a much lower dominant frequency than other species in the complex (2454–2497 Hz versus 4000 Hz or more in the other species).

Description of the holotype. Specimen in good state of preservation (Fig. 4), muscle tissue sample removed from left thigh, damage and limited tissue removal also on right thigh; tongue removed. Snout-vent length 21.8 mm, for further measurements see Table 1. Body slender; head longer than wide, approximately of same width as body. Snout rounded in dorsal view, pointed in lateral view, nostrils directed laterally, slightly protuberant, much nearer to tip of snout than to eye; canthus rostralis distinct, slightly concave; loreal region concave; tympanum distinct, rounded, its horizontal diameter 60% of eye diameter; supratympanic fold relatively distinct, running above the tympanum, then bending downwards and running straight towards forelimb insertion; tongue missing (removed); vomerine teeth absent, maxillary present; choanae small, rounded. Arms slender, subarticular tubercles single; fingers without webbing; relative length of fingers 1<2<4<3; finger disks enlarged; nuptial pads absent. Hind limbs slender; tibiotarsal articulation reaches snout tip when the hind limb is adpressed along the body; lateral metatarsalia largely separated; inner metatarsal tubercles distinct, outer metatarsal tubercle not recognizable; webbing formula between toes rudimentary, with traces of web between toes 3, 4 and 5; relative length of toes 1<2<5<3<4; third toe slightly but clearly longer than fifth. Skin on the upper surface smooth, without folds or ridges; ventral skin smooth. Femoral glands not recognizable in external or internal view.

After 10 years in preservative, the dorsum is washed with brown and greenish brown tones and some indistinct and irregular light beige dots, without distinct borders between the colors, brown color being especially seen on the anterior dorsum. Limbs greenish brown with two distinct brown crossbands on lower arm, and three brown crossbands on shanks. Ventrally irregularly and indistinctly mottled brown; hindlimbs ventrally with somewhat more distinct brown color. Color in life not documented by photos.

Variation. Besides the holotype, only one further specimen (female KU340867; not sequenced) from the type locality was available for examination (Table 1). Compared to the holotype, this specimen is slightly larger, supporting that the holotype is probably a subadult. Compared to the holotype the specimen had a somewhat more obvious light spotting on the dorsum, and a dense dark vermiculation on the ventral side. In life, the specimen had a dorsum with irregular mottling in brown and yellowish-olive elements. The border between dorsal and flank color was relatively clear, the flanks being dark brown with sharp delimited yellowish -beige spots and markings. From snout tip over nostrils to eye, a reddish-brown line was present, and some reddish-brown spots were also present along the dorsolateral separation. A second female specimen, CRH 678 (UADBA unaccessioned), largely agreed with this pattern (without the reddish-brown elements, and the light markings on the dorsum being more olive-greenish), and in life, had dark vermiculation on a silvery white throat, chest and anterior belly whereas the posterior belly was uniformly grayish brown.

We tentatively assign to this species specimens from another population, Andemaka, which was found divergent genetically, ecologically and bioacoustically. The single sequenced specimen KU340884 (CRH 781) had a 16S distance of 1.4% to the paratype KU340868 (CRH 752) from the type locality Miranony. In this specimen, an adult male determined by well-developed femoral glands, the light dorsal pattern was overall olive greenish, and the belly pattern was more whitish on gray. Femoral glands were distinct but relatively small, and the single gland granules not clearly distinguishable in external view. The advertisement call of this specimen furthermore had a very short note (pulse) duration of less than 20 ms (vs. >25 ms in Miranony), suggesting a possible bioacoustic differentiation.

Call. The advertisement call from the type locality Miranony consists of a note series of regularly repeated short bell–like tonal notes (Fig. 5). Several calls are emitted in a call series. In one series of nine calls of specimen CRH 752, calls consisted of 7–10 notes (8.5±1.7 notes; N=9), had a duration of 562–1150 ms (987±220 ms; N=9), and an inter–call interval duration of 473–752 ms (584±96 ms; N=8). Within calls, note duration was 67–105 ms (86±13 ms; N=16) and inter–note interval duration was 0–58 ms (27±15 ms; N=15). Dominant frequency was 2454–2497 Hz and approximate prevalent band width was 2200–2800 Hz.

Distribution. *Spinomantis lakolosy* sp. nov. is only known from Miranony Forest (21.1468°S, 47.5447°E; ca. 1100 m a.s.l.) in high altitude rainforest within northern Ranomafana National Park in Southern Central East Madagascar, Fianarantsoa province (Fig. 2). The identity of the specimens from the second site, Andemaka, remains to be studied in depth.

Natural history. *Spinomantis lakolosy* sp. nov. is locally moderately abundant, and found only within undisturbed, primary forests at high elevations (ca. 1000–1100 m). Individuals were perched on the surfaces of vegetation less than 50 cm in height or on mossy rocks calling over a fast-flowing stream (Fig. 6). The species' advertisement call was loud and could easily be heard over the sound of the rushing water in the stream, and many individuals could be heard calling in a light mist, on a cloudy night. Other syntopic *Spinomantis* include *S. peraccae* and a species from the *S. aglavei* complex.

Conservation status. The new species is only reliably known from Ranomafana National Park at a high elevation forest site near the village of Miranony (the status of the population from Andemaka requires further study). The distribution of this species is therefore only known from a single location, in the northern section of Ranomafana National Park, where many villages in the area have left the forest fragmented with no connectivity. Furthermore, the forest in which the species occurs is experiencing intense deforestation pressure. Ongoing anthropogenic threats are continually reducing the quality and extent of its habitat. For example, slash-and-burn agriculture and forest products are frequently extracted directly from this species' habitat. Given this information, we propose to categorize this species as "Endangered" [B1ab(iii)] following IUCN criteria (IUCN 2001).

