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The arboreal frogs in the genus *Spinomantis* (Amphibia: Mantellidae) from Madagascar: a survey of molecular, morphological and bioacoustic variation, with descriptions of four new species

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Abstract. We review the systematics of the Madagascar-endemic frogs of the genus *Spinomantis* based on DNA sequences of mitochondrial and nuclear-encoded genes from 368 individuals. We find the arboreal species in the genus, the focus of this study, to form a well-supported clade in a mitochondrial multi-gene tree, containing three subclades, here named the *peraccae* clade, the *aglavei* clade, and the *massi* clade. Each of these contained numerous deep mitochondrial lineages differing by at least 3.1% uncorrected pairwise distance in a fragment of the mitochondrial 16S rRNA gene. Our preferred partition distinguishes 20 mitochondrial species-level lineages in the arboreal *Spinomantis* clade, including seven nominal species, four new species described herein, and nine additional candidate species that require further study. The four new species described herein are delimited by a combination of several lines of evidence, including high divergence in mitochondrial DNA (> 3.5% 16S divergence to nominal species), isolated phylogenetic position, differentiation in nuclear-encoded gene fragments, and morphological and bioacoustic divergence: *S. chlorostictus* sp. n. is a species of the *peraccae* clade primarily from northern Madagascar differing by color pattern and bioacoustics from *S. peraccae*; *S. royae* sp. n. and *S. leonieae* sp. n., belonging to the *aglavei* clade, are morphologically similar to *S. fimbriatus* but differ by color pattern and advertisement call; and *S. fohitsilo* sp. n. is morphologically similar to *S. massi* but not that species' direct sister group, and differs by its advertisement call. Our study provides a baseline for understanding the diversity and biogeography of *Spinomantis*, highlights the enormous amount of yet unexplored amphibian diversity in Madagascar, and points to geographical regions and taxa where further field exploration, including the collection of voucher specimens and of bioacoustic data, is needed to complete the herpetofaunal inventory of the island.

Key words. Anura, Mantellinae, molecular genetics, morphology, bioacoustics, systematics, taxonomy, *Spinomantis fohitsilo* sp. n., *Spinomantis leonieae* sp. n., *Spinomantis chlorostictus* sp. n., *Spinomantis royae* sp. n.

Introduction

Among the Madagascan-Comoroan frogs of the endemic mantellid radiation, the genus *Spinomantis* Dubois, 1992, originally proposed as a subgenus of *Mantidactylus* and elevated to genus level by Glaw & Vences (2006), stands out as an ecomorphologically diverse clade. *Spinomantis*, endemic to Madagascar, contains saxicolous species such

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as *S. microtis, S. guibei* or *S. bertini* and allies, as well as numerous arboreal taxa (Table 1). Arboreal *Spinomantis* include some of the most bizarre-looking frogs in Madagascar, such as *S. aglavei* with numerous spiny skin appendages on the limbs and an apparent bark-mimicking color pattern, or *S. phantasticus* with an integument scattered with spiny dermal tubercles and a greenish color appearing to mimic mossy surfaces (Table 1, Fig. 1). According to current classification (Frost 2026), *Spinomantis* contains 16 species (Table 1), but molecular surveys have identified numerous additional undescribed candidate species whose morphology and bioacoustics have remained unstudied and whose taxonomic status is thus unassessed (Vieites et al. 2009, Perl et al. 2014, Carné & Vieites 2024). To complicate the situation, no DNA sequences have so far been published for two species, *S. tavaratra* and *S. nussbaumi* described by Cramer et al. (2008), and it is therefore unclarified whether these may correspond to some of the DNA-characterized candidate species.

Among Malagasy frogs, *Spinomantis* may also be indicators for undisturbed ecosystems, as they are usually found in pristine or only mildly disturbed rainforest (e.g., Glaw & Vences 2007, Fulgence et al. 2022, Rakotozafy et al. 2025), except for *S. elegans* which also occurs in montane habitats above the tree line (Glaw & Vences 2007). Many of the arboreal *Spinomantis* are very vocal, with loud, often metallic-sounding advertisement calls which are regularly heard along streams in rainforests (Blommers-Schlösser 1979, Glaw & Vences 1997, Andreone et al. 1998). Although the calling individuals are usually located on high perches in trees, often on leaves or branches covered by moss and lichens, and thus difficult to find, these species can be useful taxa for bioacoustic monitoring purposes due to their characteristic loud calls and restriction to rather intact ecosystems (Vences et al. 2008). However, the current species inventory of *Spinomantis* is far from complete. Despite several recent taxonomic treatments (e.g., Cramer et al. 2008, Vences et al. 2017, Sabino Pinto et al. 2019, Hutter et al. 2025), no comprehensive assessment of the genetic variation among and within these frogs is so far available, and numerous candidate species identified by Vieites et al. (2009), Perl et al. (2014) and Carné & Vieites (2024) have not yet been characterized morphologically. In the present study, we provide mitochondrial DNA data of all samples of *Spinomantis* available to us, along with data from two nuclear-encoded genes for representative specimens. Besides providing novel information on the geographical distribution of various *Spinomantis*, our data enable the formal scientific description and naming of four new species, as well as the identification of three additional candidate species that require additional work in future studies.

Materials and methods

Tissue samples and voucher specimens used for this study were collected during field expeditions from 1994–2022. Specimens were collected in the field mostly at night, searching for calling males with the aid of flashlights. Collected specimens were anesthetized by immersion in aqueous solutions of tricaine methanesulfonate (MS222), chlorobutanol or lidocaine, and subsequently euthanized by an overdose of the same substances. Before fixation, tissue samples were taken from the euthanized specimens and stored separately in 1.5 ml vials filled with pure ethanol or EDTA. Vouchers were then fixed in 95% ethanol or in 4% formaldehyde solution, preserved in 70% ethanol, and deposited in the following collections: Museo Regionale di Scienze Naturali di Torino (MRSN), Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK); Zoological Museum Amsterdam (ZMA; collection now included in Naturalis, Leiden); Zoologische Staatssammlung München (ZSM); the University of Kansas Biodiversity Institute (KU); and the Université d'Antananarivo, Mention Zoologie et Biodiversité Animale (UADBA). FGZC, FGMV and ZCMV refer to field numbers and catalogue numbers of F. Glaw and M. Vences. FA and FAZC refer to field numbers of F. Andreone. ACZCV, APR, CRH and MSZC refer to field numbers of A. Crottini, A.P. Raselimanana, C.R. Hutter and M.D. Scherz, respectively; ACP are laboratory numbers of A. Crottini.

Voucher specimens in the UADBA collection have in many cases not been catalogued yet due to lack of curatorial resources and are herein therefore referred to based on the physically attached field numbers, i.e., as UADBA-FGZC or UADBA-MSZC. For additional field number and catalogue number abbreviations of sequences taken from GenBank, see the respective publications as retrievable via the respective accession numbers. Geographic regions within Madagascar are named according to Boumans et al. (2007) and Brown et al. (2016). Candidate species are named according to the numbering started by Vieites et al. (2009) and continued by Carné & Vieites (2024), adding a "Ca" before each candidate number as proposed by Padial et al. (2010) and applied by Perl et al. (2014).

Morphometric measurements of voucher specimens were taken by MV with a manual caliper at an accuracy of 0.1 mm, as follows: snout–vent length (SVL); maximum head width (HW); head length from tip of snout to posterior edge of mouth opening (HL); horizontal tympanum diameter (TD); horizontal eye diameter (ED); distance between anterior edge of eye and nostril (END); distance between nostril and tip of snout (NSD); distance between both nostrils (NND); forelimb length, from limb insertion to tip of longest finger (FORL); hand length, from the articulation of the carpus with the radioulnar to the tip of the longest finger (HAL); hindlimb length, from the cloaca to the tip of the longest toe (HIL); foot length (FOL); foot length including tarsus (FOTL); and tibia length (TIBL). Webbing formula is reported according to Blommers-Schlösser (1979) to ensure comparability with previous species descriptions of Malagasy frogs.

Vocalizations were recorded in the field using various tape recorders or digital recorders with built-in microphones or attached directional microphones. In digital

Figure 1. Plate showing nominal species of *Spinomantis* according to the current classification (Table 1) in life, in dorsolateral and ventral views: (A–C) *S. aglavei* (type species of the genus *Spinomantis*), male specimen from Mandraka, with hindlimb in (B) dorsal and (C) ventral view showing femoral glands and dermal spine-like flaps of different size; (D–E) *S. fimbriatus,* male paratype ZSM 575/1999 (previously ZFMK 57440) from Andasibe; (F–G) *S. phantasticus*, male paratype ZSM 578/1999 (previously ZFMK 62208) from An'Ala; (H–I) *S. massi,* male holotype or paratype from the type locality, Benavony; (J) *S. tavaratra,* female ZSM 1635/2012 (FGZC 3569) from Sorata; (K) *S. peraccae,* male from Vohidrazana (CRH 289); (L, M) *S. nussbaumi,* male ZSM 1633/2012 (FGZC 3662) from Sorata; (N) *S. elegans*, ZSM 384/2004 from Ranomafana; (O) *S. brunae*, male holotype MRSN A1649 from Andohahela; (P) *S. microtis* from Andohahela; (Q) *S. guibei* from Andohahela; (R) *S. beckei* from Andohahela; (S) *S. bertini* from Andohahela; (T) *S. mirus* from Ivohibe. Additional images of *S. nussbaumi, S. tavaratra,* and the new species described herein are shown in subsequent figures.

Table 1. Overview of nominal species and candidate species in the genus *Spinomantis*, with information on name-bearing types and type localities from the original descriptions by Boulenger (1896), Boettger (1913), Methuen & Hewitt (1913), Guibé (1947, 1973a, 1973b), Blommers-Schlösser & Blanc (1991), Glaw & Vences (1994, 1997), Andreone et al. (1998), Cramer et al. (2008), Vences et al. (2017), Sabino-Pinto et al. (2019), Hutter et al. (2025) and the current study. Abbreviations: HT, holotype; LT, lectotype, Most type localities are given in an abbreviated form, not literally as provided in the original descriptions (for more detail, see Frost 2026). Candidate species are given following the numbering system of Vieites et al. (2009), Perl et al. (2014) and Carné & Vieites (2024), with numbers Ca13, Ca14 and Ca15 coined herein to refer to newly discovered mitochondrial lineages. * Type species of the genus. ** Synonym: *Rhacophorus sikorae* Boettger, 1913, type locality "Moramanga, O. Madagascar", LT: SMF 6815.

Species	Full original taxon name	Candidate species number	Synonyms	Name-bearing type	Type locality or reference locality	Ecomorph
Spinomantis beckei	*Spinomantis beckei* Vences, Köhler & Glaw, 2017	NA	None	HT: ZSM 173/2005	Andohahela National Park	saxicolous, small
Spinomantis bertini	*Gephyromantis bertini* Guibé, 1947	*S.* sp. Ca06	None	HT: MNHN 1935.168	Isaka-Ivondro	saxicolous, small
Spinomantis brunae	*Mantidactylus* (*Spinomantis*) *brunae* Andreone, Glaw, Vences & Vallan, 1998	NA	None	HT: MRSN A1649	between Isaka-Ivondro and Eminiminy	saxicolous, large
Spinomantis elegans	*Rhacophorus elegans* Guibé, 1973	NA	None	HT: MNHN 1953.142	"Forêt au col d'Ivohibé"	saxicolous, large
Spinomantis guibei	*Mantidactylus guibei* Blommers-Schlösser in Blommers-Schlösser and Blanc, 1991	NA	None	HT: MNHN 1972.1827	Chaînes Anosyennes	saxicolous, large
Spinomantis microtis	*Rhacophorus microtis* Guibé, 1973	NA	None	HT: MNHN 1973.1080	Chaînes Anosyennes	saxicolous, large
Spinomantis mirus	*Spinomantis mirus* Sabino-Pinto, Rakotoarison, Bletz, Edmonds, Glaw & Vences, 2019	*S.* sp. Ca12	None	HT: ZSM 818/2014	Pic d'Ivohibe	saxicolous, small
Spinomantis lakolosy	*Spinomantis lakolosy* Hutter, Andriampenomanana, Lambert & Vences, 2025	*S.* sp. Ca07	None	HT: KU340852 (CRH 726),	Ranomafana	saxicolous, small
Spinomantis lavabato	*Spinomantis lavabato* Hutter, Andriampenomanana, Lambert & Vences, 2025	NA	None	HT: KU336975 (JJW2336)	Ranomafana, Maharira	saxicolous, small
Spinomantis sp. Ca8	NA	*S.* sp. Ca08	None	Reference: ZMA 20044	Ranomafana, Maharira	arboreal (*Pandanus*-dwelling), small
Spinomantis sp. aff. *bertini* Anosy	NA	NA	None	Reference: ZCMV 14809	Ambahavala	saxicolous, small
Arboreal clade						
Spinomantis aglavei	*Rhacophorus aglavei* Methuen and Hewitt, 1913 *	NA	*Rhacophorus sikorae* Boettger, 1913 **	HT: TMP 10073 (formerly 1100)	forests adjacent to Analamazotra	arboreal, dermal spines
Spinomantis fimbriatus	*Mantidactylus* (*Spinomantis*) *fimbriatus* Glaw and Vences, 1994	NA	None	HT: ZFMK 57441	Andasibe	arboreal, dermal spines
Spinomantis massi	*Mantidactylus* (*Spinomantis*) *massi* Glaw and Vences, 1994,	NA	None	HT: ZFMK 57442	Benavony	arboreal, few dermal spines
Spinomantis nussbaumi	*Spinomantis nussbaumi* Cramer, Rabibisoa & Raxworthy, 2008	NA	None	HT: AMNH R-167949	Befosa River-Antetikalambazaha, Tsaratanana	arboreal, no dermal spines
Spinomantis peraccae	*Rhacophorus Peraccae* Boulenger, 1896	NA	None	HT: BMNH 1947.2.9.70 (originally 1896.10.9.35)	Ivohimanita	arboreal, no dermal spines
Spinomantis phantasticus	*Mantidactylus* (*Spinomantis*) *phantasticus* Glaw and Vences, 1997 "1996"	NA	None	HT: ZFMK 60000	An'Ala	arboreal, dermal tubercles and spines
Spinomantis tavaratra	*Spinomantis tavaratra* Cramer, Rabibisoa & Raxworthy, 2008	NA	None	HT: AMNH A-167935	Sorata Mountain	arboreal, few dermal spines

Table 1 continued

Species	Full original taxon name	Candidate species number	Synonyms	Name-bearing type	Type locality or reference locality	Ecomorph
Spinomantis fohitsilo sp. n.	newly named and described herein	NA	None	HT: ZSM 102/2016	Andranonafindra	arboreal, few dermal spines
Spinomantis leonieae sp. n.	newly named and described herein	NA	None	HT: ZSM 212/2022	Makira	arboreal, dermal spines
Spinomantis chlorostictus sp. n.	newly named and described herein	*S.* sp. Ca11	None	HT: ZSM 104/2016	Ampotsidy	arboreal, no dermal spines
Spinomantis royae sp. n.	newly named and described herein	NA	None	HT: ZSM 258/2005	Marojejy	arboreal, dermal spines
Spinomantis sp. Ca02 DQ060236	NA	*S.* sp. Ca02	None	Reference: ZSM 445/2004	Ranomafana	probably arboreal, adult morphology unknown
Spinomantis sp. Ca03 AY848387	NA	*S.* sp. Ca03	None	Reference: MRSN A3999, FN 7629	Masoala: Ambatoledama Corridor: Beanjada	probably arboreal, adult morphology unknown
Spinomantis sp. Ca04 FJ559306	NA	*S.* sp. Ca04	None	Reference: FGZC 2278	Marojejy	probably arboreal, adult morphology unknown
Spinomantis sp. Ca05 FJ559307	NA	*S.* sp. Ca05	None	Reference: MRSN A6737	Tsaratanana	probably arboreal, no dermal spines
Spinomantis sp. Ca09 FJ559308	NA	*S.* sp. Ca09	None	Reference: ZCMV 8817	Mahasoa	probably arboreal, dermal spines
Spinomantis sp. Ca10 KF611623	NA	*S.* sp. Ca10	None	Reference: ZCMV 12403	Tsaratanana	arboreal, no dermal spines
Spinomantis sp. Ca13	NA	new candidate species	None	Reference: FAZC 15529	Maromizaha	arboreal, dermal spines
Spinomantis sp. Ca14	NA	new candidate species	None	Reference: ZCMV 7298	Befanjana	arboreal, dermal spines
Spinomantis sp. Ca15	NA	new candidate species	None	Reference: ZCMV 15226	Marojejy	probably arboreal, morphology unknown

recordings, files were saved in uncompressed wave format at 44.1 kHz. Recordings were sampled or resampled at 22.05 kHz and 32-bit resolution and analyzed using the software Cool Edit Pro 2.0. Temporal parameters were measured in the oscillograms. Frequency information was obtained through Fast Fourier Transformation (FFT; width 1024 points) at Hanning window function. Spectrograms were produced at Blackman window function with 256 bands resolution. For a clearer graphical presentation, in some cases, careful band-pass filtering was applied to remove background sounds, applied only to frequencies outside the prevalent bandwidths of calls. Temporal measurements are summarized as range with mean ± standard deviation in parentheses. Description, terminology, and methods follow those recommended by Köhler et al. (2017), using the note-centered terminological scheme. All call recordings mentioned were analyzed herein using the same methodology, even if calls from the same recordings had been published previously (possibly resulting in slightly differing numerical parameters compared to previous descriptions). Representative sections of call recordings analyzed were archived in the Zenodo repository at https://doi.org/10.5281/zenodo.18020638.

Genetic divergence between individuals and lineages was assessed using DNA fragments of mitochondrial and nuclear-encoded genes, determined using Sanger sequencing after extracting genomic DNA from tissue samples using a salt-extraction protocol (Bruford et al. 1992) and PCR amplifying the respective DNA fragments with primers and protocols as specified below. Successfully amplified PCR products were purified with Exonuclease I and Shrimp Alkaline Phosphatase digestion and sequenced by LGC Genomics (Berlin) on an automated capillary sequencer or purified and sequenced with an ABI3730XL automated sequencer at Macrogen Inc. (Spain). Chromatograms were checked for base-calling errors and edited with CodonCode Aligner v 3.7.1 (Codon Code Corporation, Dedham, MA, USA). From the holotype of *S. fimbriatus* (tissue sampled from specimen ZFMK 57441), sequences were also assembled from archival DNA analyses (museomics) following a simple DNA shotgun sequencing protocol as will be described in detail in a forthcoming paper (Vences et al. in review). Newly determined sequences were submitted to GenBank (accession numbers PZ311231–PZ311399, PZ314434–PZ314435, PZ315192, PZ316684–PZ316891, and PZ320028–PZ320037). All alignments and a spreadsheet with sequence metadata is available from Zenodo (https://doi.org/10.5281/zenodo.18020638).

We compiled various datasets (A–D) using the following laboratory and bioinformatic methods:

(A) As an initial means to assess genetic variation within *Spinomantis*, we compiled DNA sequences of the 3'-terminal fragment of the 16S rRNA gene (16S) which has often been used for DNA barcoding of Malagasy anurans (e.g., Vieites et al. 2009). PCR was carried out using the primers 16SAL (5'–CGCCTGTTTATCAAAAACAT–3') and 16SBH-new (5'–CCTGGATTACTCCGGTCTGA–3'), modified from Palumbi et al. (1991), with cycling proto-

col 94 °C (90 s), [94 °C (45 s), 55 °C(45 s), 72 °C (90 s)] x 33, 72 °C (300 s). Newly obtained 16S sequences were combined with all homologous sequences of *Spinomantis* available from GenBank. We used the G-INS-i algorithm in MAFFT (Katoh & Standley 2013) as implemented in Concatenator (Vences et al. 2022) for alignment, determined the substitution models best fitting the data under the Bayesian Information Criterion in MEGA 7 (Kumar et al. 2016) (GTR+G), and inferred a Maximum Likelihood (ML) tree in RAxML (Stamatakis 2014) using raxmlGUI v. 2.0 (Edler et al. 2020). Node support was tested with 500 full ("thorough") bootstrap replicates. A sequence of *Guibemantis liber* was used as the outgroup.

(B) A trimmed alignment of 16S was prepared for analysis of primary species hypotheses, genetic distances and diagnostic sites, by removing sequences with large amounts of missing data and trimming the entire alignment to equal length of remaining sequences, to ensure all major lineages were represented. On this alignment, for an algorithmic inference of primary species hypotheses, we used ASAP (Puillandre et al. 2021) as implemented in iTaxoTools (Vences et al. 2021). Pairwise sequence distances between ASAP-inferred lineages were then calculated using the program TaxI2 (Vences et al. 2024a). The trimmed alignment is available from the Zenodo repository, https://doi.org/10.5281/zenodo.18020638).

(C) To more reliably assess the phylogenetic relationships among species-level mitochondrial lineages within *Spinomantis*, we compiled a dataset of DNA sequences from five mitochondrial gene fragments: cytochrome b (*cytb*), cytochrome oxidase subunit I (cox1), 12S rRNA (12S), and 16S rRNA (two adjacent fragments, 3' and 5'-terminal fragments). For primers and cycling conditions, see Vences et al. (2003) and Hutter et al. (2018). The 3'-16S barcoding fragment from dataset A was available for all species and candidate species, while several of the other fragments were missing for certain candidate species. Sequences were aligned with the MAFFT G-INS-i algorithm (Katoh & Standley 2013), and concatenated in Concatenator (Vences et al. 2022). An ML tree was inferred using by-gene and codon partitioned searches using IQ-Tree v.2.2.6 (Nguyen et al. 2015) after determining substitution models and data partitions using ModelFinder (Kalyaanamoorthy et al. 2017), assessing bootstrap support with 1000 full non-parametric bootstrap replicates.

(D) To evaluate the primary species hypotheses derived from dataset A, we sequenced two fragments of nuclear-encoded, single-copy, protein coding genes: recombination activation gene 1 (RAG-1) and leucine-rich repeat and WD repeat-containing protein (KIAA1239), using primers and PCR protocols given in the forthcoming paper by Vences et al. (in review), using a nested PCR approach for KIAA1239 (see Shen et al. 2012). The alignments of the nuclear-encoded genes were analyzed independently to understand concordance (or absence thereof) in the differentiation of these unlinked genetic markers. We used a genealogy visualization approach to graphically represent the relationship among alleles (haplotypes). Haplotypes were estimated with the PHASE algorithm (Stephens et al. 2001), and haplotype genealogies were reconstructed with the Fitchi approach (Matschiner 2016) in Hapsolutely (Vences et al. 2024b; part of iTaxoTools) following the methodological approach of Salzburger et al. (2011).

We follow the general lineage concept (de Queiroz 1998, 2007) in combination with a relaxed biological species criterion, i.e., demanding reproductive isolation indicated by restricted gene flow among lineages (e.g., Speybroeck et al. 2020, Dufresnes et al. 2021). Because reproductive barriers generated through time increase genealogical depth and agreement among unlinked loci (Avise & Wollenberg 1997), we use genealogical concordance (Avise & Ball 1990) between mitochondrial and nuclear loci, especially in populations occurring in sympatry or close geographical proximity, as an indicator for restricted gene flow. Species status is then assigned to lineages based on combined evaluation of genetic, morphological and (where available) bioacoustic evidence (Padial et al. 2010).

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 is 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 Science Identifier) for this publication is: urn:lsid:zoobank.org:pub:003AFDC9-72AB-4E98-B198-D227039C54BE. 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

Molecular systematics

The Maximum Likelihood tree calculated from 3'-16S rRNA sequences (511 bp) of 368 individuals of the genus *Spinomantis* (Fig. 2) revealed a striking amount of genetic variation within *Spinomantis*, including several genetic lineages in addition to those identified in previous studies (Vieites et al. 2009, Perl et al. 2014, Carné & Vieites 2024). For many of the genetic lineages only sequences of tadpoles were available (e.g., *S.* sp. Ca2 from Ranomafana), from others we had only small specimens probably representing subadults (e.g., *S.* sp. Ca10), and for some, no specimens could be morphologically examined in the framework of this study (e.g., specimens of a deep lineage assigned to *S. aglavei* from Betampona; Rosa et al. 2012, Piccoli et al. 2025).

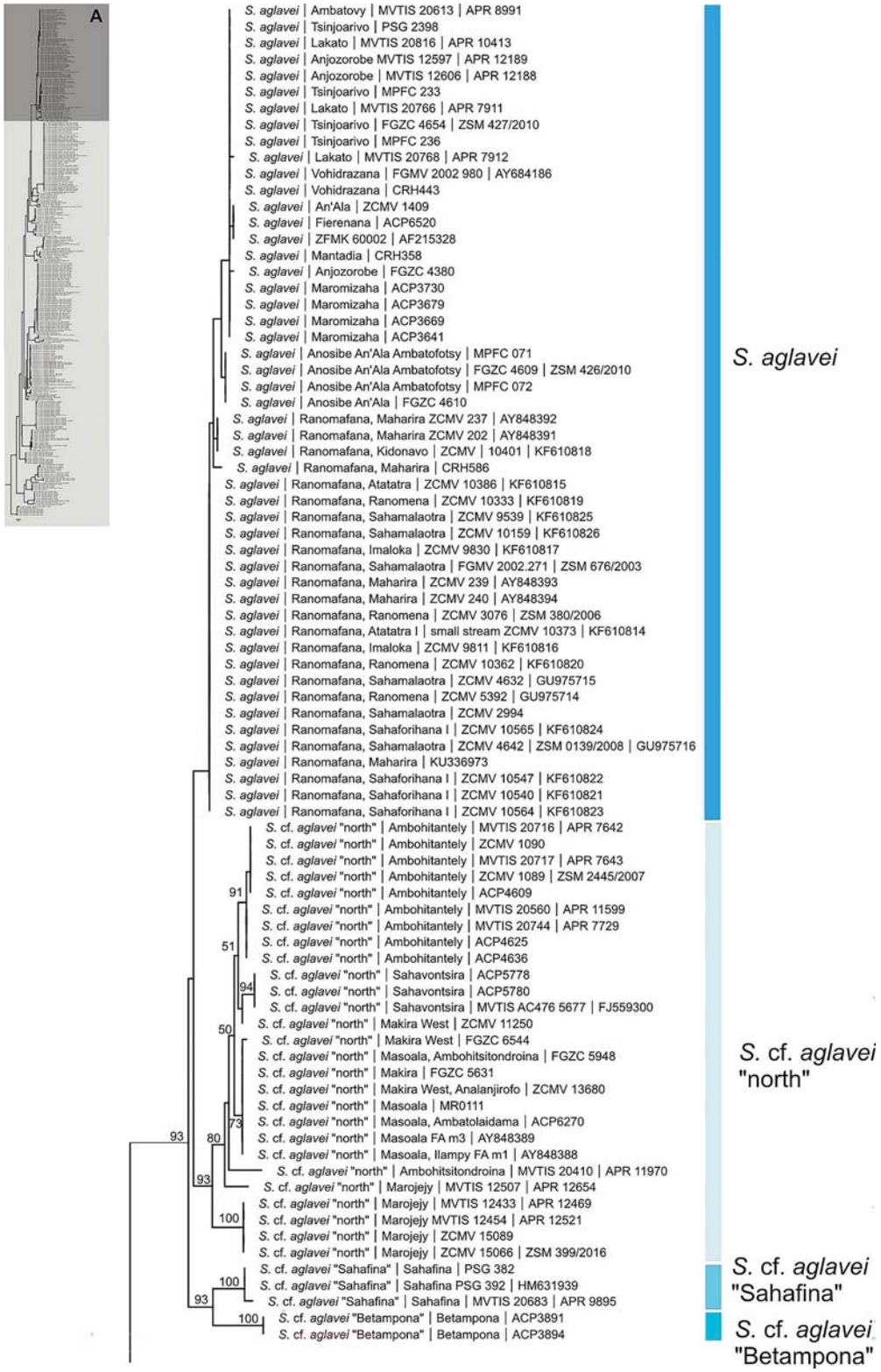

Figure 2A–E. Maximum Likelihood tree calculated from DNA sequences (511 bp) of the mitochondrial 16S rRNA gene, for 368 individuals of the genus *Spinomantis*. Tip labels include taxonomic assignment, collection location, field number, museum number, and/or GenBank accession number. Numbers at nodes are support values in percent from a bootstrap analysis (500 full replicates; not shown for values < 50% and for shallowest nodes). *Guibemantis liber* was used as the outgroup (removed graphically to better resolve branch lengths of the ingroup).

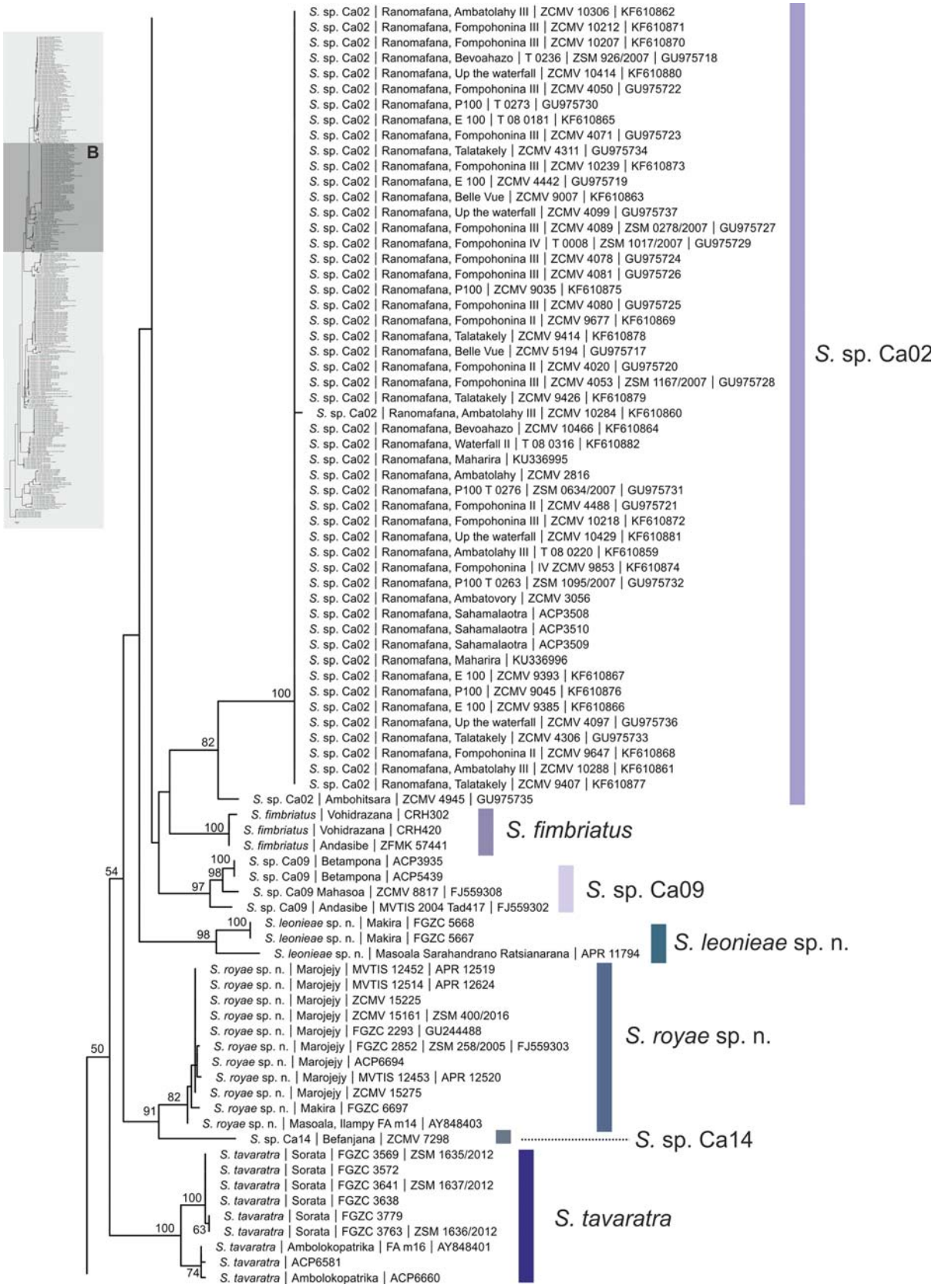

Figure 2 continued

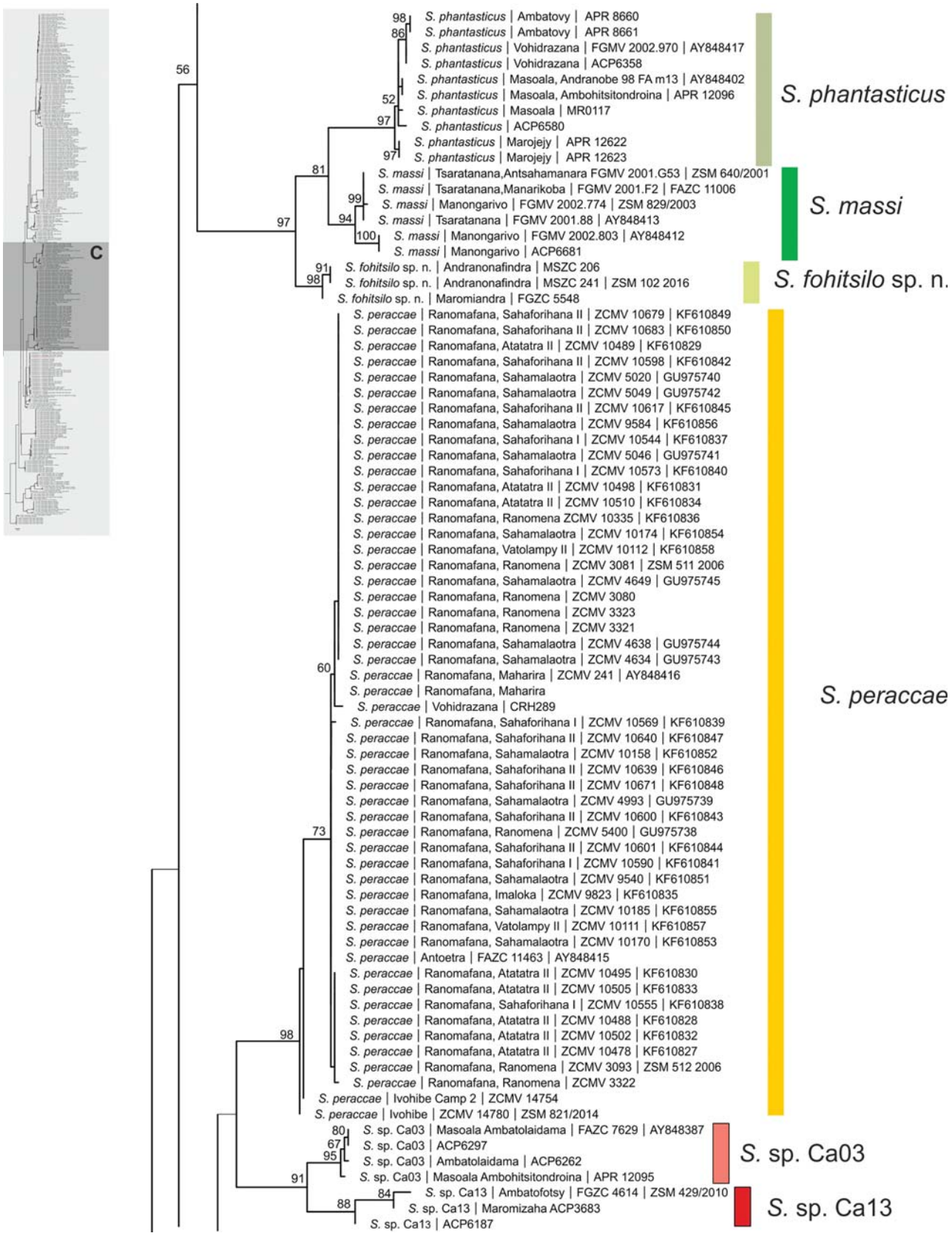

Figure 2 continued

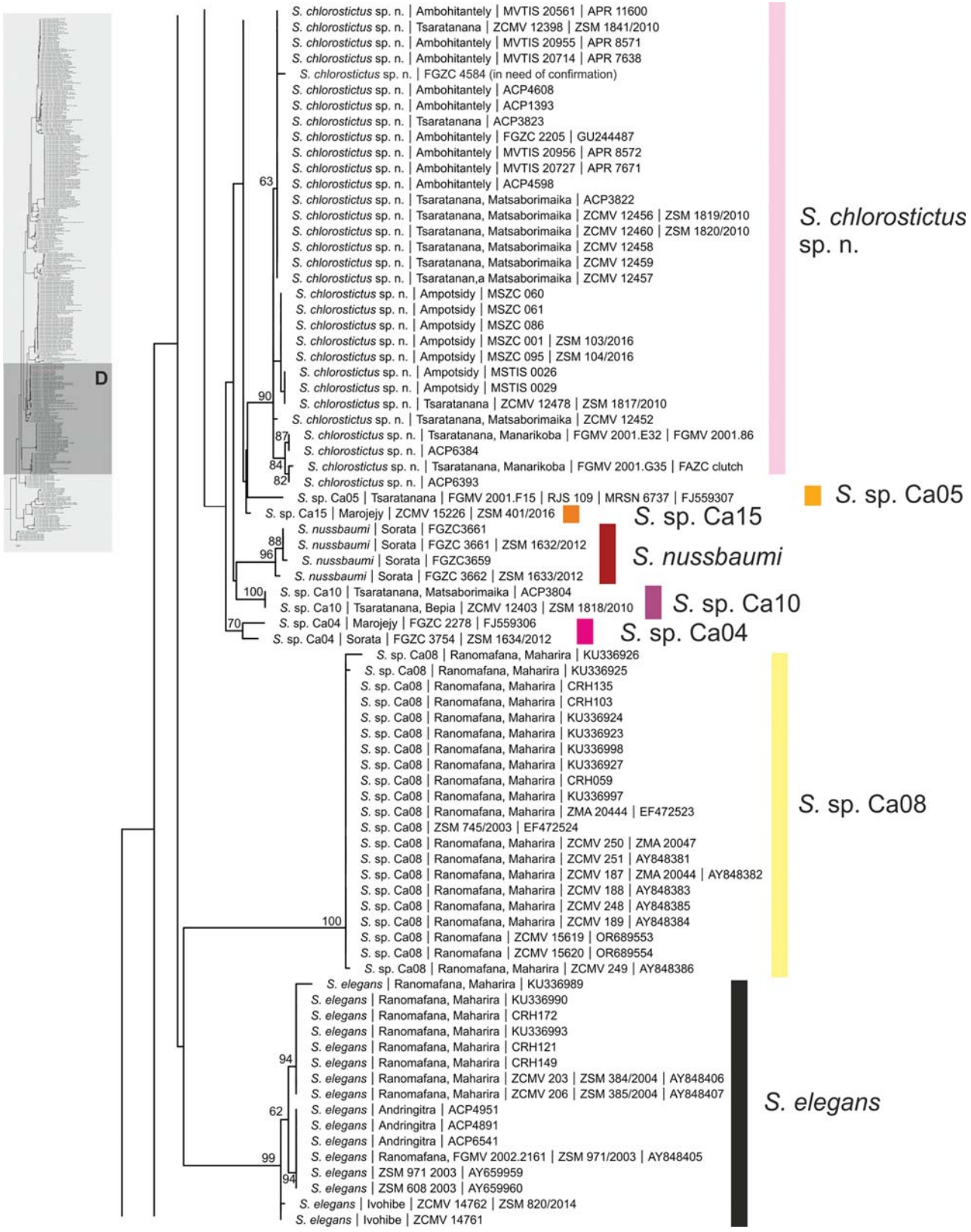

Figure 2 continued

The tree includes representatives of all nominal species of *Spinomantis* except *S. brunae*, which we hypothesize is related to other saxicolous species (which are not the target of this study); for the morphological differentiation of this species, see Andreone et al. (1998) and Cramer et al. (2008). Our work also includes the first published sequences of specimens assigned to *S. nussbaumi*, and new sequences of *S. tavaratra* from its type locality, Sorata. *Spinomantis nussbaumi*, in our molecular tree, is represented only by individuals collected in Sorata. Although this is ca 77 km from the type locality (Befosa River–Antetikalambazaha, Tsaratanana Massif, 14.1742° S, 48.9450° E), these specimens closely resemble that species morphologically (see below). For the non-arboreal species of *Spinomantis*, the topology of our tree is largely in agreement with that published by Hutter et al. (2025), and it is worth mentioning here that in Fig. 1 of that paper, the species labels of *S. lakolosy* and *S. lavabato* were accidentally swapped.