Spinomantis lavabato sp. nov.

https://zoobank.org/54D933F3-B996-4336-A901-57213941FDBC

Figs 4, 7; Table 1

Common English name. Cave Madagascar Frog.

Common Malagasy name. Ny sahona mitoetra ao anaty lavabato.

Available names. There are no junior synonyms available in the *S. bertini* complex that could represent earlier available names for the new species.

Etymology. The specific epithet *lavabato* is a Malagasy word/phrase literally meaning "rock hole" or in other words a "cave". The name was chosen to describe the

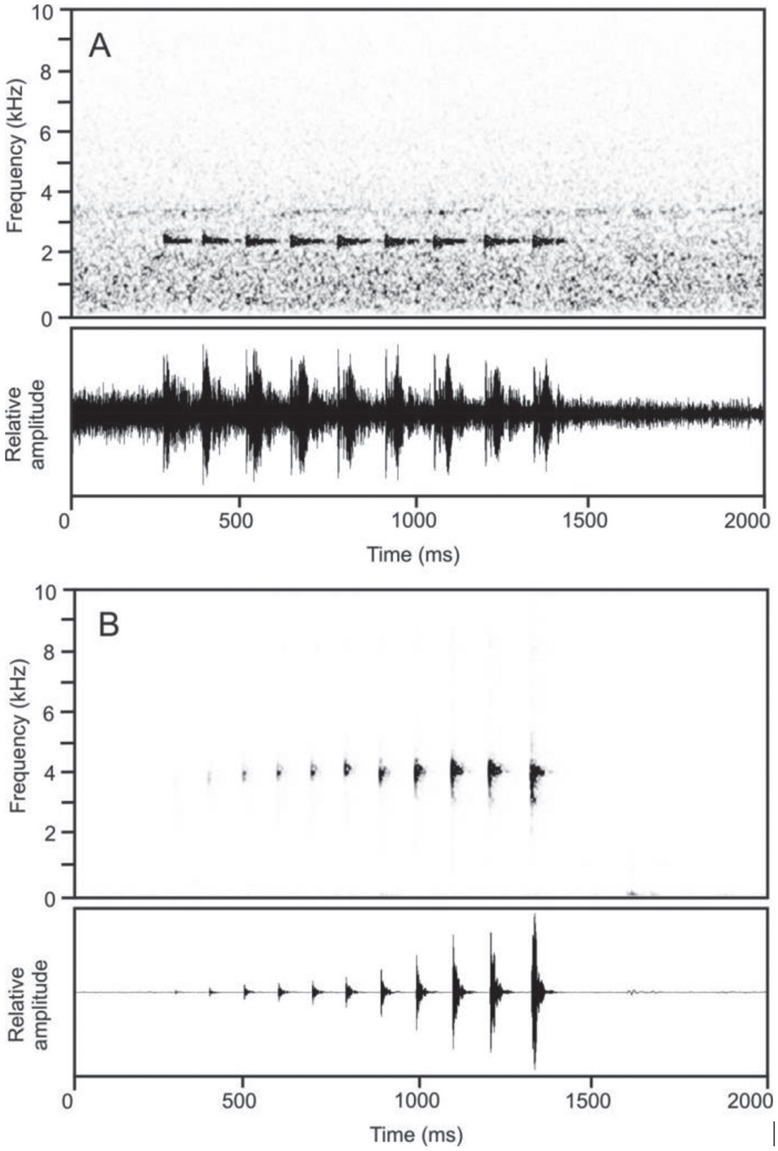

Figure 5. Oscillograms and spectrograms of the call of (**A**) *Spinomantis lakolosy* (paratype: KU340869, CRH 752) and (**B**) *S. lavabato* (holotype: KU336975, JJW 2336).

general micro-habitat of this species, where it dwells in cave-like rocky structures. The name is to be treated as an invariable noun in apposition.

Remarks. Previously referred to as *Spinomantis* aff. *bertini* (Glaw and Vences 2007) and designated as a candidate species *Spinomantis* sp. Ca07 (Vieites et al. 2009).

Type material. *Holotype*. KU336975 (field number JJW 2336). An adult male collected by Carl R. Hutter, Shea M. Lambert, and Solo Justin collected on January 10th, 2013, at Maharira Forest (21.3326°S, 47.4103°E; ca. 1300 m a.s.l.) alongside a trail with rocky formations in mid-altitude rainforest within Ranomafana National Park, in Southern Central East Madagascar, Fianarantsoa province (Fig. 2).

***Paratypes*.** KU336978 (CRH 118) adult female, KU336979 (CRH 122) adult male and KU336980 (CRH 175) adult male collected by Carl R. Hutter, Zo F. Andriampenomanana, April Hillman, and Solo Justin from caves at the peak of Maharira (21.3334°S, 47.4120°E; ca. 1340 m a.s.l.). KU336975 (JJW 2336), KU336976 (JJW 2350), and KU336977 (JJW 2352) all males collected along a trail with rocky formations in Maharira Forest (21.3312°S, 47.4106°E; ca. 1300 m a.s.l.), Fianarantsoa province, Madagascar. ZSM 806/2003 (FGMV 2002.693), adult male, collected at Maharira, Ranomafana National Park, at unknown coordinates, on 26 January 2003 by E. Rajeriarison and T. Rajoafiarison.

Diagnosis. *Spinomantis lavabato* is placed in the family Mantellidae, subfamily Mantellinae as diagnosed by Glaw and Vences (2006). Phylogenetic evidence assigns the new species to the genus *Spinomantis* with phylogenetic affinities to *S. bertini*. The new species can be diagnosed to the genus *Spinomantis* morphologically by presence of intercalary elements between ultimate and penultimate phalanges of fingers and toes, presence of distinct femoral glands (type 1: Glaw et al. 2000) in males, outer metatarsal tubercle present, maxillary teeth present, and adults living along streams in rainforests.

The new species is distinguished by a combination of the following characters within *Spinomantis*: (1) small

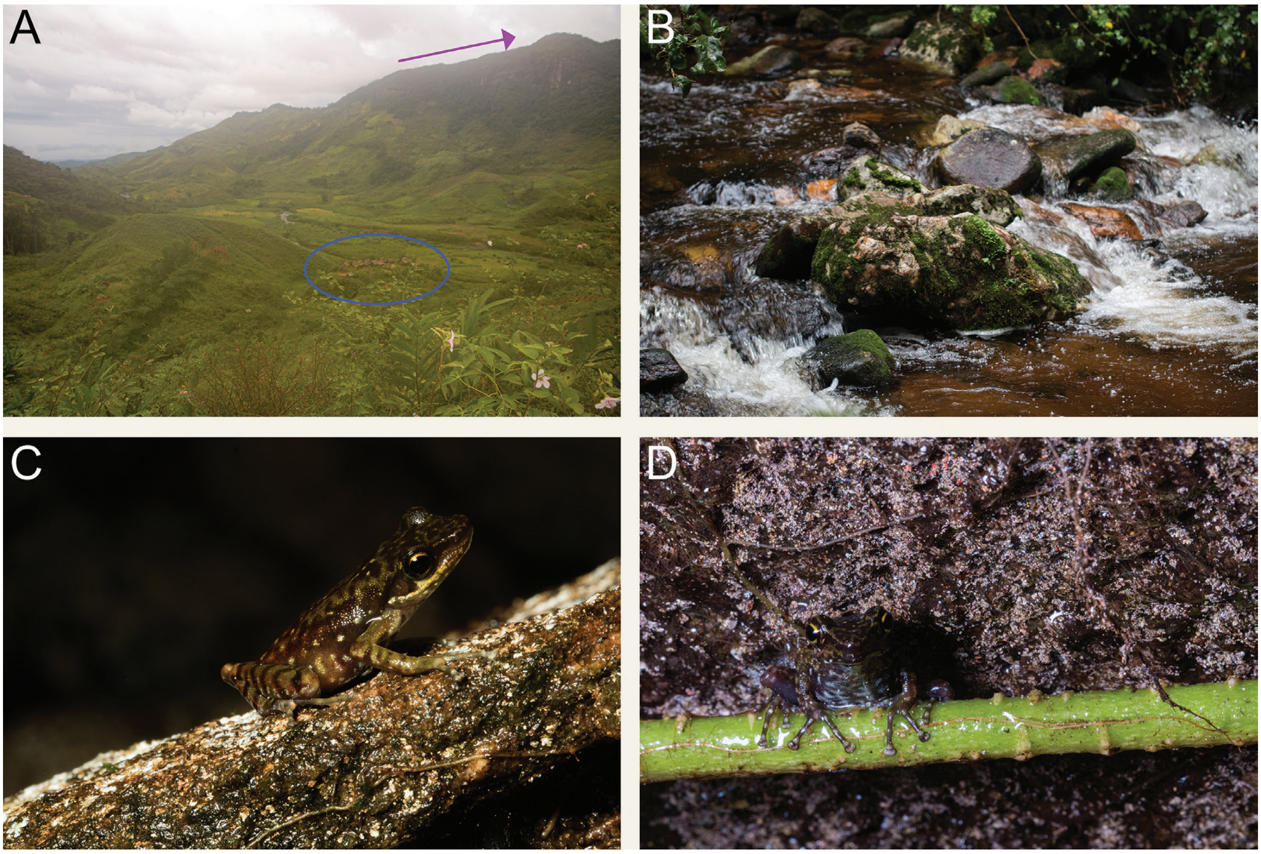

Figure 6. *In-situ* photographs of the habitat and microhabitat of *Spinomantis lakolosy*. The panels show: (**A**) the outskirts of the village of Miranony (blue circle) that leads to the primary forest habitat in the top right of the photograph (purple arrow); (**B**) within the primary forest habitat, the fast-flowing stream where *S. lakolosy* calls at night; (**C**) male paratype KU340868 (CRH 752) perched on a rock ledge alongside the stream; and (**D**) female paratype KU340867 (CRH 751) perched on a small branch alongside a rock ledge.

adult male body size of SVL 24.2–24.4 mm, adult females also small at 26.7 mm; (2) a dorsal color pattern of dark brown with yellow-olive mottling and whitish dots along the flanks; (3) darker flank coloration with mottling of white with a transition between flank and dorsal coloration somewhat diffuse as light dorsal markings can extend onto flanks and brown flank color is of similar tone as brown color on dorsum; (4) dark bands on the dorsal surface of limbs; (5) mottled frenal stripe; (6) absence of dermal fringes or spines; (7) advertisement calls are short notes arranged in a series with a combination of a very short note duration, short inter-note interval, and high dominant frequency.

Spinomantis lavabato sp. nov. can easily be distinguished from other *Spinomantis* species not in the *S. bertini* species complex by many morphological characters (size ranges in the following are given for males and females combined as body size dimorphism in *Spinomantis* is low). The new species differs from the arboreal species *S. aglavei*, *S. fimbriatus*, *S. massi*, *S. nussbaumi*, *S. peraccae*, *S. phantasticus*, and *S. tavaratra* by having a terrestrial habitat and smaller body size (SVL 24.2–24.4 versus 31–56 mm). The new species differs from *S. aglavei*, *S. fimbriatus*, *S. massi*, *S. phantasticus*, and *S. tavaratra* by smooth skin and an absence of dermal spines or fringes; from *S. elegans* by a lack of a clearly delimited ocellated dorsal pattern and smaller body size (versus 50–60 mm); from *S. guibei* by a smaller body size (versus 29–40 mm) and a brown-yellow color pattern versus green; from *S. microtis* by a smaller body size (versus 30–48 mm), smaller terminal discs on fingers and toes, and smooth skin; and from *S. brunae* by a smaller size (versus 32–35 mm) and absence of gold and black mottling on the dorsum.