As a first step, to structure this mitochondrial diversity, we examined the results of the ASAP analysis which, however, suggested unrealistic partitions: either a partial merger of clearly heterospecific lineages, or unrealistically high numbers of subsets such as 41 subsets suggested for the partition of second-best ASAP score of 7.5. The suggested partition with best (lowest) ASAP score of 5.5 divided the individuals in 22 subsets that largely corresponded to previously defined species and candidate species, with the exception of two subsets that merged samples clearly belonging to distinct species of strong morphological and bioacoustic differences (i.e., *S. massi* and *S. phantasticus* together in one subset, and *S. peraccae* and *S. nussbaumi* together in another subset). We therefore, in our preferred species partition for downstream analysis, deviate from the ASAP hypothesis by (i) considering the partition with highest ASAP score and 22 subsets but (ii) separating two of these subsets further, based on previous candidate species assessments and morphological/bioacoustic evidence. We used this preferred (primary) species partition as a starting point to assign names to genetic lineages and delimit putative species based on integrative evidence from (i) mitochondrial phylogeny, (ii) amount of mitochondrial divergence, (iii) differentiation in nuclear-encoded genes,

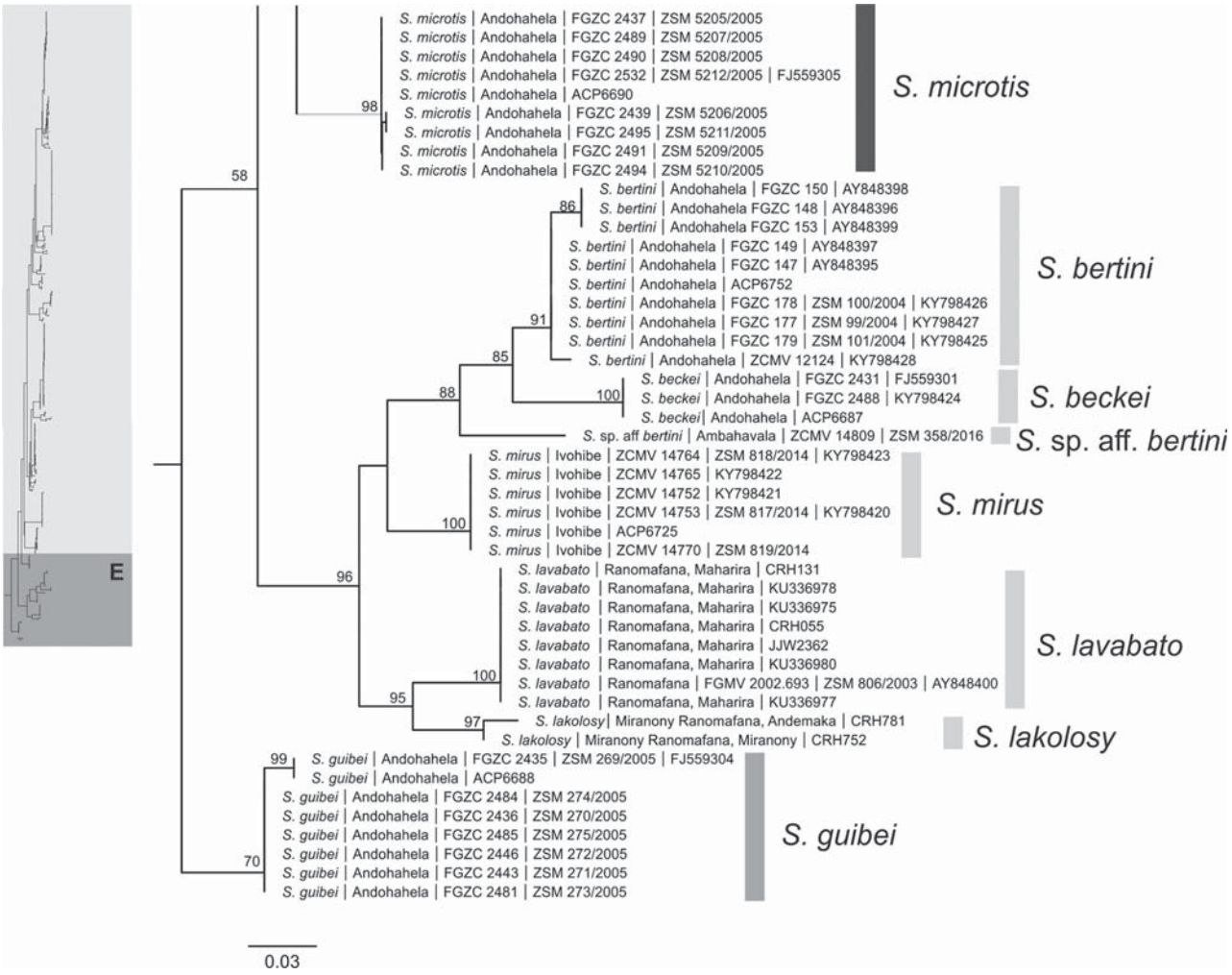

Figure 2 continued

Table 2. Uncorrected pairwise distances in percent, calculated from partial DNA sequences of the mitochondrial 16S rRNA gene (alignment length 511 bp) within and between nominal species of *Spinomantis* of the arboreal clade, including the four new species described herein. Values are mean, with min–max in parentheses. Deep conspecific lineages of *S. aglavei* from Betampona and Sahafina are not considered. See full table with all lineages and candidate species at https://doi.org/10.5281/zenodo.18020638.

	aglavei	*fimbriatus*	*royae* sp. n.	*leonieae* sp. n.	*tavaratra*	*massi*	*phantasticus*	*fohitsilo* sp. n.	*peraccae*	*nussbaumi*	*chlorostictus* sp. n.
S. aglavei	0.7 (0.0–1.4)										
S. fimbriatus	6.6 (6.3–7.2)	NA									
S. royae sp. n.	6.5 (6.2–7.0)	6.0 (5.5–6.3)	0.2 (0.0–0.9)								
S. leonieae sp. n.	7.9 (7.7–8.4)	7.2 (6.6–7.9)	7.9 (7.3–8.8)	3.9 (3.9–3.9)							
S. tavaratra	8.4 (7.7–9.0)	7.9 (7.5–8.8)	7.4 (6.6–7.9)	8.9 (7.9–9.3)	1.5 (0.0–3.2)						
S. massi	10.8 (10.1–11.8)	11.5 (11.2–12.3)	9.6 (9.0–10.5)	10.9 (10.3–11.6)	11.3 (10.3–12.8)	1.0 (0.0–2.1)					
S. phantasticus	9.8 (9.0–10.8)	10.4 (10.1–11.0)	7.9 (7.5–8.9)	11.6 (11.0–12.2)	10.6 (10.1–11.4)	5.6 (5.0–6.3)	0.7 (0.0–1.1)				
S. fohitsilo sp. n.	8.6 (8.3–9.4)	9.3 (9.0–9.4)	8.5 (7.9–9.1)	9.4 (9.2–9.6)	10.2 (10.1–10.4)	5.0 (4.6–5.8)	6.4 (5.9–6.8)	0.3 (0.0–0.4)			
S. peraccae	8.5 (8.1–9.6)	9.7 (9.2–10.5)	9.2 (8.6–9.9)	9.7 (9.2–10.5)	9.0 (7.7–10.1)	11.1 (10.5–12.5)	10.6 (10.1–11.7)	11.4 (10.7–12.4)	0.6 (0.0–2.2)		
S. nussbaumi	7.8 (7.4–8.2)	8.4 (8.3–8.5)	6.9 (6.4–7.4)	7.8 (6.8–8.8)	7.7 (6.6–8.3)	9.6 (9.2–10.4)	8.4 (7.9–9.2)	8.0 (7.7–8.1)	6.7 (6.3–7.2)	0.4 (0.0–0.9)	
S. chlorostictus sp. n.	8.2 (7.4–9.1)	6.9 (6.3–7.4)	7.2 (6.6–7.9)	7.9 (7.7–8.6)	6.8 (6.4–7.7)	11.1 (10.5–12.0)	10.0 (9.4–11.1)	9.2 (8.8–10.0)	6.3 (5.0–7.2)	4.2 (3.7–5.0)	0.6 (0.0–1.5)

(iv) morphology, and (v) bioacoustics. Our preferred partition, indicated in Figure 2 and not counting deep lineages considered to be conspecific, divides *Spinomantis* into 19 species (including the four newly described herein and not counting *S. brunae*, for which genetic data is still unavailable) plus 11 additional candidate species and three lineages provisionally considered as deep conspecific lineages (DCLs) of *S. aglavei*. Of these, 11 species and 9 candidate species belong to the clade of arboreal *Spinomantis* as defined herein (see below). Several of these appear to be rather widespread across Madagascar, with linear distances of 400–500 km between localities, while others might be microendemics restricted to a few neighboring mountain ranges (Fig. 3).

Uncorrected genetic distances for the 3'-16S fragment between all species and candidate species of *Spinomantis* range between 3.1–16.5%. Very high distances characterize especially the comparisons between lineages of the arboreal clade and the phylogenetically distant saxicolous species (a full distance matrix is included in Supplementary materials: https://doi.org/10.5281/zenodo.18020638). Within the arboreal clade, currently accepted nominal species differ between 5.0% (*S. massi* vs. *S. phantasticus*) and 12.5% (*S. massi* vs. *S.* cf. *aglavei* "north") (Table 2). The four lineages described as distinct species herein (see below) differ by minimum distances of 3.7% (*S.* sp. Ca11 vs. *S. nussbaumi*) to > 4.5%. Mitochondrial lineages considered as conspecific lead to high distances within nominal species as defined herein, of up to 3.2% in *S. tavaratra,* and up to 6.7% within *S. aglavei* when lineages from Betampona and Sahafina are included (see full distance table in Supplementary materials).

The Maximum Likelihood tree based on 2902 bp of five mitochondrial DNA fragments, corresponding to parts of the 12S rRNA, 16S rRNA (two fragments), cox1, and cytb genes for representative samples of the majority of species and candidate species in the genus (Fig. 4), agrees with previous, less comprehensive analyses (e.g., Wollenberg et al. 2011) in distinguishing two main clades within the genus, corresponding to: (i) the mainly saxicolous species *S. guibei, S. microtis,* and the *S. bertini* complex (*S. beckei, S. bertini, S. mirus*, *S. lavabato*, and *S. lakolosy*) (bootstrap support BS = 74%), and (ii) the arboreal species (all other species except *S. elegans* and the candidate species *S.* sp. Ca08; BS = 70%). *Spinomantis elegans* and *S.* sp. Ca08 were placed with the arboreal clade, but with low support (BS = 63%) and their phylogenetic placement thus requires additional study. Within the arboreal clade, three highly supported subclades could be distinguished, which are here called the *aglavei* clade (with *S. aglavei, S. fimbriatus*, and related lineages; BS = 99%), the *massi* clade (with *S. massi, S. phantasticus*, and one further lineage; BS = 100%), and the *peraccae* clade (with *S. peraccae, S. nussbaumi,* and several related lineages; BS = 99%). Within each of these three clades, one or several candidate species were phylogenetically arranged in separate positions and could not be assigned as deep conspecific lineages to any nominal species without an assumption of non-monophyletic species.

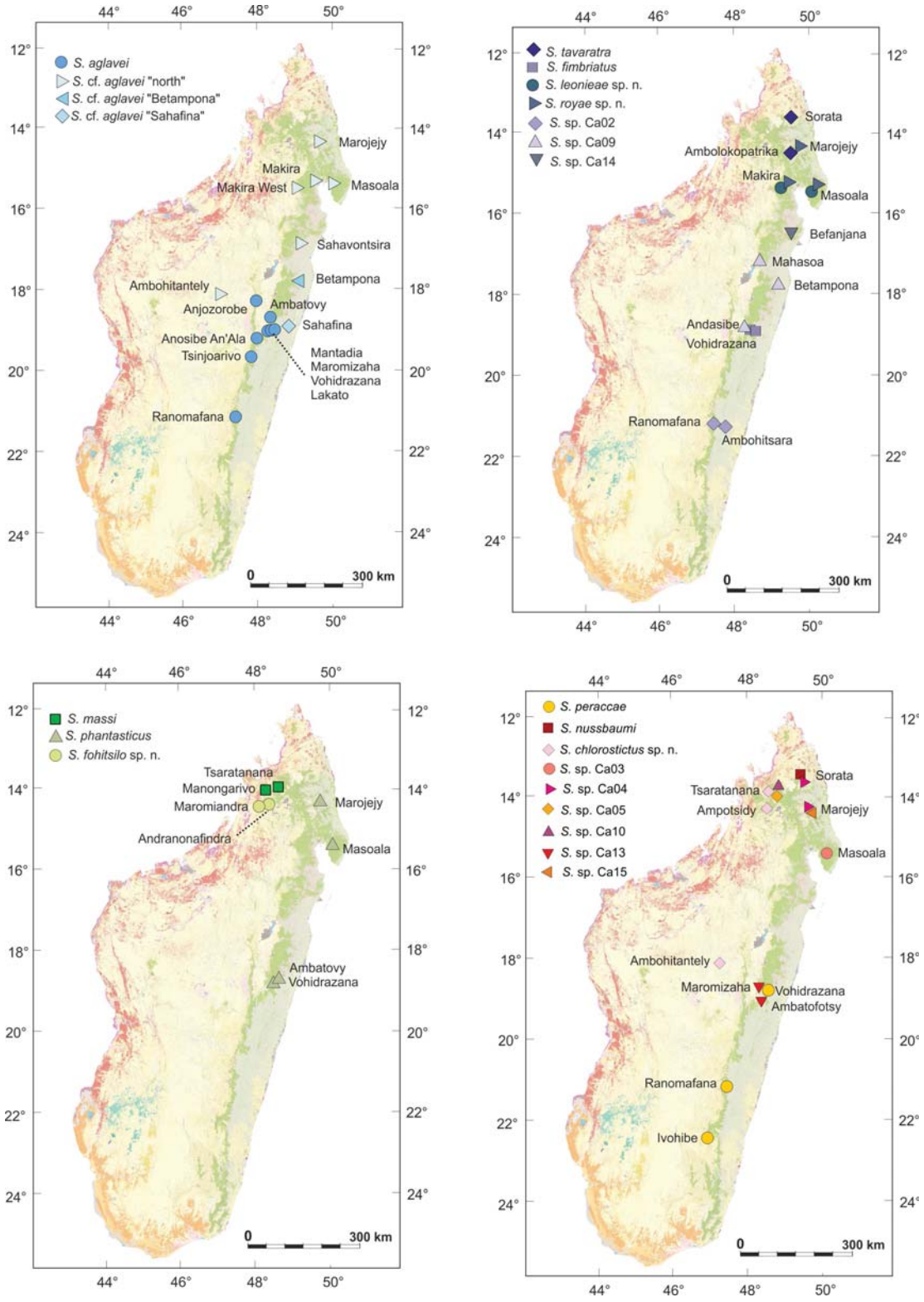

Figure 3. Maps of Madagascar showing the distribution of genetically confirmed records of species and candidate species in the arboreal clade of *Spinomantis*, as included in Figure 1. The base map shows vegetation across Madagascar from the Madagascar Vegetation Mapping Project (Moat & Smith 2007), available at https://web.archive.org/web/20180419112513/http://www.vegmad.org/). Vegetation is colored as follows: green, humid forest (rainforest); red, western dry deciduous forest; pink, mangroves; orange, spiny forest-thicket; greenish blue, western subhumid forest; yellow, Tapia forest; pale yellow, cultivation and grasslands.

Haplotype networks (Fitch genealogies) reconstructed from two nuclear gene fragments (KIAA 1239 and RAG-1; Fig. 5) separated individuals of the *aglavei* clade, *massi* clade, and *peraccae* clade into relatively well separated phylogroups, with only one instance of haplotype sharing between individuals of different clades (one haplotype in KIAA1239 shared between a representative of the *aglavei* clade and the *peraccae* clade). One individual of *S.* sp. Ca13 had a unique RAG-1 haplotype deeply nested within the *aglavei* clade, despite being assigned by mitochondrial evidence to the *peraccae* clade; its haplotype in KIAA1239 was placed well within the *peraccae* clade. Within the *massi* clade, the three included lineages were well separated, without haplotype sharing between them. *Spinomantis tavaratra* in KIAA1239, *S. nussbaumi* in RAG-1 and *S. phantasticus* in both genes were separated from all other lineages by several mutational steps.

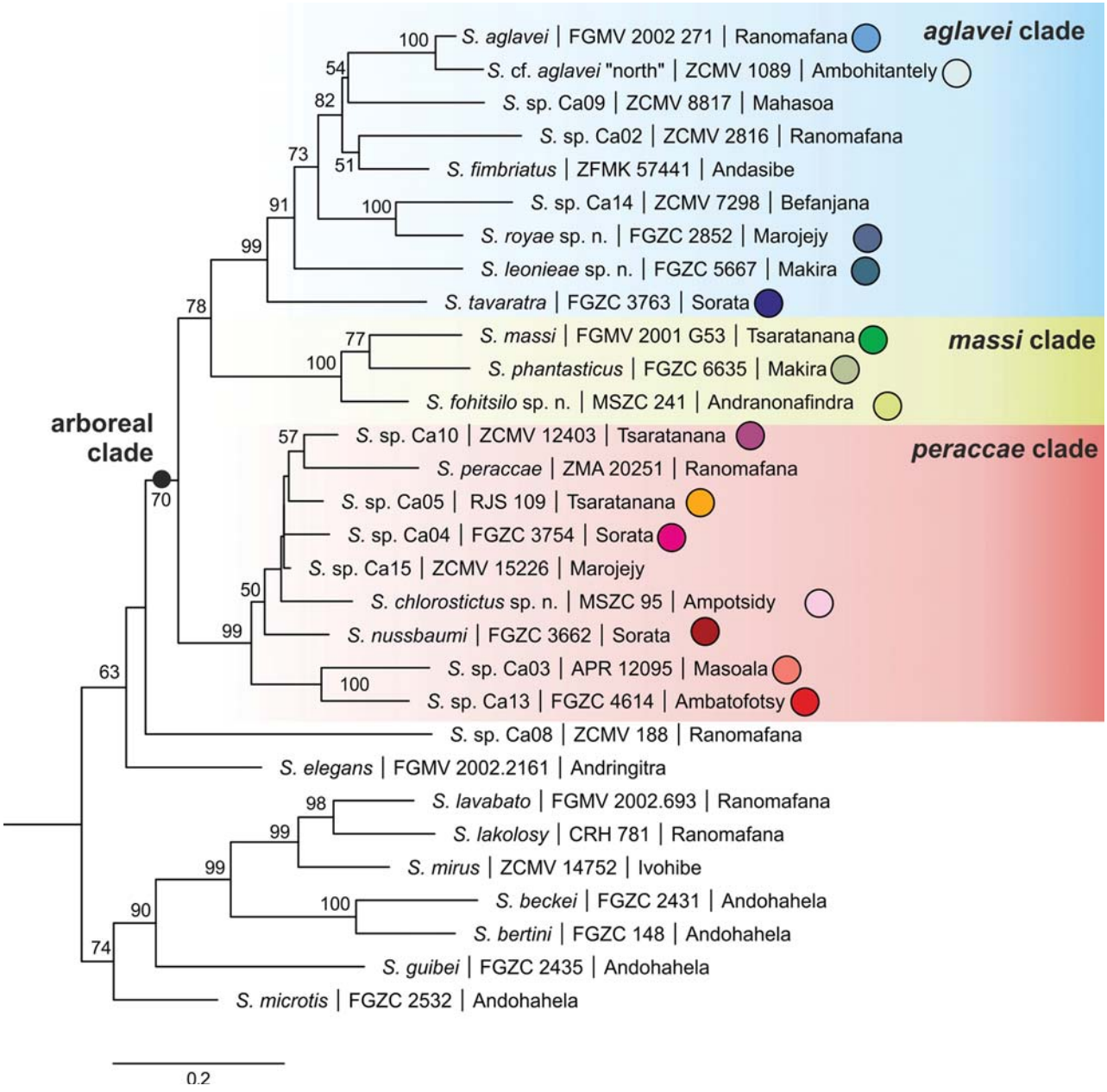

Figure 4. Maximum Likelihood tree inferred from a partitioned analysis of concatenated DNA sequences of the five mitochondrial gene fragments: 12S, 16S (3' and 5'), cox1 and cytb (2902 bp). Numbers at nodes are support values in percent from a bootstrap analysis (500 full replicates; not shown for values < 50%). *Guibemantis liber* was used as the outgroup (removed graphically to better resolve branch lengths of the ingroup).

Bioacoustics and morphology

Despite a limited number of available recordings and generally similar call characters, comparisons of advertisement calls of focal lineages with those of known nominal species (and among each other) revealed qualitative and/or quantitative differences that unequivocally allow for an identification of lineages by bioacoustics alone. Calls of most species considered are easy to identify by the human ear. The differences here observed between advertisement calls of *Spinomantis* lineages for which reliably assigned recordings were available are far beyond those that could be considered intra-specific call variation, particularly in cases of qualitative differences and/or quantitative differences without any overlap in measured parameters (see Köhler et al. 2017). In summary, the bioacoustic results are concordant with the genetically identified lineages and support the existence of unnamed clades at the species level. Bioacoustic parameters of advertisement calls considered are summarized in a comparative manner in Table 3, displayed in Figs 6–8, and further detailed in the species accounts and diagnostic paragraphs below.

Morphologically, differences between species in the arboreal *Spinomantis* clade extend to body size, presence and expression of dermal spines on limbs and body (Figs 1, 9), relative tympanum size, relative size of femoral glands in males (Fig. 10), and color pattern (Figs 1, 11–17). In general, species of the *peraccae* clade are characterized by absence of dermal spines on limbs, and by mostly relatively large tympanum sizes (usually TD ≥ 50% of ED and ≥ 6.5 of SVL). In contrast, species of the *aglavei* and *massi* clades have at least some small dermal spines on tibia and tarsus, and usually a smaller relative tympanum size (usually TD < 50% of ED and ≤ 6% of SVL) (see original measurements in Table 4). Several species are well-defined and differ from all others by unique combinations of characters, such as *S. phantasticus* by having large numbers of spiny dermal tubercles on dorsum (see Glaw & Vences 1997), or *S. aglavei* by strong expression of dermal spines on tibia and tarsus, with alternating short and long spines (Fig. 1). Other species and candidate species are more difficult to diagnose morphologically, and species delimitation is in the following thus performed by integrating molecular, phylogenetic, morphological, and bioacoustic evidence.

Species delimitation and justification in arboreal *Spinomantis*

Of the *Spinomantis* candidate species in our data set, those not belonging to the arboreal clade will be dealt with in separate studies and therefore are not further evaluated here. Within the arboreal clade, we discuss separately the *aglavei* clade, *massi* clade, and *peraccae* clade as defined above.

In the *peraccae* clade, there are three lineages that conform to the general morphology of *S. peraccae* (holotype

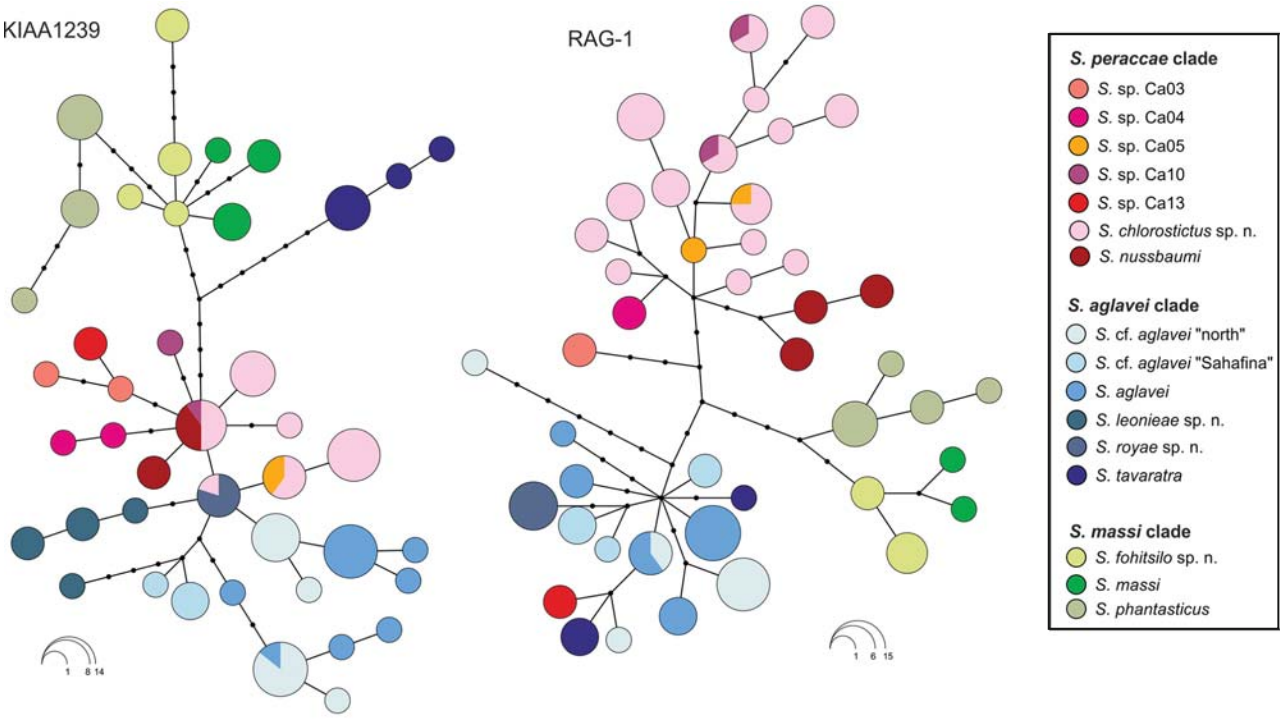

Figure 5. Haplotype networks (Fitch genealogies) reconstructed from DNA sequences of fragments of two nuclear-encoded genes, KIAA1239 (65 individuals, 819 bp) and RAG-1 (62 individuals, 412 bp), for individuals of the arboreal clade of *Spinomantis*. Black dots represent unsampled haplotypes. Networks were reconstructed from phased sequences, and each individual is therefore represented twice in the network.

Table 3. Comparative numerical parameters and characters of advertisement calls of selected *Spinomantis* species/populations.

	call duration [ms]	notes/call	note duration [ms]	inter-note interval [ms]	dominant frequency [Hz]	character of notes	calls analyzed
S. fimbriatus Andasibe	267–344	8	6–45 (13.3±9.7)	10–57 (27.8±12.4)	2186–2426 (2256±99)	pulsatile + tonal	2
S. phantasticus An'Ala	1275–1822 (1455.0±248.5)	10–14 (11.0±2.0)	42–63 (49.8±6.0)	28–170 (92.3±61.6)	2120–2403 (2289±119)	pulsatile	4
S. massi Manongarivo	54–109 (68.1±18.9)	2–3 (2.2±0.4)	9–19 (13.8±2.9)	27–38 (33.2±3.3)	2700–2836 (2753±57)	pulsatile	12
S. massi Benavony	45–63 (52.6±5.6)	2 (2.0±0.0)	10–23 (16.2±3.6)	16–30 (21.3±5.3)	2863–3219 (3043±154)	pulsatile	8
S. fohitsilo sp. n. Andranonafindra	119–133 (124.4±4.7)	3 (3.0±0.0)	7–21 (12.7±3.6)	41–46 (42.8±1.5)	2573–2598 (2587±13)	tonal	8
S. royae sp. n. Marojejy	180–269 (210.8±31.8)	5–7 (6.2±0.8)	8–30 (16.4±5.2)	3–43 (22.7±13.0)	2292–2497 (2391±79)	tonal	6
S. leonieae sp. n. Makira	1323–2894 (2164.3±419.9)	6–15 (11.5±2.5)	7–11 (8.2±1.0)	175–285 (220.0±35.3)	2386–2566 (2469±58)	pulsatile	11
S. peraccae Vohiparara	512–604 (552.5±40.5)	2 (2.0±0.0)	106–181 (147.1±21.0)	223–260 (242.5±16.3)	2583–2756 (2670±73)	pulsatile	4
S. chlorostictus sp. n. Ampotsidy	526–2417 (1347.9±630.6)	2–6 (3.8±1.5)	47–59 (53.0±2.6)	360–524 (415.9±50.1)	2713–2820 (2771±33)	tonal	11
S. chlorostictus sp. n. Manarikoba	732–831 (772.0±40.3)	2 (2.0±0.0)	38–51 (45.6±4.5)	653–719 (687.8±27.0)	2784–2807 (2792±9)	tonal	5
S. aglavei An'Ala	1941–2309 (2067.0±166.4)	6–7 (6.3±0.5)	52–79 (64.6±9.2)	263–390 (308.1±40.5)	1830–1929 (1893±37)	tonal	4
S. aglavei Ankeniheny	1723	6	57–71 (64.0±6.4)	307–406 (349.0±40.2)	1925–2011 (1969±43)	tonal	1

pictured by Andreone et al. 1998): (1) one occurring in the South East, Southern Central East, and Northern Central East, spanning at least from Ivohibe to Vohidrazana according to genotyped samples; we here consider this lineage as *S. peraccae* because the type locality of *S. peraccae* (Ivohimanita = Ivohimanitra; see Andreone et al. 1998) is within its geographical range; (2) a lineage from various sites on the Masoala Peninsula, in agreement with previous assessments (Vieites et al. 2009), is here called *S.* sp. Ca03; and (3) a lineage from Maromizaha and Ambatofotsy for which we here coin the new candidate species number *S.* sp. Ca13. Individuals of these three lineages have a distinctly contrasting pattern of dark brown markings on a light brown dorsum, often with an overall yellowish-greenish tint, yellowish femoral glands in males, and a uniformly whitish venter without extended dark spotting. Unfortunately, for the present study, no call recordings assignable to genotyped vouchers of *S.* sp. Ca03 and Ca13, and no sequences of the nuclear-encoded genes for *S. peraccae* were available. In the haplotype networks (Fig. 5), the few included specimens of *S.* sp. Ca03 and *S.* sp. Ca13 included did not share haplotypes.

Three further lineages in the *peraccae* clade originate from rather high elevations in northern Madagascar and as far as can be assessed with the material at hand, they roughly conform morphologically to *S. nussbaumi*. We have here provisionally assigned one of these genetic lineages, from the Sorata Massif, to *S. nussbaumi* because the relatively large-sized adult specimens (one male 42.8 mm, one female 51.2 mm; Table 4, Fig. 11A–E) collected by us agree rather well with the original description of the species (Cramer et al. 2008) in color pattern, absence of dermal spines on the limbs, body size, and extent of webbing. In agreement with the type specimens of *S. nussbaumi,* the Sorata specimens have dark brown rounded markings on a light brown to beige dorsum, with each dark marking surrounded by a blackish line (Fig. 11F–I). The venter is whitish with dark spotting. Specimens of *S.* sp. Ca10 from Tsaratanana, for which only probable subadults were available for examination, have a similar color pattern with large longitudinal dark brown markings on the back (rather than rounded spots), but the dark dorsal markings are surrounded by a whitish, not blackish, line (a feature that could of course also be attributable to their immaturity). A third lineage, *S.* sp. Ca05, is only known from a single specimen from Ampiboahanala on the Tsaratanana Massif (adult male, MRSN A6737: see Andreone et al. 2009; field number RJS 109) that by body size (SVL 42.1 mm) is reminiscent of *S. nussbaumi*, but as far as can be assessed from the preserved specimen, has dark brown dorsal patches less contrasted and not distinctly delimited by blackish lines, and is ventrally quite densely marbled with dark pigment which extends onto the throat (vs. usually with sparser small isolated dark spots, and not extending

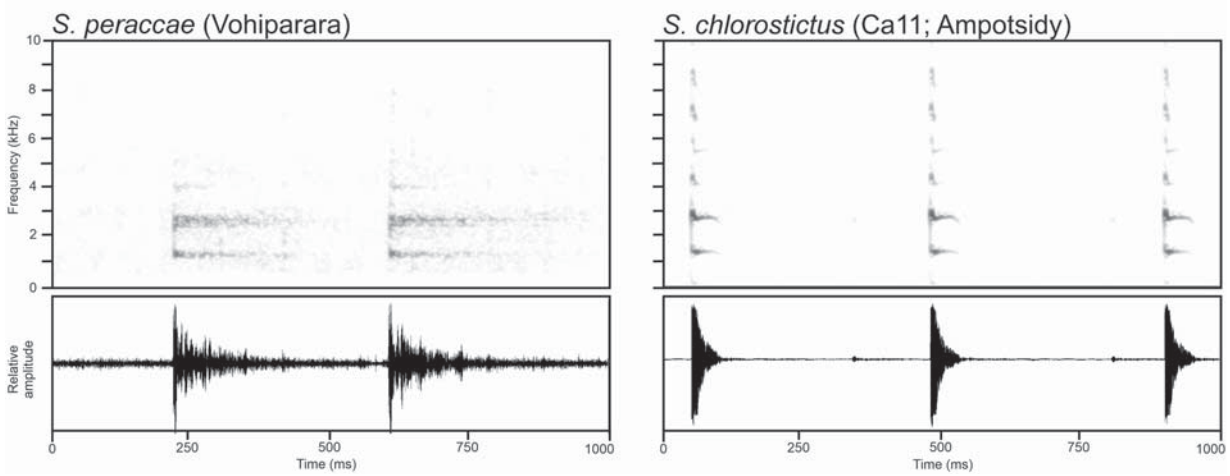

Figure 6. Comparative audiospectrograms and corresponding oscillograms of advertisement calls of *Spinomantis peraccae* and *S. chlorostictus* sp. n. The plot of the *S. chlorostictus* sp. n. call from its type locality displays only three notes (out of six) at 1000 ms time scale.

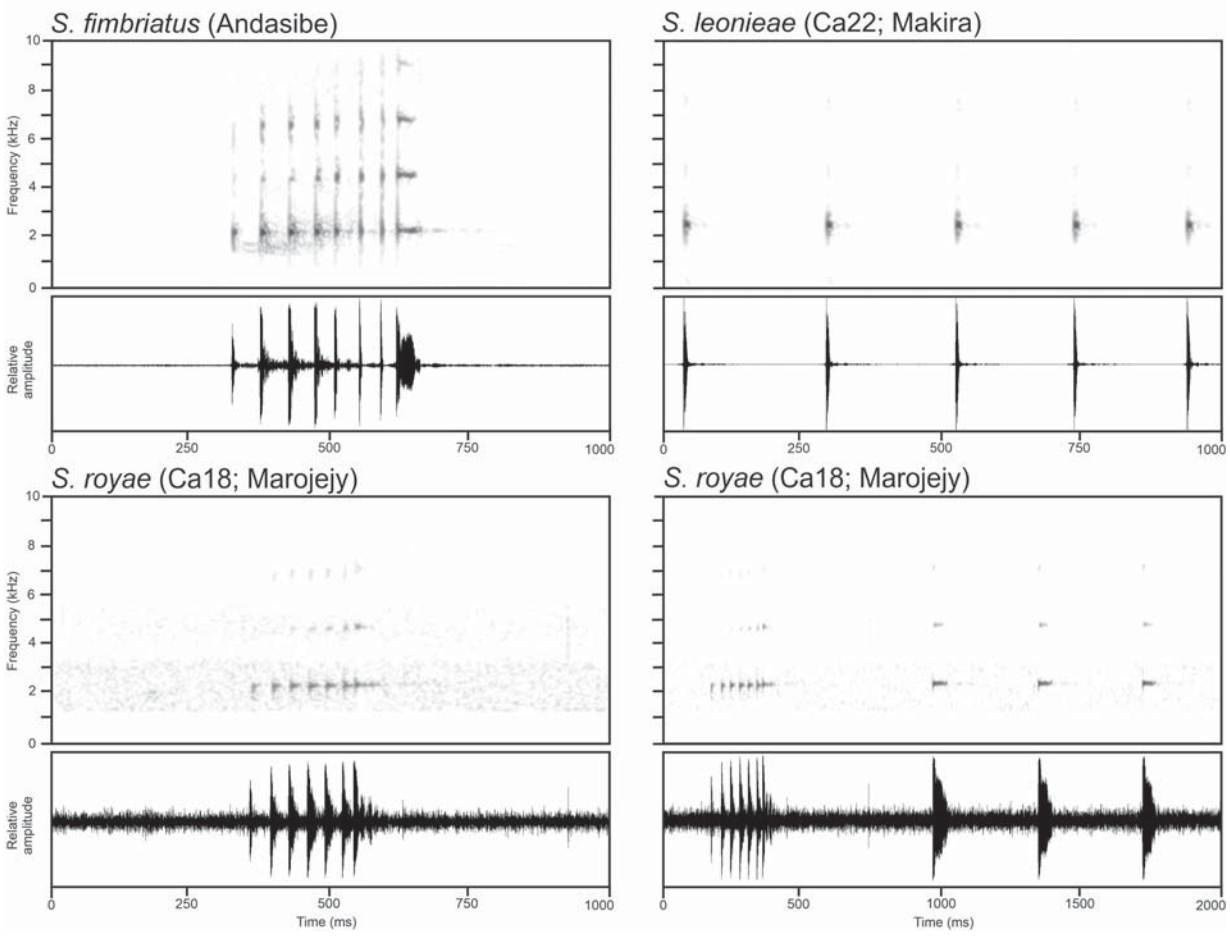

Figure 7. Comparative audiospectrograms and corresponding oscillograms of advertisement calls of *Spinomantis fimbriatus*, *S. leonieae* sp. n., and calls here tentatively assigned to *S. royae* sp. n. The plot of the *S. leonieae* sp. n. call from its type locality (top right) displays five notes only of the entire call at 1000 ms time scale; the plot of the call assigned to *S. royae* sp. n. at bottom right displays two call types at 2000 ms time scale, namely the advertisement call followed by three longer tonal notes, here interpreted to have territorial function (see text).

onto the throat in males; see Cramer et al. 2008). In the haplotype networks of the two nuclear genes (Fig. 5), the lineages of the *peraccae* clade were poorly separated, with several instances of haplotype sharing between lineages, but at least in RAG-1, the sequences of *S. nussbaumi* (as defined herein) formed a separate phylogroup, separated by a minimum of four mutational steps from all other lineages, including *S.* sp. Ca05 and *S.* sp. Ca10 (Fig. 5). Without further data, the status of these various lineages cannot be clarified, but given their strong mitochondrial divergences and indications of at least faint morphological differences between them, we suspect that they belong to more than just one species-level lineage, and whether the Sorata specimens are correctly assigned to *S. nussbaumi* requires confirmation from DNA sequences from the type material of this species or from specimens collected at the type locality.

For two additional lineages in the *peraccae* clade, only very limited data are available. *Spinomantis* sp. Ca04 is known only from a tadpole collected in the Marojejy Massif, and a neometamorph from Sorata; and the newly identified candidate species *S.* sp. Ca15 is only known from a tadpole sequence from Marojejy. Rakotoarimalala & Raselimanana (2023) identified specimens collected recently at Marojejy, which were rather common in their Campsites 4 and 5 on branches overhanging small streams, as *S. nussbaumi*. These specimens, which according to available photos indeed are very similar to this complex of species, may correspond to one of the genetic lineages *S.* sp. Ca04 or *S.* sp. Ca15, and the respective samples and voucher specimens should be included in future taxonomic revisions. The Sorata specimen of *S.* sp. Ca04 did not share haplotypes with any other lineage in the haplotype networks of both nuclear-encoded genes analyzed (Fig. 5), indicating it may likely represent an independent evolutionary lineage.