When comparing *Spinomantis lavabato* sp. nov. to other species in the *S. bertini* complex, the following differences are apparent: (1) *S. bertini*: has more white coloration on ventral side and a more distinct frenal stripe that extends farther to the tip of the snout and is more yellow in coloration (versus a less distinct frenal stripe mottled in coloration), a dorsal-lateral line with yellow borders (versus absence of line), dorsal coloration that is more uniform (versus mottled in the new species); (2) *S. beckei*: has a distinct dorsolateral line and much smaller brown spotting, a thin frenal stripe that extends past the arm but does not extend to the snout, whiteish coloration on the hind limbs and less distinct bands, and brown spots on a yellow background versus yellow spots on a brown background; (3) *S. mirus*: has a more yellow-brown background dorsal coloration while the new species is more brown in background dorsal coloration, the new species has dark brown flanks versus yellow in *S. mirus*; and (4) *S. lakolosy* above: has a distinct frenal stripe, more yellow dorsal background coloration, hints of red color on the flanks and

Figure 7. *Ex-situ* dorsal-lateral, dorsal, and ventral photographs of (**A**) male *Spinomantis lavabato* (holotype: KU336975, JJW 2336) and (**B**) female (paratype: KU336978, CRH 118) in life.

limbs, and golden colored eyes (versus copper). Also, in most individuals of all these species except *S. lakolosy*, the transition between dorsal and flank color occurs along a sharp and distinguishable straight color border which is less distinctly expressed in the new species.

Bioacoustically, *Spinomantis lavabato* sp. nov. differs from other species in the *S. bertini* complex by: (1) *S. bertini*: a shorter note duration (20–26 ms versus 27–67 ms); (2) *S. beckei*: a shorter note duration (20–26 ms versus 27–67 ms) and frequency modulation with a terminal end note; and (3) *S. lakolosy* above: a much longer note duration (67–105 ms versus 27–67 ms) and lower dominant frequency than expected by body size. Additionally, a unique characteristic of this call compared to the other species is that the amplitude of each note starts out low and increases to maximum call amplitude in the final note.

Description of the holotype. Specimen in excellent state of preservation (Fig. 4), some tissue removed dorsoanteriorly from right thigh. Snout-vent length 24.4 mm, for further measurements see Table 1. Body slender; head longer than wide, slightly wider than body. Snout slightly pointed in dorsal view, rounded in lateral view, nostrils directed laterally, slightly protuberant, nearer to tip of snout than to eye; canthus rostralis distinct, concave; loreal region slightly concave; tympanum distinct, rounded, its diameter 60% of eye diameter; supratympanic fold distinct, straight; tongue ovoid, bifid and free posteriorly; vomerine teeth absent, maxillary teeth present; choanae small, rounded. Arms slender, subarticular tubercles single; fingers without webbing; relative length of fingers 1<2<4<3; finger disks distinctly enlarged; nuptial pads absent. Hind limbs slender; tibiotarsal articulation reaches nostrils when the hind limb is adpressed along the body; lateral metatarsalia partly connected; inner metatarsal tubercles distinct, outer metatarsal tubercle not recognizable; webbing formula between toes rudimentary, with traces between toes 3, 4 and 5; relative length of toes 1<2<3=5<4. Skin on the upper surface smooth, without folds or ridges; ventral skin smooth. Throat skin with recognizable folds laterally, indicating the presence of a vocal sac. Femoral glands large and distinctly elevated, of type 2 sensu Glaw et al. (2000), distance between femoral glands 1.3 mm.

After almost 13 years in preservative, the dorsum is dark brown with distinctly delimited beige spots and vermiculation. Limbs with distinct dark brown patterns which form clear crossbands on the forelimbs (four on lower arm, about three on upper arm) and less clearly delimited crossbands on hindlimbs (about five on thigh, five on shank, and four on tarsus and hand). Ventrally, dark brown with light spots and vermiculation on throat, chest and belly, more uniformly brown on limbs. In life, the light vermiculation on the dorsum was light brown with an olive greenish tint and rather poorly contrasted, especially in the anterior part of the dorsum. The light spots on the flanks were more distinctly contrasting with the dark brown flank color, yellowish where adjacent to the dorsum and white in the center of the flanks. Strongly contrasting yellowish spots were also present laterally on the head. The iris was copper in its dorsal part (not visible in its ventral half on the available images). The limbs were olive brownish with dark brown crossbands. Ventrally dark brown with very strongly contrasting silvery white vermiculation with a slightly bluish tint. Limbs ventrally brownish with indistinct pattern.

Variation. Table 1 contains measurements of two males and one female. The female paratype KU336978 (SVL 26.7 mm) is slightly larger than the two males (24.2–24.4 mm) and lacks femoral glands, and in preservative has a pattern of numerous narrow crossbands on the limbs, especially on the forelimbs. and a more vermiculated pattern on the throat. There does not seem to be a conspicuous sexual dimorphism in relative tympanum size (TD/ED 0.51 in the female, 0.49–0.62 in the two males). In paratype KU336977 the dorsal pattern is more uniformly green rather than yellowish green as in the holotype (Fig. 7).