Finally, for one lineage of the *peraccae* clade (previously named *S.* sp. Ca11; Perl et al. 2014), we had a relatively large number of specimens from various sites available for morphological examination, as well as call recordings. This

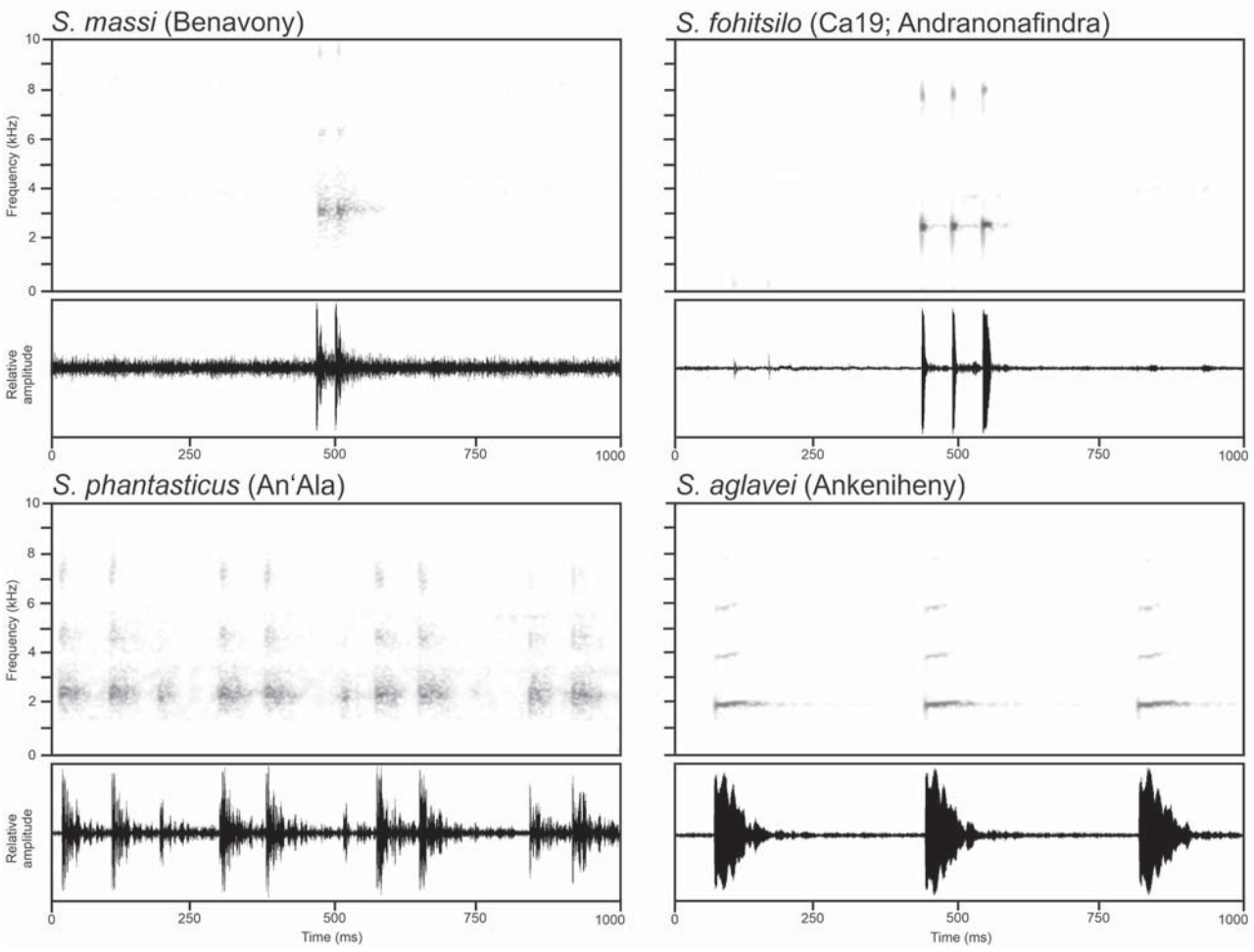

Figure 8. Comparative audiospectrograms and corresponding oscillograms of advertisement calls of *Spinomantis massi* (from its type locality), *S. fohitsilo* sp. n. (from its type locality), *S. phantasticus* (from its type locality) and *S. aglavei*. The plots of the *S. phantasticus* call (bottom left) and of the *S. aglavei* call (bottom right) display eight and three notes only, respectively, of the entire call at 1000 ms time scale.

Table 4. Morphological measurements (all in mm) of specimens of arboreal *Spinomantis* newly measured for this study. For abbreviations of measurements, see Materials and methods. Additional abbreviations: HT, holotype; PT, paratype; M, male; F, female, SA, subadult.

Specimen-voucher	Field number	Locality	Status	Sex	SVL	HW	HL	TD	ED	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIL	FGL	FGW
S. aglavei																				
ZSM 676/2003	FGMV 2002.271	Ranomafana		M	46.7	16.7	17.8	2.8	5.3	5.0	3.0	4.1	32.0	15.7	78.1	34.7	21.5	25.4	11.4	4.5
ZSM 380/2006	ZCMV 3076	Ranomafana		M	45.2	15.7	17.1	2.3	5.7	4.9	3.5	4.4	29.3	13.8	72.4	31.7	18.8	24.5	9.4	3.3
ZSM 427/2010	FGZC 4654	Tsinjoarivo		M	46.4	16.5	17.0	2.4	5.4	5.1	2.8	4.3	29.8	14.5	76.0	33.6	20.4	25.0	8.4	3.0
S. cf. *aglavei* N																				
ZSM 244/2007	ZCMV 1089	Ambohitantely		M	42.0	13.9	15.4	2.0	5.2	4.4	2.7	3.4	27.7	13.1	62.2	27.2	16.7	21.0	8.7	3.7
ZSM 399/2016	ZCMV 15066	Marojejy		M	44.4	15.4	17.8	2.4	5.7	4.6	3.0	3.5	29.0	13.4	72.6	31.8	18.7	24.2	9.3	3.6
S. fimbriatus																				
ZSM 575/1999	ex. ZFMK 57440	Andasibe	PT	M	35.9	12.8	13.6	1.7	4.5	3.5	2.1	3.5	24.5	10.8	62.0	26.1	15.4	20.2	8.0	3.5
S. massi																				
ZSM 577/1999	ex. ZFMK 57443	Benavony	PT	M	33.6	13.0	14.2	1.9	4.4	4.0	2.2	3.2	22.2	10.3	54.2	24.5	14.9	17.4	10.6	4.0
ZSM 829/2003	FGMV 2002.774	Manongarivo		M	40.0	14.1	15.6	2.1	4.9	5.0	2.7	3.7	27.0	13.1	63.5	28.7	17.5	20.3	10.3	3.4
ZSM 640/2001	FGMV 2001.90	Manarikoba, Tsaratanana		M	37.7	12.9	14.6	2.2	4.3	4.1	2.5	3.3	24.9	12.3	57.5	25.3	15.7	18.5	10.0	3.7
ZSM 639/2001	FGMV 2001.88	Manarikoba, Tsaratanana		M	42.1	14.5	15.7	2.1	4.7	4.2	3.0	3.9	27.6	13.8	64.3	28.4	17.7	20.3	12.4	4.6
S. nussbaumi Ca20																				
ZSM 1633/2012	FGZC 3662	Sorata		M	42.8	15.5	16.2	2.8	5.6	3.4	2.8	4.5	32.4	16.1	74.5	34.9	23.1	24.2	8.5	4.3
ZSM 1632/2012	FGZC 3661	Sorata		F	51.2	19.3	19.0	3.5	6.9	4.7	3.6	5.1	35.3	17.6	84.4	40.1	27.3	26.6	NA	NA
S. peraccae																				
ZSM 821/2014	ZCMV 14780	Ivohibe		F	37.6	14.4	14.7	2.8	5.0	3.4	2.9	4.2	27.4	14.3	61.8	30.4	19.9	19.6	NA	NA
ZSM 512/2006	ZCMV 3093	Ranomafana		M	40.2	15.1	15.8	3.1	5.3	3.4	3.1	4.2	26.1	13.5	63.1	30.2	19.5	20.2	10.1	3.5
ZSM 511/2006	ZCMV 3081	Ranomafana		M	37.6	14.7	15.0	2.8	5.3	3.6	3.1	4.6	26.2	13.4	62.6	29.6	20.0	19.3	8.6	4.3
S. phantasticus																				
ZSM 692/2022	FGZC 6635	Makira		F	42.4	16.5	18.0	2.3	5.9	5.0	2.9	4.0	28.7	14.5	67.3	29.9	18.0	21.4	NA	NA
S. tavaratra																				
ZSM 1636/2012	FGZC 3763	Sorata		M	34.7	12.9	13.2	2.0	4.8	3.9	2.5	3.0	23.1	11.5	55.2	22.9	14.8	16.6	6.3	2.6
ZSM 1635/2012	FGZC 3569	Sorata		F	36.6	14.1	15.2	1.9	5.4	3.8	2.7	3.3	25.2	12.4	60.2	22.1	17.0	19.1	NA	NA
ZSM 1637/2012	FGZC 3641	Sorata		M	35.3	13.2	13.6	2.0	4.8	3.2	2.5	2.9	23.9	12.2	53.6	23.0	15.0	16.5	7.2	3.2
S. sp. Ca10																				
ZSM 1818/2010	ZCMV 12403	Tsaratanana		SA	31.6	11.6	12.6	2.4	4.5	2.7	2.4	3.3	22.2	12.4	56.3	26.7	16.2	18.2	NA	NA
S. sp. Ca13																				
ZSM 429/2010	FGZC 4616	Ambatofotsy		F	32.6	13.1	14.0	2.3	4.3	3.3	2.4	3.8	23.7	12.0	58.0	26.5	17.0	18.1	NA	NA
S. sp. Ca14																				
ZSM 769/2009	ZCMV 7298	Befanjana		F	32.4	12.0	13.1	1.6	5.0	3.1	2.0	2.5	21.6	10.5	54.8	24.1	14.0	17.9	NA	NA

Table 4 continued

Specimen-voucher	Field number	Locality	Status	Sex	SVL	HW	HL	TD	ED	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIL	FGL	FGW
Spinomantis chlorostictus sp. n.																				
ZSM 103/2016	MSZC 1	Ampotsidy	PT	M	39.4	13.9	15.9	2.8	5.1	3.6	2.6	3.8	25.7	13.2	60.6	29.6	19.1	19.4	8.5	3.4
ZSM 104/2016	MSZC 95	Ampotsidy	HT	M	42.3	15.1	16.0	3.2	6.2	3.4	2.5	4.4	27.2	14.1	65.2	30.3	19.9	21.1	9.1	3.5
ZSM 1841/2010	ZCMV 12398	Tsaratanana	PT	F subad	33.0	12.7	13.1	2.6	5.0	3.8	2.6	3.3	24.0	12.0	55.5	26.1	17.6	17.6	NA	NA
ZSM 637/2001	FGMV 2001.122	Manarikoba, Tsaratanana	PT	M	38.0	14.4	15.4	2.9	4.9	3.8	2.9	3.9	25.1	13.0	59.9	28.2	18.2	18.8	7.7	2.8
ZSM 638/2001	FGMV 2001.126	Manarikoba, Tsaratanana	PT	M	37.9	14.2	15.1	2.5	5.3	3.5	3.1	3.6	24.0	13.0	60.9	27.6	18.1	19.0	7.5	3.2
ZSM 636/2001	FGMV 2001.63	Manarikoba, Tsaratanana	PT	M	38.9	15.0	15.4	2.5	5.4	3.5	3.1	4.0	25.4	12.2	61.6	27.8	17.3	19.2	7.1	2.6
Spinomantis royae sp. n.																				
ZSM 400/2016	ZCMV 15161	Marojejy	PT	F	36.6	13.5	14.6	1.8	5.3	3.5	2.6	3.2	26.3	11.6	60.2	26.6	15.5	20.0	NA	NA
ZSM 258/2005	FGZC 2852	Marojejy	HT	M	36.4	13.9	14.8	2.0	5.1	3.7	2.9	3.6	26.3	12.5	61.0	26.6	15.8	20.0	7.3	3.4
Spinomantis fohitsilo sp. n.																				
ZSM 102/2016	MSZC 241	Andranonafindra	HT	M	43.0	14.9	16.2	2.1	5.3	3.9	3.2	3.8	27.8	13.0	64.3	29.4	18.6	20.4	11.1	4.1
Spinomantis leonieae sp. n.																				
ZSM 211/2022	FGZC 5667	Makira	PT	M	33.9	13.1	14.4	1.5	4.8	3.4	2.2	3.0	24.7	11.8	59.3	25.2	16.0	19.4	6.2	2.1
ZSM 212/2022	FGZC 5668	Makira	HT	M	35.3	13.3	14.6	2.1	5.4	4.0	2.7	3.2	23.8	11.4	57.0	26.0	15.7	19.2	6.2	3.1

lineage from various sites in northern Madagascar, especially on the Tsaratanana Massif, differs morphologically and genetically from the other two nominal species of the *peraccae* clade. Compared to *S. nussbaumi*, it has a smaller body size (males 37.9–42.3 mm vs. 42.8–56.4 mm; Table 1 and Cramer et al. 2008) and less distinctly contrasting dark patterns on the back (Fig. 14); also, in at least one nuclear-encoded gene fragment (RAG-1), the two lineages do not share haplotypes (Fig. 5). Compared to *S. peraccae*, it lacks the usually regular dorsal pattern of rounded dark patches and largely unspotted belly typical for that species and instead has a variable and often indistinct dorsal pattern with green elements, usually some dark spots on belly (Fig. 14), and furthermore differs by qualitative and quantitative bioacoustic differences (Fig. 6, Table 3; see diagnosis below for more details). This lineage is described herein as *S. chlorostictus* sp. n.

For populations here subsumed under *S. aglavei*, our data suggest a high genetic variation which is also reflected by the fact that Carné & Vieites (2024) distinguished four deep conspecific lineages for this species. In our dataset, a mitochondrial lineage of samples from mid-elevation sites in the Southern Central East and Northern Central East, between Ranomafana and Fierenana, differed from those further northwards, from an area spanning from Ambohitantely to Marojejy, by 2.6–4.6% uncorrected distance in the 16S gene. Furthermore, two sites at lower elevation in the Northern Central East, Betampona and Sahafina, each harbor a similarly deep mitochondrial lineage, which differed by 3.9–5.4%. Morphological examination of three sequenced specimens (male ZSM 399/2016 from Marojejy, male ZSM 244/2007 from Ambohitantely; and female FAZC 10065 = MRSN A3766 from Masoala) did not reveal obvious morphological differences to those from Ranomafana and Tsinjoarivo, besides possibly slightly smaller body sizes of the two males (Table 2). All these specimens had numerous alternating long and short dermal spines on tibia and tarsus and an immaculate venter. In the two nuclear-encoded gene fragments, haplotype sharing between the lineages was detected (Fig. 5). We tentatively assign all these populations to *S. aglavei* and refer to the lineage from the Northern and Southern Central East as *S. aglavei* and to the others as *S.* cf. *aglavei* "north", *S.* cf. *aglavei* "Betampona", and *S.* cf. *aglavei* "Sahafina". An in-depth taxonomic revision of this complex should be undertaken in the future.

Besides *S. aglavei* and the genetically quite divergent *S. tavaratra* (Fig. 12), which differs by a 16S pairwise distance of > 6.3% (Table 2) from all other species and is separated by a minimum of nine mutational steps in the KIAA1239 haplotype network (Fig. 5), the *aglavei* clade includes several other lineages with known or suspected morphological similarity to *S. fimbriatus*.

Because no molecular data from reliably identified individuals of *S. fimbriatus* were available, we obtained mitochondrial sequences from the holotype (ZFMK 57441) of the species from Andasibe, which clustered with two additional specimens from Vohidrazana. For a possibly related

lineage already identified by Vieites et al. (2009), no reliable information of the adult morphology or bioacoustics was available for the present study: *S.* sp. Ca02 from the Ranomafana area.

Spinomantis sp. Ca09 known from Betampona and Mahasoa, and apparently also occurring syntopically with *S. fimbriatus* in Andasibe based on a sequence from a tadpole (Fig. 2) is known by only a few specimens and no bio-

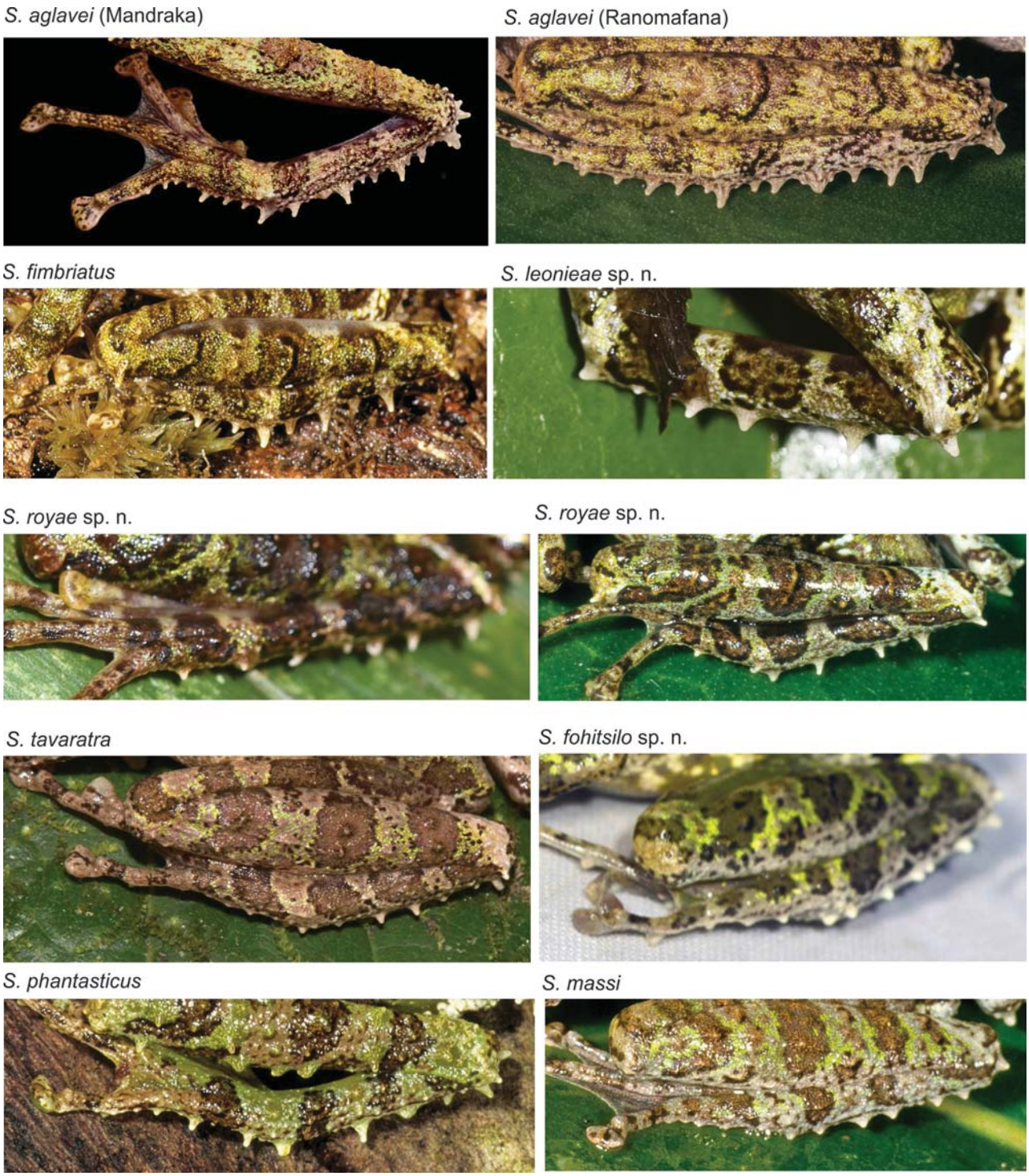

Figure 9. Hindlimbs (tibia, tarsus and foot) of selected species of arboreal *Spinomantis* with dermal spines and tubercles in this body region, illustrating differences in number, size and periodicity of these structures in life. Not to scale.

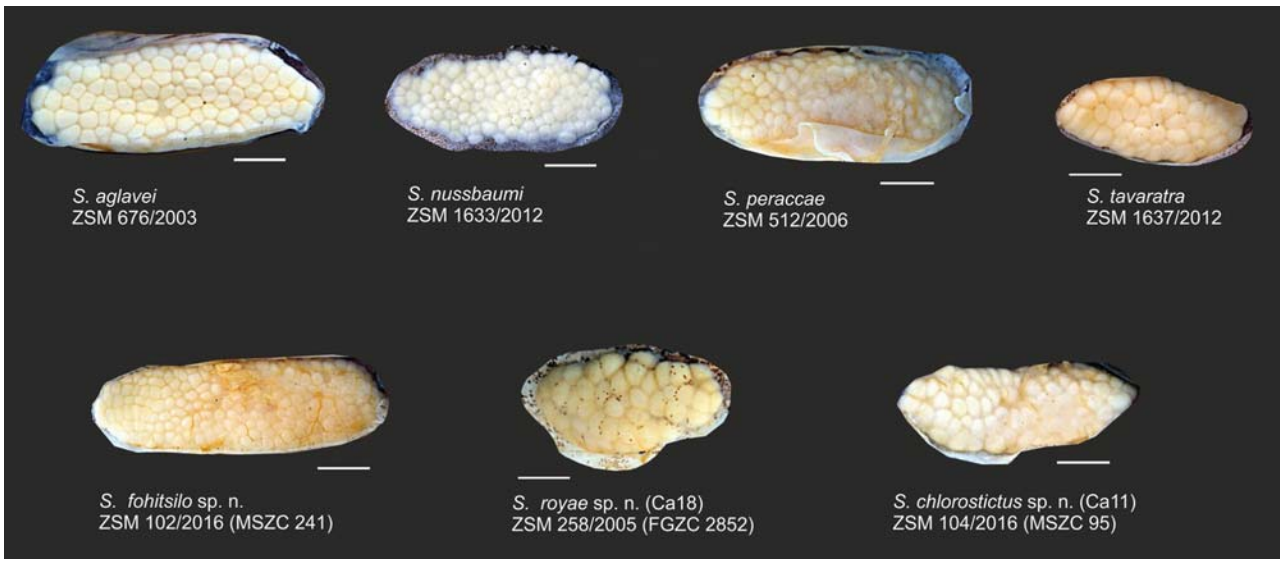

Figure 10. Femoral glands of males of selected species of arboreal *Spinomantis* in internal view (i.e., after dissection and reflection of skin), showing number and relative size of gland granules. Scale bars = 2 mm.

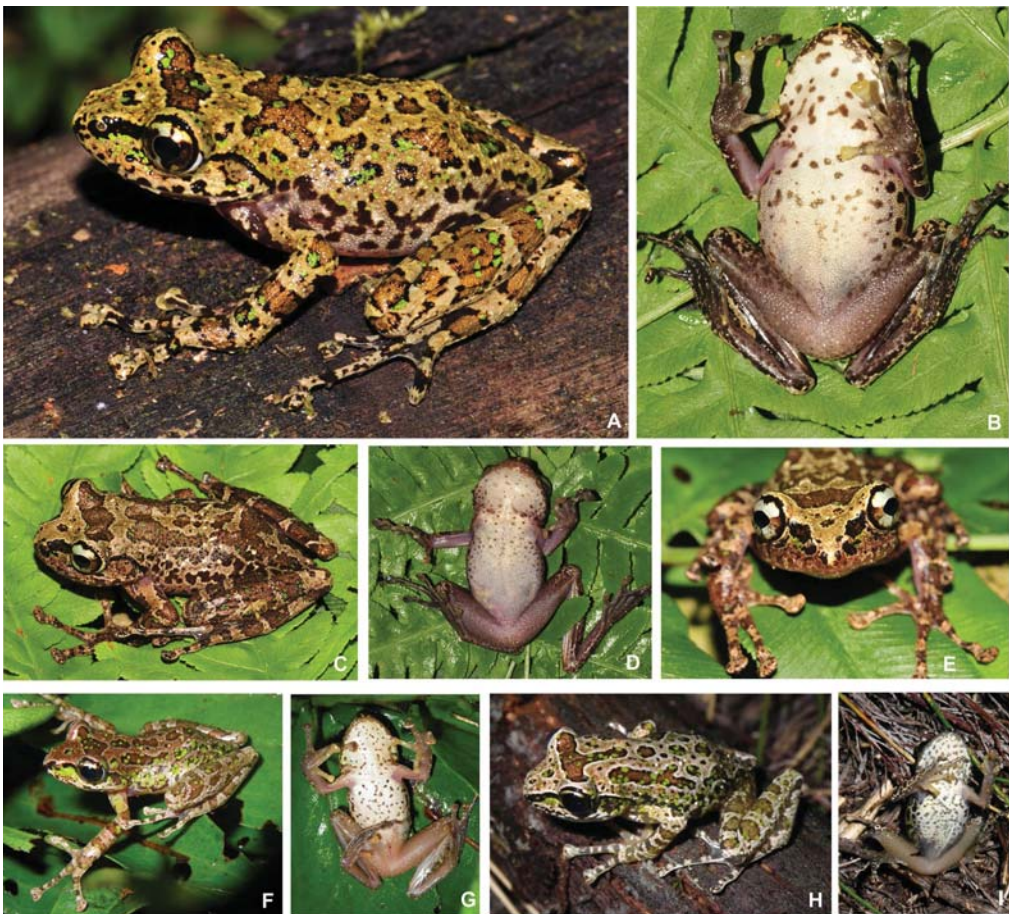

Figure 11. Specimens assigned to *Spinomantis nussbaumi* and the related *S.* sp. Ca10 in life, in dorsolateral and ventral views: (A–B) female of *S. nussbaumi* from Sorata (images not assignable to a voucher specimen); (C–E), female of *S. nussbaumi* from Sorata, ZSM 1632/2012 (FGZC 3661); (F–G) subadult of *S.* sp. Ca10 from Tsaratanana (Bepia campsite) (images not assignable to a voucher specimen); (H–I) subadult of *S.* sp. Ca10 from Tsaratanana (way to Maromokotro) (images not assignable to a voucher specimen).

acoustic data are available. Based on a photograph of one genotyped specimen (ACP5439) the species is morphologically similar to *S. aglavei*, with distinct alternating long and short dermal spines on hindlimbs, but perhaps with more expressed and more irregular large dorsal tubercles than in *S. aglavei*. One lineage from Marojejy, Makira and Masoala included specimens that in the past were provisionally assigned to *S. fimbriatus* (e.g., Glaw & Vences 1997, 2007) but differ by a more distinct dorsal pattern and a conspicuous bluish outer iris area (Fig. 15). Advertisement calls of this species from Marojejy differ from those of *S. fimbriatus*, and we here describe this lineage as *S. royae* sp. n. One specimen from Befanjana (ZSM 769/2009) is placed sister to *S. royae* sp. n. but differs from it by 5.1% pairwise distance in 16S; we here refer to this specimen as *S.* sp. Ca14. One additional lineage from Makira and Masoala is morphologically similar to *S. fimbriatus* (Fig. 16) but differs by a radically different advertisement call; it is herein described as *S. leonieae* sp. n.

Finally, the *massi* clade consists of three lineages: two of them corresponding to the morphologically highly distinct species *S. massi* and *S. phantasticus*, and a third one from northern Madagascar. This third lineage is morphologically similar to *S. massi* (Fig. 17) but differs bioacoustically and by a high mitochondrial divergence. It also lacks haplotype sharing with *S. massi* in one of the nuclear gene fragments studied (Fig. 5), despite geographical proximity of their populations, and is therefore herein described as *S. fohitsilo* sp. n.

Descriptions of new species

Spinomantis chlorostictus sp. n.

Figs 13–14

ZooBank LSID: urn:lsid:zoobank.org:act:93E29B02-2261-429A-AB72-0D64521E2C79

Remark: This species was depicted as *S. peraccae* in Glaw & Vences (2007: Fig. 5b on p. 207), and corresponds to *S.* sp. aff. *peraccae* of Andreone et al. (2009), *S.* sp. Ca11 in Perl et al. (2014), and *S.* sp. 11 in Carné & Vieites (2024). Phylogenetically it belongs to the *peraccae* clade where its phylogenetic relationships to other mitochondrial lineages are largely unresolved (Fig. 4).

Holotype: ZSM 104/2016 (field number MSZC 0095), adult male collected by M. D. Scherz, J. Borrell, L. Ball, T. Starnes, E. Razafimandimby, D. H. Nomenjanahary, and J. Rabearivony on 28 December 2015 at Ampotsidy, 15.7 km NNW of Bealanana (14.41965° S, 48.71943° E, 1347 m above sea level), northern Madagascar.

Paratypes: Seven specimens: ZSM 103/2016 (MSZC 0001), adult male, collected at the type locality by the same collectors as the holotype, on 18 December 2015. ZSM 1841/2010 (ZCMV 12398), probably a subadult female, collected by M. Vences, D. R. Vieites, R. D. Randrianiaina, S. Rasamison, A. Rakotoarison, E. Rajeriarison,

Figure 12. Specimens assigned to *Spinomantis tavaratra* from Sorata in life, in dorsolateral and ventral views: (A–B) female (images not assignable to a voucher specimen); (C–E) female ZSM 1635/2012 (FGZC 3569); (F–G) female (images not assignable to a voucher specimen).

and T. Rajoafiarison in June 2010 in Tsaratanana National Park (exact collecting information not available). ZSM 636/2001 (FGMV 2001.63), ZSM 637/2001 (FGMV 2001.122), and ZSM 638/2001 (FGMV 2001.126), three adult males, collected by F. Andreone, F. Mattioli, J. Randrianirina, and M. Vences from 3–9 February 2001 at Antsahamanara Campsite, Manarikoba Forest, Tsaratanana Massif (14.045° S, 48.784° E, ca. 1000 m a.s.l.). Two adult male specimens, UADBA-A 62241 (MSZC 0060), and UADBA-A 62298 (MSZC 0086), collected at the type locality by the same collectors as the holotype, on 23 and 24 December 2015, respectively, and at the following exact coordinates, respectively: 14.41965° S, 48.71943° E, 1347 m a.s.l.; 14.41227° S, 48.71187° E, 1480 m a.s.l.

Diagnosis: The new species is placed in the genus *Spinomantis* based on presence of intercalary elements between ultimate and penultimate phalanges of fingers and toes (verified by external examination), presence of distinct femoral glands (type 2; Glaw et al. 2000) in males, outer metatarsal tubercle present, maxillary teeth present, adults living along streams in rainforests, and molecular phylogenetic relationships. Within *Spinomantis*, it phylogenetically belongs to the *peraccae* clade and differs from all members of the *aglavei* and *massi* clades by a relatively large tympanum (tympanum diameter up to 59% of eye diameter) and absence (vs. presence) of dermal spines on tibia and tarsus. It differs from *S. nussbaumi* by a smaller body size (males 37.9–42.3 mm vs. 42.8–56.4 mm; Table 1 and Cramer et al. 2008) and less distinctly contrasting dark pattern on the back (see Fig. 14 vs. Fig. 11). It differs from *S. peraccae* by usually indistinct dorsal pattern (vs. distinct pattern with rounded dark markings), presence of opaque green spots and markings on dorsum (vs. absence), absence of translucent greenish-yellowish tint, especially on femoral glands (vs. presence), and black spots on venter (vs. usually absent).

Advertisement calls of the new species differ from those of *S. peraccae, S. massi, S. phantasticus*, and *S. fimbriatus* by an entirely tonal character of notes (vs. pulsatile, or a combination of pulsatile and tonal in *S. fimbriatus*). Furthermore, calls of *S. chlorostictus* differ from those of *S. peraccae* by shorter note duration (38–59 vs. 106–181 ms) and from those of *S. aglavei* by higher dominant frequency (2713–2820 vs. 1830–2011 Hz) (see Table 3).

Description of the holotype: Adult male in excellent state of preservation, with part of left thigh muscle removed for tissue sample (Fig. 13). SVL 42.3 mm, for all morphometric measurements see Table 4. Body moderately slender; head longer than wide, similar in width to body; snout rounded in dorsal, ventral, and lateral views; nostrils nearer to tip of snout than to eye, protuberant and directed laterally;

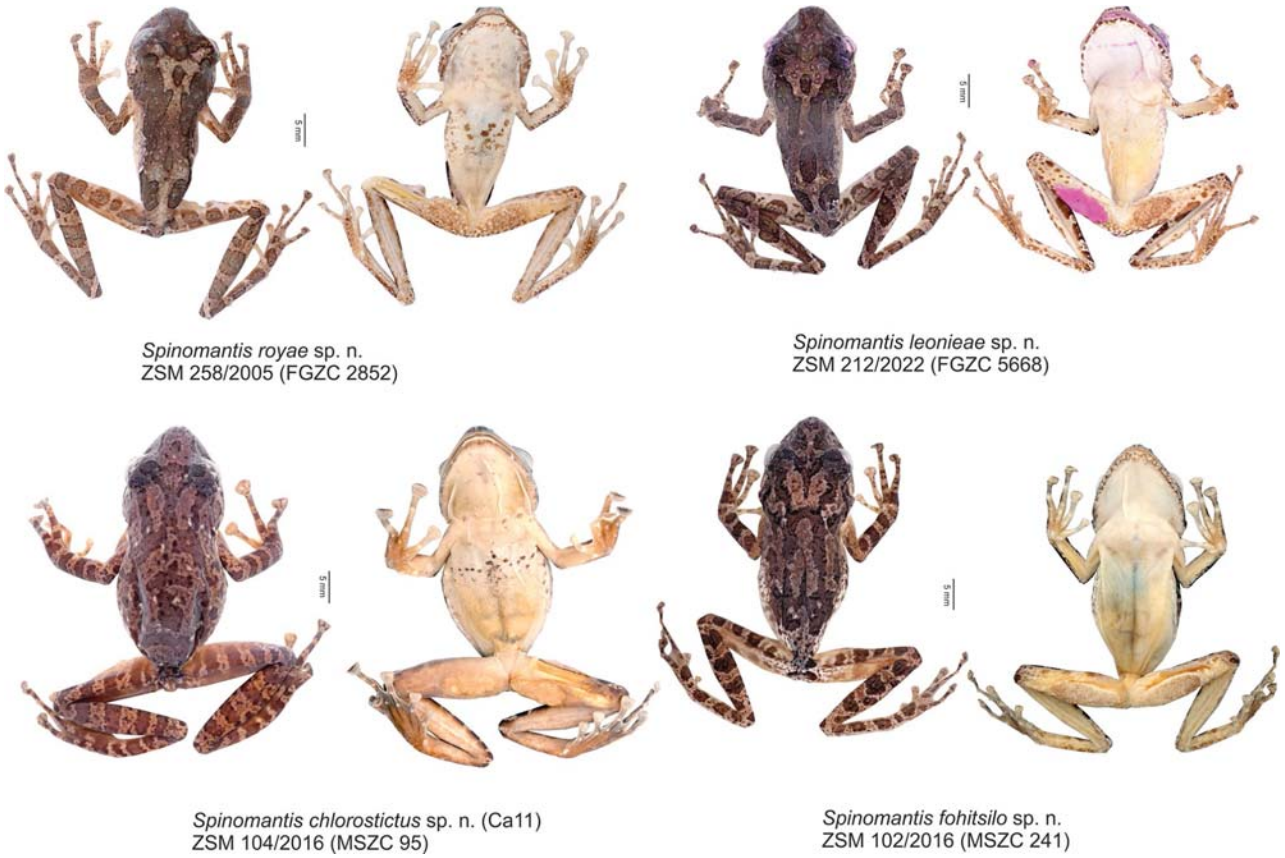

Figure 13. Preserved holotypes of the four new species of *Spinomantis* described herein in dorsal and ventral views.

canthus rostralis distinct, concave; loreal region concave; tympanum distinct, its diameter 52% of eye diameter; distinct supratympanic fold, regularly curved, bending slightly upwards behind eye, then downwards towards forelimb insertion; tongue ovoid, strongly bifid posteriorly; vomerine teeth distinct, forming a rounded aggregation posterolateral of each choana; choanae small to moderately sized, their openings rounded and connected to an elongated lateral furrow; maxillary teeth present. Forelimbs slender; subarticular tubercles distinct and single; inner metacarpal tubercle relatively small but distinct; outer metacarpal tubercle distinct, smaller than inner metacarpal tubercle; central metacarpal tubercle rounded but not very prominent. Hands with traces of webbing between fingers; relative finger length I<II<IV<III; finger discs distinctly enlarged; nuptial pads absent. Hind limbs slender; when adpressed along body, the tibiotarsal articulation reaches the center of the eye; lateral metatarsalia separated by webbing; inner metatarsal tubercle distinct, ovoid; outer metatarsal tubercle distinct, tiny and rounded; webbing formula of the foot 1(1), 2i(1.25), 2e(0.5), 3i(1.5), 3e(1), 4i(2), 4e(2), 5(1); relative toe length I<II<III<V<IV, fifth toe slightly longer than third. Skin dorsally with numerous small irregularly scattered granules; ventral skin smooth with some granulations on anterior and posterior belly and in inguinal region. No recognizable dermal flaps on heel and elbow, no dermal spines or tubercles on limbs. Femoral glands recognizable from external view, distinct and coarsely granular, consisting of many small gland granules in a very distinct area, of type 2 as defined by Glaw et al. (2000).

In preservative, dorsally brown with a poorly contrasted symmetrical pattern of dark brown patches connected to each other, forming a large marking dorsally connecting the eyes, a W-shaped marking behind the eyes, and additional patches on the posterior dorsum. In between, numerous irregular dark brown spots and small markings, and a few scattered beige spots. Flanks beige with irregular brown spotting. Ventral side uniformly cream, with a series of small brown dots on the anterior belly.

In life, similar to preservative, but on dorsal side several small irregular opaque green spots and markings. Ventrally grayish to white with dark spotting especially on chest. Femoral glands light brown. Iris dark with a beige-yellowish area in its upper third.

Variation: SVL of adult males varies between 37.9–42.3 mm; adult females have not been studied. For morphometric variation, see Table 4. The species shows a remarkable variation of color and pattern in life, with some specimens having rather indistinct dark pattern dorsally and others having more regular dark brown dorsal markings; most specimens with small or large opaque green spots or markings that sometimes cover most of the dorsum (Fig. 14). Ventral side in life grayish, with all examined specimens exhibiting at least some black spots.

Etymology: The species epithet *chlorostictus* is derived from the Greek words χλωρός (chlōrós), meaning 'green', and στικτός (stiktós), meaning 'spotted', referring to the characteristic, green-spotted coloration of this species in life. The name is an adjective in the masculine nominative singular form.

Natural history: At Antsahamanara campsite (Tsaratanana), calling males of this species were regularly heard at night from a small stream in primary rainforest. At Ampotsidy, individuals were regularly encountered along flowing streams and never encountered more than a few meters from flowing water. Males were usually found sitting in small *Pandanus* plants, seldom more than two meters above the ground. They were not found together with *Pandanus*-dwelling *Guibemantis* (which were instead always encountered in areas with slower or non-flowing water). Calling activity was mostly crepuscular and nocturnal but also coincided especially with rain. The calls (described below) were found to be so loud that they could often be heard from the open grassland ridges between tiny forest fragments in the fragmented landscape of forest around Ampotsidy at the southern edge of the Réserve de Ressources Naturelles de Mahimborondro, often together with the calls of *Gephyromantis* (*Asperomantis*) *angano.*

Vocalization: Advertisement calls of *S. chlorostictus* were recorded on 28 December 2015 at Ampotsidy (air temperature unknown) from the holotype (ZSM 104/2016, MSZC 0095). The call consists of a series of short, tonal notes, repeated at regular inter-note intervals (Fig. 6). Calls vary greatly in duration and number of notes contained. Amplitude modulation within notes is evident with the highest call energy occurring at the beginning of each note, rapidly decreasing to the middle of the note and then gradually decreasing towards its end. Frequency is distributed in a broad band with numerous harmonic frequency bands being evident. Numerical parameters of eleven analyzed calls emitted by call voucher ZSM 104/2016 are as follows: call duration 526–2417 ms (1347.9 ± 630.6 ms); notes/call 2–6 (3.8 ± 1.5); note duration 47–59 ms (53.0 ± 2.6 ms); inter-note interval 360–524 ms (415.9 ± 50.1 ms); dominant frequency 2713–2820 Hz (2771 ± 33 Hz), with a second energy peak of almost the same intensity at around 1400 Hz; prevalent bandwidth 1000–6200 Hz.

Advertisement calls recorded in February 2001 at Manarikoba Forest (air temperature 20.5 °C; CD2 Track 55 of Vences et al. 2006) agree in general characteristics with those described above from Ampotsidy, with the exception that exclusively two-note calls were recorded, with notes separated by slightly longer inter-note intervals. Numerical parameters of five analyzed calls are as follows: call duration 732–831 ms (772.0 ± 40.3 ms); notes/call 2 (2.0 ± 0.0); note duration 38–51 ms (45.6 ± 4.5 ms); inter-note interval 653–719 ms (687.8 ± 27.0 ms); dominant frequency 2784–2807 Hz (2792 ± 9 Hz); prevalent bandwidth 1000–5800 Hz.