Call. The advertisement call consists of a note series of regularly repeated click notes (Fig. 5). Several calls are often emitted in a call series, and in such a case, the number of notes per call gradually increases. Based on one call series of five calls of paratype specimen KU336977 (JJW 2352), call parameters were as follows: 4, 5, 8, 11, 11 notes per call, call duration 368, 496, 794, 1115 and 1118 ms. Intervals between calls were 1552–3859 ms (2373±1033 ms, n=4). Note duration was 27–67 ms (44±16 ms, n=18) and interval duration between notes was 48–68 ms (60±7 ms; n=16). Amplitude increased from first to last note of a call. Dominant frequency was 3789–4134 Hz (3996±88 ms), approximate prevalent band width was between 2600–4400 Hz. Calls of a second specimen KU336976 (JJW2350) were very similar in structure and parameters, one call series consisting of six calls consisting of 4, 5, 7, 9, 11, 9 notes per call.

Distribution. *Spinomantis lavabato* sp. nov. is known only from Ranomafana National Park at Maharira (Fig. 2), where cave-like rock formations can be found. The subsites being caves at the peak of Maharira (21.3334°S, 47.4120°E; ca. 1340 m a.s.l.) and along a trail with rocky formations in Maharira Forest (21.3312°S, 47.4106°E; ca. 1300 m a.s.l.).

Natural history. *Spinomantis lavabato* sp. nov. is locally abundant, and found only within undisturbed, primary forests at high elevations (ca. 1100–1300 m). Individuals were perched on the surfaces of rocks either within cave-like rock formations or alongside streams that were surrounded by large rock structures (Fig. 8A, B). Many

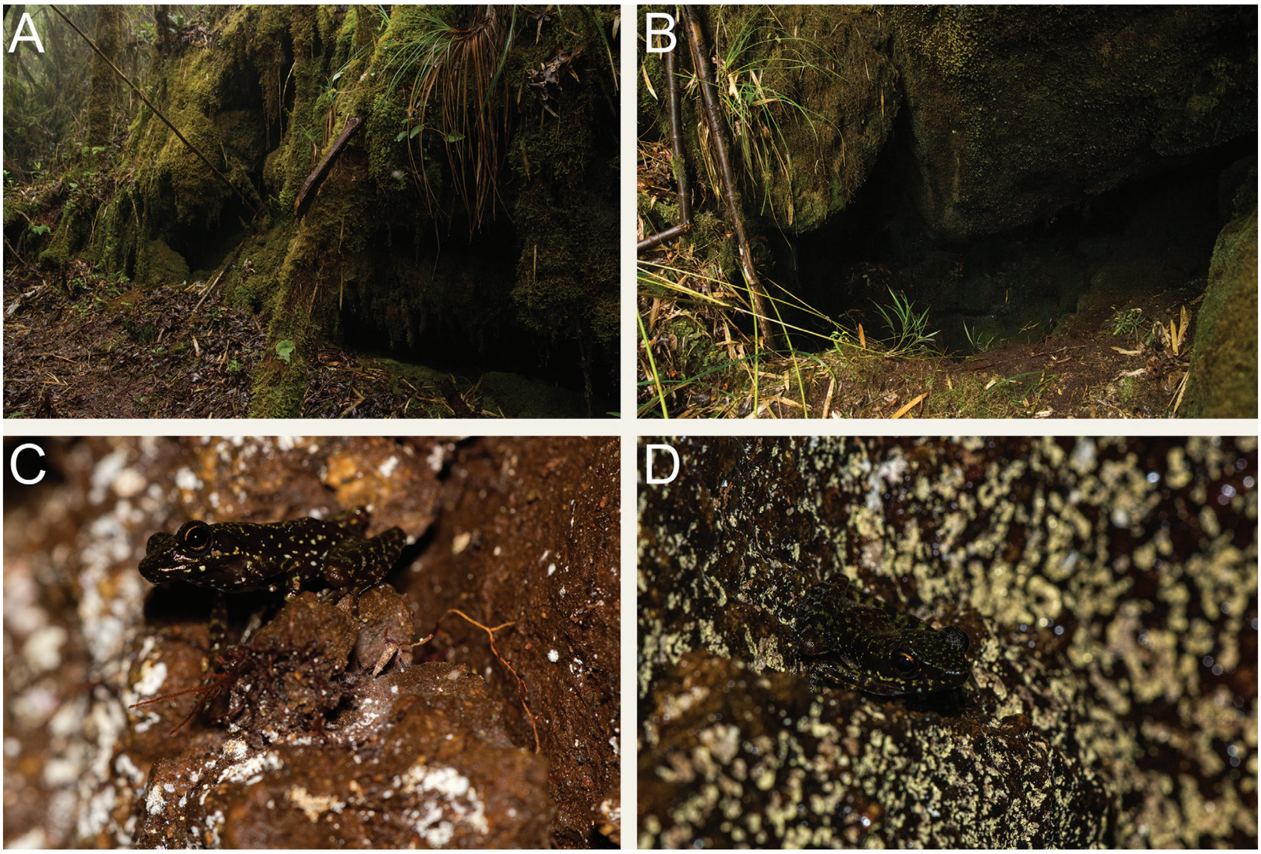

Figure 8. *In-situ* photographs of the habitat and microhabitat of *Spinomantis lavabato* found after locating through advertisement call. The panels show: (**A**) cave-like rock formations found along trails at Mahrira within Ranomafana National Park; (**B**) A closer look into the cave where individuals of this species can be found calling; (**C**) unidentified male individual perched on an earthen ledge within an enclosed cave-like rock formation; and (**D**) unidentified male individual perched on a crevice of a rock within a cave-like rock formation.

individuals of the species were always located on these rocks, and usually with a slow flowing stream alongside or underneath them and occasionally with only standing water that may flood during the rain and wash the tadpoles out. The species advertisement call was quiet and therefore calling males could only be heard if nearby when the sound of flowing water was quiet; the sound also echoed from the insides of the cave-like rock structures. Furthermore, the species called during the day, which is not something observed in many other *Spinomantis* except for *S. elegans* which also calls from the same microhabitat. Other syntopic *Spinomantis* include *S. peraccae*, a species from the *S. aglavei* complex, and *S. elegans*.