Distribution and suggested threat status: According to genotyped samples (Fig. 2), the species is known from (1) the type locality, Ampotsidy, within the Réserve de Res-

sources Naturelles de Mahimborondro; (2) the Tsaratanana Massif, at least from Antsahamanara Campsite (Manarikoba) on the western slope of the massif, and Matsaborimaika; and (3) Ambohitantely in the central highlands. The known elevational range of the species spans from ca. 1000 m a.s.l. at Antsahamanara to ca. 2000 m a.s.l. at Matsaborimaika. All three known occurrence records are located within protected areas (Réserve de Ressources Naturelles de Ma-

Figure 14. Specimens of *Spinomantis chlorostictus* sp. n. in life, in dorsolateral and ventral views: (A–B) male holotype ZSM 104/2016 (MSZC 0095) from Ampotsidy; (C) male paratype ZSM 103/2016 (MSZC 0001) from Ampotsidy; (D–E) non-type specimen MSZC 0061 from Ampotsidy; (F) paratype UADBA-A 62298 (MSZC 0086) from Ampotsidy; (G–H, I–J, K, L), four unsexed specimens from Tsaratanana (Matsaborimaika Campsite), photos not assignable to voucher specimens; (M–N) adult male from Tsaratanana (Manarikoba), photos not assignable to voucher specimen.

himborondro, Tsaratanana Strict Nature Reserve, and Ambohitantely Special Reserve). However, in Ambohitantely, the small remaining forest fragments are threatened especially by bush fires (Andrianambinina et al. 2025), while Tsaratanana has recently witnessed high rates of deforestation (Rafanoharana et al. 2021), and Ampotsidy is part of a patchwork of diminishing rainforest fragments at the southern edge of Mahimborondro. It is uncertain whether the distribution of the species is continuous or not, but assuming a fragmented distribution, a status of Near Threatened or Vulnerable (as e.g. in *S. massi*) might be considered as adequate in a future Red List assessment of the species.

Spinomantis royae **sp. n.**
Figs 13, 15

ZooBank LSID: urn:lsid:zoobank.org:act:
A983FE16-90E0-462C-B025-533FE3FA15D4

Remark: This species was depicted as *S. fimbriatus* in Glaw & Vences (1997 and 2007: Fig. 2b on p. 207). It has not previously been considered as a separate candidate species due to the lack of genetic data. It belongs into the *aglavei* clade where it is sister to the candidate species *S.* sp. Ca14 from Befanjana, and the two lineages together are sister to a clade containing *S. aglavei, S. fimbriatus, S.* sp. Ca02, and *S.* sp. Ca09 (Fig. 4).

Holotype: ZSM 258/2005 (field number FGZC 2852), adult male, collected by F. Glaw, M. Vences and R. D. Randrianiaina on 16 February 2005 at Camp Simpona (Campsite 3), Marojejy National Park (14.43665° S, 49.74335° E, 1326 m a.s.l.), northern Madagascar.

Paratype: One specimen: ZSM 400/2016 (ZCMV 15161), female, collected by M. D. Scherz, A. Rakotoarison, M. Bletz, M. Vences and J. Razafindraibe on 17 November 2016 at Camp Simpona (Campsite 3), Marojejy National Park (14.43661° S, 49.74335° E, 1325 m a.s.l.).

Additional specimens: Three males and one female from Marojejy, collected in 1995 and listed by Glaw & Vences (1997) most likely belong to this species, but are not included in the paratype series because they have not been genotyped: ZFMK 59900, ZFMK 59926, ZFMK 59927, and ZFMK 59928.

Diagnosis: The new species is placed in the genus *Spinomantis* based on presence of intercalary elements between ultimate and penultimate phalanges of fingers and toes (verified by external examination), presence of distinct femoral glands (type 2; Glaw et al. 2000) in males, outer metatarsal tubercle present, dermal spines on tibia and tarsus, maxillary teeth present, adults living along streams in rainforests, and molecular phylogenetic relationships.

Within *Spinomantis*, it phylogenetically belongs to the *aglavei* clade and differs from all members of the *peraccae* clade (*S. chlorostictus, S. nussbaumi, S. peraccae*) by a relatively small tympanum (diameter only 34–39% of eye diameter vs. 46–59%) and presence (vs. absence) of dermal spines on tibia and tarsus. It differs from *S. phantasticus* by the absence of dorsal spines (vs. presence), from *S. massi* and *S. tavaratra* by longer dermal spines on tibia and tarsus (vs. shorter; Fig. 9), and from *S. aglavei* by smaller body size (adult SVL 34.4–36.4 mm vs. > 40 mm; see Table 4 and Glaw & Vences 1997) and presence of only about 7 dermal spines of relatively similar length on tibia and tarsus (vs. a larger number of dermal spines with alternating shorter and longer ones). Morphologically, the new species is most similar to *S. fimbriatus* but differs by slightly smaller adult body size (adult SVL 34.4–36.4 mm vs. 35.9–38.6 mm; see Table 4 and Glaw & Vences 1997), spotted ventral side (vs. usually unspotted), and presence of a distinct blue outer iris area (vs probably absent according to available data).

Advertisement calls probably belonging to the new species differ from calls of *S. fimbriatus, S. phantasticus, S. massi,* and *S. peraccae* by an entirely tonal character of notes (vs. pulsatile, or a combination of pulsatile and tonal in *S. fimbriatus*). Calls assigned to *S. royae* sp. n. furthermore differ from those of *S. aglavei* and *S. chlorostictus* by distinctly shorter call duration (180–269 vs. 526–2417 ms) (see Table 3).

Description of the holotype: Adult male in good state of preservation, with part of right thigh muscle removed for tissue sample (Fig. 13). SVL 36.4 mm, for all morphometric measurements see Table 4. Body slender; head longer than wide, wider than body; snout rounded in dorsal, ventral, and lateral views; nostrils nearer to tip of snout than to eye, protuberant and directed laterally; canthus rostralis rather indistinct and strongly concave, the whole canthal area forms an elevated ridge towards the nostril area; loreal region strongly concave; tympanum distinct, rather small, its diameter 40% of eye diameter; distinct supratympanic fold, regularly curved behind eye, then bending downwards and continuing rather straight towards forelimb insertion; tongue ovoid, strongly bifid posteriorly; vomerine teeth distinct, forming a rounded aggregation posterolateral of each choana; choanae small to moderately sized, their openings rounded and connected to an elongated lateral furrow; maxillary teeth present. Forelimbs slender; subarticular tubercles distinct and single; inner metacarpal tubercle relatively small but distinct; both central and outer metacarpal tubercles distinct, similarly sized and larger than inner metacarpal tubercle. No webbing between fingers; relative finger length I<II<IV<III; finger discs distinctly enlarged; nuptial pads absent. Hind limbs slender; when adpressed along body, the tibiotarsal articulation reaches the snout tip; lateral metatarsalia separated by webbing; inner metatarsal tubercle distinct, ovoid; outer metatarsal tubercle distinct, smaller than inner; webbing formula of the foot 1(1.5), 2i(2), 2e(1), 3i(2), 3e(1), 4i(2.5), 4e(3), 5(1.75); relative toe length I<II<V<III<IV, fifth toe shorter than third. Skin dorsally with numerous irregularly scattered granules, two pairs of spiny tubercles on the posterior head and anterior dorsum, a pair of distinct interocular tubercles; ventral skin smooth

with small granulation on belly and recognizable even on throat. No dermal flaps on elbow, but a recognizable dermal tubercle on heel which in life formed a distinct dermal spine. Tarsus with about six distinct spiny dermal tubercles which in life formed dermal spines. Femoral glands recognizable from external view, distinct and coarsely granular, consisting of many small gland granules in a very distinct area; type 2 as defined by Glaw et al. (2000).

In preservative, dorsally brown with a central symmetric beige marking forming an elongated X starting behind the eyes and running over most of the dorsum and continuing as a single broad vertebral band on the posteriormost dorsum. Flanks cream with some brown spotting. Much of tympanal area and lips light in color, partly with a slightly pinkish tone, and interrupted by a rounded brown patch anteroventrally of the eye. Limbs beige with distinct brown crossbands. Ventral side cream, with a distinct brown spotting on anterior belly and diffuse larger brown spots on throat. Color in life not documented.

Variation: See Table 4 for morphometric measurements of holotype and one paratype. Paratype ZSM 400/2016 (Fig. 15), probably a subadult female, is extremely similar to the holotype in skin texture, morphometric proportions, and color pattern, despite having been collected 11 years later. In life (Fig. 15B–C), the symmetric dorsal marking was light brown, the dark areas of the dorsum were dark olive green, with some opaque green markings. The flanks were yellowish green. The ventral side was white on throat and gray on belly, with large dark spots. The outer iris area (not recognizable on Fig. 15B but documented in other images) was light blue. Morphometric measurements of three males and one female from Marojejy probably assignable to this species were reported by Glaw & Vences (1997); SVL was 31.3–34.3 in the males and 33.2 mm in the female. One of these specimens in life also showed a distinct blue outer iris area (Fig. 15A), somewhat darker blue than in the paratype ZSM 400/2016.

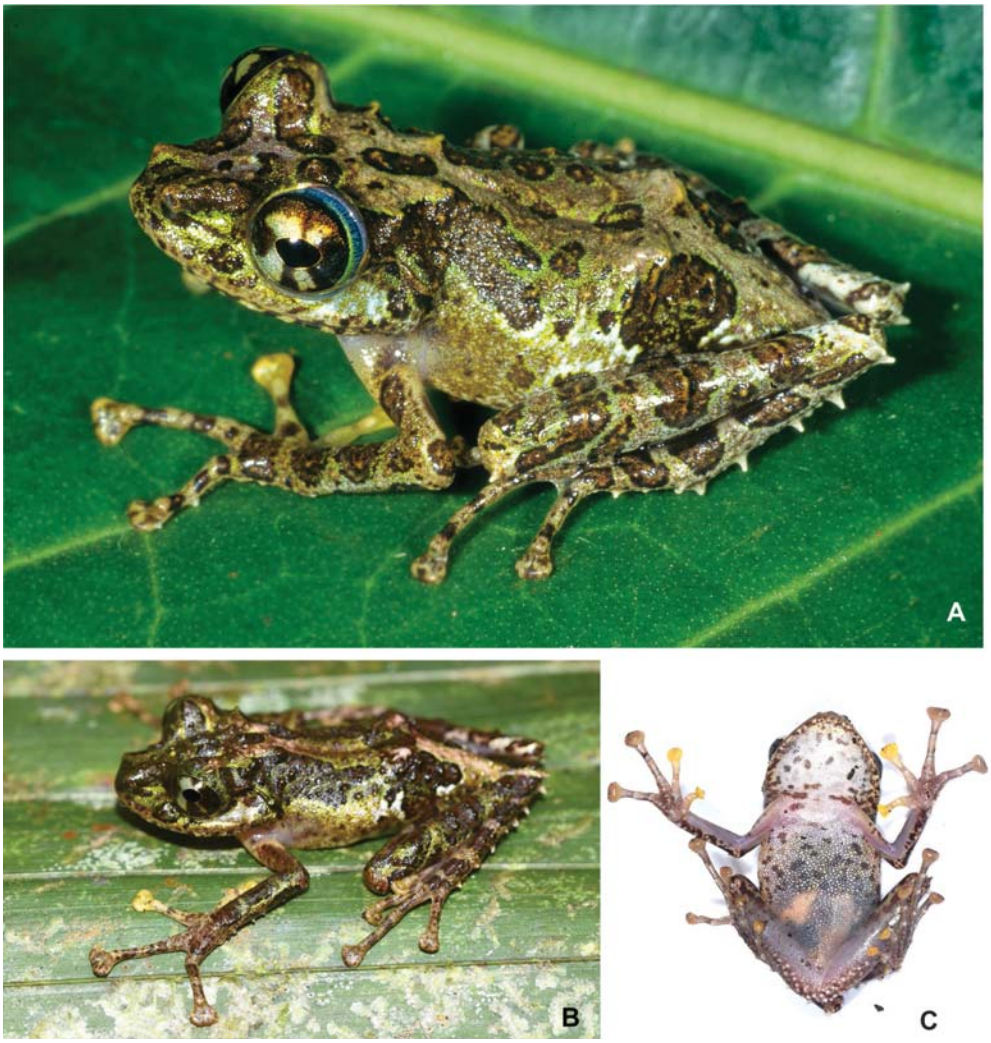

Figure 15. Specimens of *Spinomantis royae* sp. n. from Marojejy in life, in dorsolateral and ventral views: (A) specimen photographed 1995 (not genotyped and not assigned to a voucher specimen); (B–C) female paratype ZSM 400/2016 (ZCMV 15161).

Etymology: The species is dedicated to Roya Sophie Kupitz, in recognition of the support of the Kupitz family (Bünde, Germany) to biodiversity research and nature conservation in Madagascar. The epithet is the genitive singular of a first-declension feminine noun.

Natural history: Glaw & Vences (1997) reported on a female probably assignable to this species (ZFMK 59927) sitting on a fresh clutch of 12 whitish-yellowish eggs, on a leaf, ca. 2.5 m above a slowly running, swampy stretch of a brook in Marojejy, found on 26 February 1995.

Vocalization: Vocalizations that we here tentatively assign to *S. royae* sp. n. (call vouchers not collected) were recorded on 26 February 1995 at Marojejy National Park (air temperature 21.6 °C) and include two different call types (Fig. 7). One call type consists of a multi-note call of short duration with considerable modulation of temporal parameters of notes and their repetition. This call type was emitted regularly, although at irregular intervals, and we here classify it as the advertisement call. In some cases, this call type was followed by a series of 3–4 tonal notes, repeated at regular intervals. We here classify this second call type as possibly being of territorial function, given its emission during presence of other conspecific males calling.

The advertisement call is characterized by containing 5–7 notes of variable duration and emitted at rather variable intervals within the call, with the tendency of inter-note intervals to become distinctly shorter towards the end of the call. Numerical parameters of six analyzed calls are as follows: call duration 180–269 ms (210.8 ± 31.8 ms); notes/call 5–7 (6.2 ± 0.8); note duration 8–30 ms (16.4 ± 5.2 ms); inter-note interval 3–43 ms (22.7 ± 13.0 ms); dominant frequency 2292–2497 Hz (2391 ± 79 Hz); prevalent bandwidth 1700–3100 Hz.

The territorial call consists of a series of 3–4 tonal notes, repeated at relatively long intervals and usually follows an advertisement call. Numerical parameters of three analyzed call series are as follows: note duration 45–61 ms (54.0 ± 5.2 ms); inter-note interval 298–322 ms (312.2 ± 12.1 ms); dominant frequency 2383–2400 Hz (2391 ± 7 Hz).

Distribution and suggested threat status: According to genotyped samples (Fig. 2), the species is known from (1) the type locality, Marojejy; (2) the Makira Reserve, and (3) at Menamalona (15.39200° S, 50.04700° E) along the Ilampy Corridor on the Masoala Peninsula. The known elevational range spans from 510 m a.s.l. at Menamalona to 1326 m a.s.l. at "Simpona" campsite on the Marojejy Massif. All known sites are in protected areas, and extend into relatively high elevations at Marojejy, which can be assumed to be under less anthropogenic pressure than the low-elevation forests. Based on on ongoing threats in parts of its distribution area and its current distribution, which covers an area of approximately 5,000 km², it could be classified as Vulnerable under IUCN Red List criteria. Its distribution range is similar to e.g. *Boophis ulftunni*, which is likewise currently categorized as Vulnerable.

***Spinomantis leonieae* sp. n.**

Figs 13, 16

ZooBank LSID: urn:lsid:zoobank.org:act:3F128CEB-900E-4B7C-896C-EB12D90882B7

Remark: This species has been newly discovered in the framework of this study and has not been considered a candidate species previously. It belongs to the *aglavei* clade where it is sister to a clade containing *S. aglavei, S. fimbriatus, S. royae,* and the three candidate species *S.* sp. Ca02, *S.* sp. Ca09, and *S.* sp. Ca14 (Fig. 4).

Holotype: ZSM 212/2022 (field number FGZC 5668), adult male, collected by J. M. Rafanoharana, H. Raherinjatovo and F. Glaw on 22 March 2022 at Park Naturel Makira (at geographical coordinates 15.17806° S, 49.62444° E, 890 m above sea level), northern Madagascar.

Paratype: One specimen: ZSM 211/2022 (FGZC 5667), male, with same collecting data as holotype.

Diagnosis: The new species is placed in the genus *Spinomantis* based on presence of intercalary elements between ultimate and penultimate phalanges of fingers and toes (verified by external examination), presence of distinct femoral glands (type 2; Glaw et al. 2000) in males, outer metatarsal tubercle present, dermal spines on tibia and tarsus, maxillary teeth present, adults living along streams in rainforests, and molecular phylogenetic relationships.

Within *Spinomantis*, it phylogenetically belongs to the *aglavei* clade and differs from all members of the *peraccae* clade (*S. chlorostictus, S. nussbaumi, S. peraccae*) by a relatively small tympanum (its diameter only 31–39% of eye diameter vs. 46–59%) and presence (vs. absence) of dermal spines on tibia and tarsus. It differs from *S. phantasticus* by the absence of dorsal spines (vs. presence), from *S. massi* and *S. tavaratra* by longer dermal spines on tibia and tarsus (vs. shorter; Fig. 9), and from *S. aglavei* by smaller body size (adult SVL 33.9–35.3 mm vs. > 40 mm; see Table 4 and Glaw & Vences 1997) and presence of only about 7 dermal spines of relatively similar length on tibia and tarsus (vs. a larger number of dermal spines with alternating shorter and longer ones).

Morphologically, the new species is most similar to *S. fimbriatus* and *S. royae* but differs from *S. fimbriatus* by probably slightly smaller adult body size (adult SVL 33.9–35.3 mm vs. 35.9–38.6 mm; see Table 4 and Glaw & Vences 1997), and from *S. royae* by an unspotted ventral side (vs. spotted), and greenish outer iris area (vs. blue).

Advertisement calls of the new species differ from calls of all other species, except those of *S. phantasticus*, *S. chlorostictus* and *S. aglavei*, by distinctly longer call duration. Furthermore, *S. leonieae* calls differ from those of *S. fimbriatus*, *S. royae*, *S. chlorostictus*, and *S. aglavei* by a pulsatile character of notes (vs. tonal, or a combination of tonal and pulsatile in *S. fimbriatus*), from those of *S. phantasticus* by distinctly shorter note duration (7–11 vs. 42–63 ms), and

from calls of *S. peraccae* and *S. massi* by a higher number of notes per call (see Table 3).

Description of the holotype: Adult male in good state of preservation, with part of right thigh muscle and tongue removed for tissue sample and area of tissue removal stained with unknown pinkish substance which also left some pinkish spots on the throat (Fig. 13). SVL 35.3 mm, for all morphometric measurements see Table 4. Body slender; head longer than wide, wider than body; snout rounded in dorsal and ventral view, truncate in lateral view; nostrils much nearer to tip of snout than to eye, protuberant and directed laterally; canthus rostralis moderately distinct and strongly concave, the whole canthal area forms a somewhat elevated ridge towards the nostril region; loreal region concave; tympanum moderately distinct, rather small, its diameter 39% of eye diameter; moderately distinct supratympanic fold, slightly curved dorsally behind eye then bending downwards and continuing rather straight; tongue removed as tissue sample for molecular analysis; vomerine teeth distinct, forming a rounded aggregation posterolateral of each choana; choanae small to moderately sized, their openings rounded and connected to an elongated lateral furrow; maxillary teeth present. Forelimbs slender; subarticular tubercles distinct and single; inner metacarpal tubercle relatively small but distinct; central metacarpal tubercles not recognizable due to strong fixation; inner metacarpal tubercle recognizable, small. Only rudiments of webbing between fingers; relative finger length I<II<IV<III; finger discs distinctly enlarged; nuptial pads absent. Hind limbs slender; when adpressed along body, the tibiotarsal articulation reaches the nostril; lateral metatarsalia separated by webbing; inner metatarsal tubercle distinct, ovoid; outer metatarsal tubercle distinct, tiny; webbing formula of the foot 1(1.5), 2i(2), 2e(1.25), 3i(2), 3e(1.25), 4i(3), 4e(3), 5(2); relative toe length I<II<V<III<IV, fifth toe slightly shorter than third. Skin dorsally with numerous irregularly scattered granules, partly forming ridge-like patterns, and a pair of small interocular tubercles; ventral skin smooth with small granulation on belly and recognizable even on throat. No dermal flaps on elbow, but a recognizable dermal tubercle on heel which in life formed a distinct dermal spine. Tarsus with about five distinct spiny dermal tubercles which in life formed dermal spines. Femoral glands recognizable from external view, distinct and coarsely granular, consisting of many small gland granules in a very distinct area, of type 2 as defined by Glaw et al. (2000).