Conservation status. The new species is known from Ranomafana National Park and only one locality within the park: Maharira. The species is locally abundant, but the microhabitats to find them are somewhat difficult to access and are a very specific specialized habitat type of rocky formations. Maharira, where the species is located, is under some deforestation pressure and faces ongoing threats that result in the reduction of quality and extent of habitat. For example, slash-and-burn agriculture and forest products are frequently extracted directly from this species' habitat. Given this information, we propose to categorize this species as "Endangered" [B1ab(iii)] following IUCN criteria (IUCN 2001).

Discussion

We have shown that *Spinomantis lakolosy* and *S. lavabato* are clearly distinct species based on morphology, bioacoustics, and molecular phylogenetics. We have also provided evidence for one deep conspecific lineage that has the potential to be a distinct species in the Anosy Massif, based on a single specimen from Ambahavala without associated bioacoustic data. This specimen is characterized by its high genetic divergence and phylogenetic position (Fig. 1) and requires further study in the future, ideally based on more extensive data from fresh collections. Our data also indicate that specimens from Andemaka, here provisionally assigned as deep conspecific lineage to *S. lakolosy*, differ from the type series from Miranony in bioacoustics, plus some moderate differences in mitochondrial DNA (1.4% divergence), and perhaps morphology. Remarkably, these two sites are only 7 km from each other but at higher elevations separated by low elevation valleys, which may have isolated this population. It is possible that the Andemaka population represents yet another species of the *S. bertini* complex, which would represent an extraordinary example of recent species formation as it has also been suggested for other species of amphibians in the Ranomafana area (Vences et al. 2012).

An interesting aspect of these species, possibly related to species formation in the complex, is the divergence in their advertisement calls and the different habitats they inhabit. *Spinomantis lakolosy* inhabits fast flowing streams, which are loud, and it becomes a challenge for males to communicate with females for reproduction. Perhaps related to these habitat characteristics, *S. lakolosy* has evolved a longer note duration (and audibly louder call) as well as a lower dominant frequency than expected by body size (given that the rest of the species in the complex are of similar body sizes but call at higher spectral frequencies) such that the males dominant frequency would be non-overlapping with the sound of the rushing water in the stream. In stark contrast, *S. lavabato* has a very quiet sounding advertisement call with very short note durations, and these males attempt to attract females to their specific and quiet cave-like habitat, using their environment to their advantage as the calls echo from within these rock formations. An interesting component of this echo is that the first notes of the call begin at a lower amplitude and increase to maximum call amplitude in the final note.

If the mitochondrial tree presented here (Fig. 1) represents the species tree, it may also contribute to hypotheses on the biogeography of the *S. bertini* complex. The phylogenetic pattern suggests a clear north to south pattern of phylogenetic speciation, with successively splitting species *S. lakolosy/lavabato* – *S. mirus* – *S.* sp. from Ambahavala – *S. beckei/bertini* occurring successively at more southern locations and suggesting a possible colonization pattern in this direction. However, the two hierarchical sister taxa of the *S. bertini* complex (*S. guibei* and *S. microtis*) both occur in the extreme South East, indicating an overall convoluted biogeographic history of ground-dwelling *Spinomantis* in the South East and Southern Central East of Madagascar.

The discoveries of one previously undocumented new species and at least one further deep species-level lineage herein exemplifies the importance of continued field work in Madagascar, as the discovery of previously undocumented new species is occurring frequently (Lambert et al. 2017; Scherz et al. 2017a, 2018; Hutter et al. 2021), despite the extensive past barcoding efforts for Malagasy frogs (e.g., Vieites et al. 2009; Perl et al. 2014). Typically, such species have either low population densities, small geographic ranges or elevational ranges, and/or are in areas that have not been extensively surveyed. The new species here are from areas not well-surveyed and have very specific habitat requirements within caves, and while they might be locally abundant their specific microhabitat is more rare. Other recent examples of new discoveries include the very distinct *Rhombophryne nilevina* (Lambert et al. 2017), *Guibemantis sioka* (Hutter et al. 2025), *Gephyromantis angano* (Scherz et al. 2017a), *G. lomorina* (Scherz et al. 2018), *G. marokoroko* (Hutter et al. 2021), *G. cornucopia*, and *G. feomborona* (Miralles et al. 2023) – many of these discovered just at Ranomafana National Park. The continuation of basic field inventories is therefore clearly necessary to fully understand the patterns of species richness and complete evolutionary histories of frogs in Madagascar and other tropical regions.

Ranomafana National Park is one of the most surveyed localities for amphibians in Madagascar (Vieites et al. 2009; Glaw and Vences 2007) but the discoveries herein exemplify that even in such well-known sites in

Madagascar the herpetofaunal inventory is still incomplete. The new species described herein, however, were only found at locations within the park that are far from the main park entrances and thus difficult to reach, requiring expeditions of several days. It is therefore important to direct survey efforts not only to the easily accessible parts of protected areas in Madagascar, but also to new sites within them. Also, conservation efforts must ensure protection of the entire ensemble of habitat and elevational diversity available in Madagascar's protected areas considering the specialization and microendemism of many representatives of their biota.

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References

AmphibiaWeb (2025) AmphibiaWeb. https://amphibiaweb.org University of California, Berkeley, CA, USA. [Accessed 07 October 2025]

Angel F (1935) Batraciens nouveaux de Madagascar récoltés par M. R. Catala. Bulletin de la Société Zoologique de France 60: 202–207.

Biomatters (2025) Geneious Prime 2025. Biomatters Ltd., Auckland, New Zealand.

Boettger O (1880) Diagnoses reptilium et batrachiorum novorum a Carolo Ebanau in insula Nossi-Bé Madagascariensis lectorum. Zoologischer Anzeiger 3: 279–283.

CodonCode Corporation (2025) CodonCode Corporation. CodonCode Aligner, Dedham, USA.

D'Cruze NC, Henson D, Olsson A, Emmett DA (2009) The importance of herpetological survey work in conserving Malagasy biodiversity: Are we doing enough? Herpetological Review 40: 19–25.

De Queiroz K (1998) The general lineage concept of species, species criteria, and the process of speciation: A conceptual unification and terminological recommendations. In: Howard DJ, Berlocher SH (Eds) Endless Forms: Species and Speciation. Oxford University Press, Oxford, 57–75. https://doi.org/10.1093/oso/9780195109009.003.0005

De Queiroz K (2005) Ernst Mayr and the modern concept of species. Proceedings of the National Academy of Sciences 102: 6600–6607. https://doi.org/10.1073/pnas.0502030102

de Queiroz K (2007) Species concepts and species delimitation. Systematic Biology 56: 879–886. https://doi.org/10.1080/10635150701701083

Gerhardt HC, Tanner SD, Corrigan CM, Walton HC (2000) Female preference functions based on call duration in the gray tree frog (*Hyla versicolor*). Behavioral Ecology 11: 663–669. https://doi.org/10.1093/beheco/11.6.663

Glaw F, Vences M, Gossmann V (2000) A new species of *Mantidactylus* (subgenus *Guibemantis*) from Madagascar, with a comparative survey of internal femoral gland structure in the genus (Amphibia: Ranidae: Mantellinae). Journal of Natural History 34: 1135–1154. https://doi.org/10.1080/00222930050020140

Glaw F, Vences M (2006) Phylogeny and genus-level classification of mantellid frogs. Organisms Diversity and Evolution 6: 236–253. https://doi.org/10.1016/j.ode.2005.12.001

Glaw F, Vences M (2007) A Field Guide to the Amphibians and Reptiles of Madagascar (3rd Edn.). Self-published, Köln, Germany, 496 pp.

Glaw F, Köhler J, Vences M (2011) New species of *Gephyromantis* from Marojejy National Park, northeast Madagascar. Journal of Herpetology 45: 155–160. https://doi.org/10.1670/10-058.1

Glaw F, Vences M (2011) Description of a new frog species of *Gephyromantis* (subgenus *Laurentomantis*) with tibial glands from Madagascar. Spixiana. München 34: 121–127.

Hutter CR, Escobar-Lasso S, Rojas-Morales JA, Gutiérrez-Cárdenas PDA, Imba H, Guayasamin JM (2013) The territoriality, vocalizations and aggressive interactions of the red–spotted glassfrog, *Nymphargus grandisonae*, Cochran and Goin, 1970 (Anura: Centrolenidae). Journal of Natural History 47: 3011–3032. https://doi.org/10.1080/00222933.2013.792961

Hutter CR, Lambert SM, Cobb KA, Andriampenomanana ZF, Vences M (2015) A new species of bright-eyed treefrog (Mantellidae) from Madagascar, with comments on call evolution and patterns of syntopy in the *Boophis ankaratra* complex. Zootaxa 4034: 531–555. https://doi.org/10.11646/zootaxa.4034.3.6

Hutter CR, Lambert SM, Andriampenomanana ZF, Glaw F, Vences M (2018) Molecular phylogeny and diversification of Malagasy bright-eyed tree frogs (Mantellidae: *Boophis*). Molecular Phylogenetics and Evolution 127: 568–578. https://doi.org/10.1016/j.ympev.2018.05.027

Hutter CR, Cobb KA, Portik DM, Travers SL, Wood Jr PL, Brown RM (2022) FrogCap: A modular sequence capture probe-set for phylogenomics and population genetics for all frogs, assessed across multiple phylogenetic scales. Molecular Ecology Resources 22: 1100–1119. https://doi.org/10.1111/1755-0998.13517

Hutter CR, Andriampenomanana ZF, Basham EW, Glaw F, Masotti MD, Lambert SM, Vences M (2025) A new species of mantellid frog of the genus *Guibemantis* from south-eastern Madagascar. Zootaxa 5647: 260–274. https://doi.org/10.11646/zootaxa.5647.3.3

IUCN (2001) IUCN Red List Categories and Criteria: Version 3.1. IUCN, Switzerland and Cambridge.

Kaffenberger N, Wollenberg KC, Köhler J, Glaw F, Vieites DR, Vences M (2012) Molecular phylogeny and biogeography of Malagasy frogs of the genus *Gephyromantis*. Molecular Phylogenetics and Evolution 62: 555–560. https://doi.org/10.1016/j.ympev.2011.09.023

Kalyaanamoorthy S, Minh BQ, Wong TK, von Haeseler A, Jermiin LS (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. Nature Methods 14: e587. https://doi.org/10.1038/nmeth.4285

Katoh K, Standley DM (2013) MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability. Molecular Biology and Evolution 30: 772–780. https://doi.org/10.1093/molbev/mst010

Köhler J, Jansen M, Rodríguez A, Kok PJR, Toledo LF, Emmrich M, Glaw F, Haddad CFB, Rödel M-O, Vences M (2017) The use of bioacoustics in anuran taxonomy: theory, terminology, methods and recommendations for best practice. Zootaxa 4251: 1–124.

Kumar S, Stecher G, Tamura K (2016) MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. Molecular Biology and Evolution 33: 1870–1874. https://doi.org/10.1093/molbev/msw054

Lambert SM, Hutter CR, Scherz M (2017) Diamond in the rough: a new species of fossorial diamond frog (*Rhombophryne*) from Ranomafana National Park, southeastern Madagascar. Zoosystematics and Evolution 93: 143–155. https://doi.org/10.3897/zse.93.10188

Methuen PA, Hewitt J (1913) On a collection of Batrachia from Madagascar made during the year 1911. Annals of the Transvaal Museum 4: 49–64.

Miralles A, Köhler J, Glaw F, Wollenberg Valero KC, Crottini A, Rosa AM, du Preez L, Gehring PS, Vieites DR, Ratsoavina FM, Vences M (2023) An endless harvest: integrative revision of the *Gephyromantis boulengeri* and *G. blanci* complexes reveals six new species of mantellid frogs from Madagascar. Salamandra 59: 1–41.

Nguyen LT, Schmidt HA, von Haeseler A, Minh BQ (2014) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Molecular Biology and Evolution 32: 268–274. https://doi.org/10.1093/molbev/msu300

Padial JM, Miralles A, De la Riva I, Vences M (2010) The integrative future of taxonomy. Frontiers in Zoology 7: 1–14. https://doi.org/10.1186/1742-9994-7-16

Perl RB, Nagy ZT, Sonet G, Glaw F, Wollenberg KC, Vences M (2014) DNA barcoding Madagascar's amphibian fauna. Amphibia-Reptilia 35: 197–206. https://doi.org/10.1163/15685381-00002942

Ryan MJ, Rand AS (1990) The sensory basis of sexual selection for complex calls in the túngara frog, *Physalaemus pustulosus* (sexual selection for sensory exploitation). Evolution 44: 305–314. https://doi.org/10.2307/2409409

Sabino-Pinto J, Rakotoarison A, Bletz MC, Edmonds D, Glaw F, Vences M (2019) A new species of the *Spinomantis bertini* species complex (Anura: Mantellidae) from Pic d'Ivohibe Special Reserve (Madagascar). Zootaxa 3248: 66–68. https://doi.org/10.11646/zootaxa.4656.1.6

Scherz MD, Razafindraibe JH, Rakotoarison A, Dixit NM, Bletz MC, Glaw, F, Vences M (2017a) Yet another small brown frog from high altitude on the Marojejy Massif, northeastern Madagascar (Anura: Mantellidae). Zootaxa 4347: 572–582.

Scherz MD, Vences M, Borrell J, Ball L, Herizo Nomenjanahary D, Parker D, Rakotondratsima M, Razafimandimby E, Starnes T, Rabearivony J, Glaw F (2017b) A new frog species of the subgenus *Asperomantis* (Anura, Mantellidae, *Gephyromantis*) from the Bealanana District of northern Madagascar. Zoosystematics and Evolution 93: 451–466.

Scherz MD, Hawlitschek O, Andreone F, Rakotoarison A, Vences M, Glaw F (2017c) A review of the taxonomy and osteology of the *Rhombophryne serratopalpebrosa* species group (Anura: Microhylidae) from Madagascar, with comments on the value of volume rendering of micro-CT data to taxonomists. Zootaxa 4273: 301–340. https://doi.org/10.11646/zootaxa.4273.3.1

Scherz MD, Hawlitschek O, Razafindraibe JH, Megson S, Ratsoavina FM, Rakotoarison A, Bletz MC, Glaw F, Vences M (2018) A distinctive new frog species (Anura, Mantellidae) supports the biogeographic linkage of two montane rainforest massifs in northern Madagascar. Zoosystematics and Evolution 94: 247–261. https://doi.org/10.3897/zse.94.21037

Simpson GG (1961) Principles of Animal Taxonomy. Columbia University Press, New York, 247 pp.

Vences M, Glaw F, Andreone F, Jesu R, Schimmenti G (2002) Systematic revision of the enigmatic Malagasy broad-headed frogs (*Laurentomantis* Dubois, 1980), and their phylogenetic position within the endemic mantellid radiation of Madagascar. Contributions to Zoology 70: 191–212. https://doi.org/10.1163/18759866-07004001

Vences M, Glaw F, Marquez R (2006) The Calls of the Frogs of Madagascar. 3 Audio CD's and booklet. Foneteca Zoológica, Madrid, Spain, 44 pp.

Vences M, Gehara M, Köhler J, Glaw F (2012) Description of a new Malagasy treefrog (*Boophis*) occurring syntopically with its sister species, and a plea for studies on non-allopatric speciation in tropical amphibians. Amphibia-Reptilia 33: 503–520. https://doi.org/10.1163/15685381-00002856

Vences M, Köhler J, Glaw F (2017) A new species of smooth-skinned *Spinomantis* frog (Anura: Mantellidae) from south-eastern Madagascar. Zootaxa 4317: 379–390. https://doi.org/10.11646/zootaxa.4317.2.12

Vences M, Guayasamin JM, Miralles A, De La Riva I (2013) To name or not to name: Criteria to promote economy of change in Linnaean classification schemes. Zootaxa 3636: 201–244. https://doi.org/10.11646/zootaxa.3636.2.1

Vences M, Köhler J, Pabijan M, Bletz M, Gehring PS, Hawlitschek O, Rakotoarison A, Ratsoavina FM, Andreone F, Crottini A, Glaw F (2017) Taxonomy and geographic distribution of Malagasy frogs of the *Gephyromantis asper* clade, with description of a new subgenus and revalidation of *Gephyromantis ceratophrys*. Salamandra 53: 77–98.

Vieites DR, Wollenberg KC, Andreone F, Köhler J, Glaw F, Vences M (2009) Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. Proceedings of the National Academy of Sciences 106: 8267–8272. https://doi.org/10.1073/pnas.0810821106

Wiley EO (1978) The evolutionary species concept reconsidered. Systematic Zoology 27: 17–26. https://doi.org/10.2307/2412809

Wollenberg KC, Vieites DR, Glaw F, Vences M (2011) Speciation in little: the role of range and body size in the diversification of Malagasy mantellid frogs. BMC Evolutionary Biology 11: e217. https://doi.org/10.1186/1471-2148-11-217