In preservative, dorsally brown with a pattern of large dark brown symmetrical patches: two patches start behind eyes and converge centrally without fusing; one small round marking on posterior head; one ovoid marking on

Figure 16. Specimens of *Spinomantis leonieae* sp. n. from Makira in life, in dorsolateral and ventral views: (A–B) male holotype ZSM 212/2022 (FGZC 5668); (C–D) male paratype ZSM 211/2022 (FGZC 5667).

central dorsum; two ovoid markings on posterior-most belly. Limbs beige with distinct brown crossbands. Ventral side whitish on throat, cream on chest and yellowish belly, without any dark spots; ventral sides of limbs yellowish, with dark spotting and marking on hindlimbs, and brown pigment also on femoral glands.

In life (Fig. 16A–B), the dark elements on the dorsal side were brown with an olive tint, and the lighter areas were light olive green. The brown patches on the posterior dorsum were surrounded by a light green to white line. Outer iris area greenish. Ventrally, the throat and chest are bright white and the belly rather unpigmented and of a translucent pinkish gray, without ventral spotting. White linea masculina showed clearly through the skin of the abdomen. Femoral glands brown.

Variation: For morphometric data of holotype and paratype, see Table 4. Both specimens are morphologically very similar to each other (Fig. 16). The paratype has a few dark spots on the throat.

Etymology: The species is dedicated to Leonie Maeva Kupitz, in recognition of the support of the Kupitz family (Bünde, Germany) to biodiversity research and nature conservation in Madagascar. The epithet is the genitive singular of a first-declension feminine noun.

Natural history: Both holotype and paratype were collected on a rainy night while emitting their advertisement calls from vertical perches on tree trunks or hanging leaves, 1.0–1.5 m above the ground along a small brook.

Vocalization: Advertisement calls of *S. leonieae* were recorded on 22 March 2022 at Makira (air temperature < 20 °C). The call consists of a series of very short, pulsatile click notes, repeated at long and regular inter-note intervals, but note repetition tends to become slightly faster towards the end of the call (Fig. 7). Calls vary greatly in duration and number of notes contained. In most notes, two barely separated pulses are recognizable. Numerical parameters of eleven analyzed calls emitted by at least four different males are as follows: call duration 1323–2894 ms (2164.3 ± 419.9 ms); notes/call 6–15 (11.5 ± 2.5); note duration 7–11 ms (8.2 ± 1.0 ms); inter-note interval 175–285 ms (220.0 ± 35.3 ms); dominant frequency 2386–2566 Hz (2469 ± 58 Hz); prevalent bandwidth 1400–3200 Hz.

Distribution and suggested threat status: According to genotyped samples (Fig. 2), the species is known from (1) the type locality, Makira Reserve, and (2) a site on the Masoala Peninsula (Sarahandrano, Ratsianarana). The known elevational range spans from 110 m a.s.l. at Ratsianarana to ca. 900 m a.s.l. at Makira. Both known sites are located in protected areas. More data on the species' distribution and area of occupancy are needed to decide whether it falls under a threat status of Vulnerable, or can be considered as Least Concern; we therefore suggest it should be assessed as Data Deficient at present.

***Spinomantis fohitsilo* sp. n.**

Figs 13, 17

ZooBank LSID: urn:lsid:zoobank.org:act:6192916E-CC72-4F8E-8352-BE404C693B1E

Remark: This species has been newly discovered in the framework of this study and has not been considered a candidate species previously. It belongs to the *massi* clade and is sister to the clade containing *S. massi* and *S. phantasticus* (Fig. 4).

Holotype: ZSM 102/2016 (field number MSZC 0241), adult male, collected by M. D. Scherz and M. Rakotondratisma on 17 January 2016 at Andranonafindra forest (30 km SW of Bealanana on the RN31; 14.73607° S, 48.54902° E, 1157 m above sea level), northern Madagascar.

Paratypes: Two specimens: UADBA-A 52263 (MSZC 0206), adult male, collected at the type locality by same collectors as holotype, on 14 January 2016 and at precise coordinates 14.73569° S, 48.5481° E, 1169 m a.s.l.; UADBA-FGZC 5548, juvenile, collected near the summit of Maromiandra Mountain (elevation 700–800 m a.s.l.), approximate geographical coordinates 13.00° S, 48.22° E, on 9 April 2019 by J. Razafindrabe, A. Razafimanantsoa and F. Glaw.

Diagnosis: The new species is placed in the genus *Spinomantis* based on presence of intercalary elements between ultimate and penultimate phalanges of fingers and toes (verified by external examination), presence of distinct femoral glands (type 2; Glaw et al. 2000) in males, outer metatarsal tubercle present, dermal spines on tibia and tarsus, maxillary teeth present, adults living along streams in rainforests, and molecular phylogenetic relationships.

Within *Spinomantis*, it phylogenetically belongs to the *massi* clade and differs from all members of the *peraccae* clade (*S. chlorostictus, S. nussbaumi, S. peraccae*) by a relatively small tympanum (its diameter only 40% of eye diameter vs. 46–59%) and presence (vs. absence) of dermal spines on tibia and tarsus.

It differs from *S. phantasticus* by the absence of dorsal spines (vs. presence); from *S. aglavei* by presence of only short dermal spines on tibia and tarsus (vs. a larger number of dermal spines with alternating shorter and longer ones); from *S. fimbriatus, S. leonieae* and *S. royae* by larger body size (SVL 43.0 vs. < 40 mm) and short dermal spines on tibia and tarsus (vs. few but relatively long spines), and furthermore from *S. royae* by an unspotted venter (vs. spotted); from *S. tavaratra* by larger body size (SVL 43.0 mm vs. < 40 mm), more distinct dermal spines on tibia and tarsus (Fig. 9) and femoral gland with more and smaller gland granules covering almost the entire shank ventrally (vs. fewer and larger granules, and only covering part of shank; Fig. 10).

Morphologically, the new species is most similar to *S. massi* but reaching larger body size (SVL 43.0 mm vs. 33.6–42.1 mm; Table 1) and having a smaller tympanum (TD/ED ratio 40% vs. 43–51%).

Advertisement calls of *S. fohitsilo* differ from those of *S. fimbriatus, S. phantasticus, S. massi, S. leonieae* and *S. peraccae* by containing notes of entirely tonal character (vs. pulsatile, or a combination of pulsatile and tonal in *S. fimbriatus*). Furthermore, the calls of *S. fohitsilo* differ from those of *S. phantasticus, S. fimbriatus, S. royae, S. leonieae* and *S. aglavei* by a lower number of notes per call (3 vs. 5–14 notes/call), and from those of *S. aglavei*, *S. phantasticus*, *S. chlorostictus* and *S. peraccae* by distinctly shorter note duration (see Table 3).

Description of the holotype: Adult male in excellent state of preservation, with part of left thigh muscle removed for tissue sample (Fig. 13). SVL 43.0 mm, for all morphometric measurements see Table 4. Body slender; head longer than wide, similar in width to body; snout rounded in dorsal, ventral, and lateral views; nostrils nearer to tip of snout than to eye, protuberant and directed laterally; canthus rostralis rather indistinct and strongly concave, the whole canthal area forms an elevated ridge towards the nostril area; loreal region strongly concave; tympanum distinct, rather small, its diameter 40% of eye diameter; distinct supratympanic fold, curved upwards behind eye, then bending downwards and continuing rather straight towards forelimb insertion; tongue ovoid, strongly bifid posteriorly; vomerine teeth distinct, forming a rounded aggregation posterolateral of each choana; choanae small to moderately sized, their openings rounded and connected to an elongated lateral furrow; maxillary teeth present. Forelimbs slender; subarticular tubercles distinct and single; inner metacarpal tubercle relatively small but distinct; central metacarpal tubercles indistinct, rounded; outer metacarpal tubercle distinct, similar in size to inner. Very rudimentary webbing between fingers, barely recognizable; relative finger length I<II<IV<III; finger discs distinctly enlarged; nuptial pads absent. Hind limbs slender; when adpressed along body, the tibiotarsal articulation reaches the center of the eye; lateral metatarsalia separated by webbing; inner metatarsal tubercle distinct, ovoid; outer metatarsal tubercle distinct, similar in size to inner; webbing formula of the foot 1(0.5), 2i(1.5), 2e(0.75), 3i(1.5), 3e(0.75), 4i(2), 4e(2.5), 5(1); relative toe length I<II<V<III<IV, fifth toe slightly shorter than third. Skin dorsally with numerous irregularly scattered granules, two pairs of large (but not spiny) tubercles on the posterior head and anterior dorsum, a pair of small interocular tubercles; ventral skin smooth with small granulations on belly. No dermal flaps on elbow, but a recognizable small dermal tubercle on heel which in life formed a distinct dermal spine. Tarsus with a few barely recognizable dermal tubercles (in life, about eight small dermal spines were visible on tarsus and about three dermal tubercles on foot). Femoral glands recognizable from external view, distinct and coarsely granular, consisting of many small gland granules in a very distinct area, of type 2 as defined by Glaw et al. (2000).

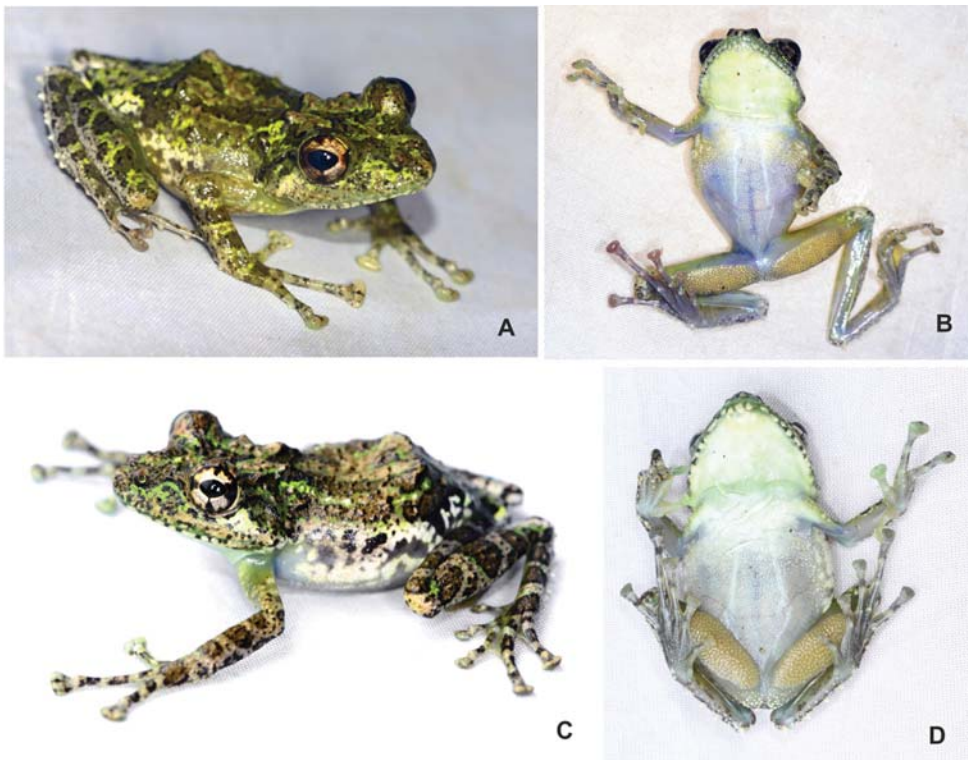

Figure 17. Specimens of *Spinomantis fohitsilo* sp. n. from Andranonafindra in life, in dorsolateral and ventral views: (A–B) male holotype ZSM 102/2016 (MSZC 0241); (C–D) male paratype UADBA-A 62253 (MSZC 0206).

In preservative, dorsally light brown with a darker brown central symmetric beige marking forming an elongated X starting behind the eyes and running over most of the dorsum and fusing on the posteriormost part of the dorsum. Numerous smaller dark brown spots and markings scattered in between these large markings. Flanks marbled with irregular white markings. Limbs beige with distinct brown crossbands. Ventral side cream on belly to whitish on throat, without any dark spots.

In life (Fig. 17A–B), the dark elements on the dorsum were dark olive green and the lighter elements were light green. Brown pigment was present within some of the light olive patches, and the posterior flanks had light beige color. Ventrally without spots; the throat was white with a greenish tint, belly unpigmented bluish-pinkish gray. Femoral glands light brown. White linea masculina showed clearly through the skin of the abdomen.

Variation: No morphometric data are available for the paratypes. From the available photos, the paratype UADBA-A 62253 (MSZC 0206) agrees well with the holotype in its dorsal color pattern, unspotted venter and large femoral glands.

Etymology: The species epithet is a noun in apposition derived from Malagasy 'fohi-' (diminutive prefix for 'short') and 'tsilo' (spine). It refers to the short dermal spines on tarsus and tibia of this species.

Natural history: The holotype was collected after recording its call, from a perch on a liana ca. 3 m above the ground, during light rain. It was several meters up a very steep slope from a narrow stream below. Paratype UADBA-A 62253 (MSZC 206) was collected on a leaf ca. 1 m above the ground, calling close to a flat area of stream in the middle of the valley. Both were collected in the degraded rainforest fragment of Andranonafindra (see Distribution and suggested threat status, below).

Vocalization: Advertisement calls of *S. fohitsilo* from the holotype (ZSM 102/2016, MSZC 0241) were recorded on 17 January 2016 (19:55 h) at Andranonafindra (air temperature not recorded). The call consists of three short, simple click notes, which are tonal in character and are repeated in rapid succession at regular inter-note intervals (Fig. 8). The terminal note of each call is slightly longer in duration compared to the first two notes of the call. There is slight amplitude modulation within notes, with maximum call energy present at the beginning of each note. Numerical parameters of eight analyzed calls of the holotype are as follows: call duration 119–133 ms (124.4 ± 4.7 ms); notes/call 3 (3.0 ± 0.0); note duration 7–21 ms (12.7 ± 3.6 ms); inter-note interval 41–46 ms (42.8 ± 1.5 ms); dominant frequency 2573–2598 Hz (2587 ± 13 Hz); prevalent bandwidth 1650–3400 Hz, with a second frequency peak at around 7900 Hz. In this respective recording, calls were repeated at an approximate rate of 1.3 calls/minute.

Distribution and suggested threat status: According to genotyped samples (Fig. 2), the species is known from (1) the type locality, Andranonafindra forest; and (2) Maromiandra forest fragment. The known elevational range is between 700–800 m a.s.l. at Maromiandra to 1157 m a.s.l. at Andranonafindra. Both known sites are small, unprotected or poorly protected forest fragments which are under high anthropogenic pressure, but the species is likely to occur in the adjacent Manongarivo reserve. In 2016, Andranonafindra had sites of active charcoal burning and logs stacked near the path, showing ongoing intensive harvesting, and lay directly below a carved road used to bring heavy mining equipment and vehicles up to the sites south of Route National 31. The species was not seen or heard in other forest fragments (which were mostly less intact than the Andranonafindra fragment) between Ampandrana (14.7113° S, 48.5788° E) and the Bealanana-Antsohihy border (14.7489° S, 48.4907° E) during rapid surveys in 2016. Under the current state of knowledge, the species could be assigned a threat status of Critically Endangered, but given the uncertainty of occurrence in Manongarivo, Data Deficient might be appropriate in this case.

Discussion

Although rarely encountered by tourists, the genus *Spinomantis* includes some of the most charismatic and fascinating anurans from Madagascar. The bizarre morphology of some species such as *S. aglavei* and *S. phantasticus*, which probably represents bark or moss mimesis and makes these frogs very hard to spot during the day; as well as their loud and typical "metallic" calls, which shape the nocturnal soundscape in prominent ecotouristic sites such as Ranomafana; make them an emblematic component of Madagascar's rainforest ecosystems. We have here presented a first assessment of genetic, morphological and bioacoustic variation in arboreal *Spinomantis*, confirming and widening the evidence for the existence of many scientifically unnamed lineages and candidate species. Despite the formal description of four new species, and the definition of three additional candidate species, our study does not provide a full taxonomic understanding of arboreal *Spinomantis* but provides a baseline to better understand which data are missing and inform future field campaigns and taxonomic revisions.

From a biogeographic perspective, our data support a clade containing most of the saxicolous species occurring in the South East and Southern Central East of Madagascar. One further species and one candidate species (*S. elegans* and *S.* sp. Ca08, both from the Southern Central East), split from the successive nodes to the arboreal clade, although the respective nodes were poorly supported (Fig. 4). In the arboreal clades, most of the species splitting from the basalmost nodes (*S. tavaratra, S. fohitsilo, S. nussbaumi,* and *S.* sp. Ca13) occur in northern Madagascar. Taken together, our data suggest a geographical and ecomorphological dichotomy in the genus with a predomi-

nantly southern saxicolous group and an arboreal group that originated and initially diversified in northern Madagascar. In this scenario, some of the arboreal taxa (*S. peraccae, S. aglavei, S.* sp. Ca02) would have secondarily colonized the Southern Central East of the island. To formally analyze this pattern, to compare it with other amphibians of either northern or southern centers of diversification in Madagascar (e.g., Wollenberg et al. 2008, Kaffenberger et al. 2012, Miralles et al. 2023), and to hypothesize on the underlying processes, a more complete knowledge of the taxonomy, morphology and distribution of several poorly known lineages of *Spinomantis* is needed.

Herein, we used a "museomics" approach to clarify the genetic identity of *S. fimbriatus*, by a simple shotgun-sequencing approach of genomic DNA and reconstructing mitochondrial barcode sequences for its holotype. But the identity of most other species of arboreal *Spinomantis* needs confirmation, too. In the *peraccae* clade, we have here assigned the nomen *S. peraccae* to the sole lineage known from the geographic area encompassing its type locality, "Ivohimanita". This site, probably corresponding to Ivohimanitra visited by the collector Charles Forsyth Major, is located NE of Fianarantsoa and in the country of the Tanala of Ambohimanga, according to Major's reports (see Jenkins & Carleton 2005), and thus somewhat north of Ranomafana. Nevertheless, we cannot exclude that *S.* sp. Ca13, also known from the Northern Central East, may also have its range extending into the same region. For *S. nussbaumi,* we have here assigned specimens from Sorata to this species due to morphological similarities, but the type locality of the species is in the Tsaratanana Massif (Befosa River–Antetikalambazaha, 14°10'27" S, 48° 56'42" E, 1650 m a.s.l.; Cramer et al. 2008), where two other morphologically similar lineages occur (herein named *S.* sp. Ca05 and *S.* sp. Ca10); with the limited data at hand, we cannot exclude that one of these lineages corresponds to *S. nussbaumi,* in which case the Sorata population would be an unnamed candidate species. For *S. massi*, we here assume that the genotyped individuals from Tsaratanana and Manongarivo are conspecific with those from the geographically close type locality Benavony, but given the existence of the related species *S. fohitsilo* at sites slightly further south, a confirmation of this assignment would improve taxonomic clarity. Lastly, the identity of *S. aglavei* appears to be clear based on its type locality (Analamazaotra close to Andasibe) and similarly that of its synonym *Rhacophorus sikorae* (Moramanga, in the same region) (Table 1), but should be confirmed, given the occurrence of several deep conspecific lineages in the wider geographical area (e.g., Ambohitantely and Sahafina). For all these species, obtaining DNA sequences from type specimens via museomics approaches would be a crucial step for further taxonomic revision of the genus.

To target future fieldwork on *Spinomantis*, we here point to three geographical regions that should be prioritized. First, the Marojejy Massif encompassed by Marojejy National Park is comparatively well accessible and is home to two largely unknown lineages of the *peraccae* clade (*S.* sp. Ca04 and *S.* sp. Ca15; Fig. 3), whose taxonomic and conservation status can only be clarified with new field collections of adult specimens. Furthermore, also at Marojejy, new material of *S. royae* with call recordings reliably assignable to genotyped vouchers would be very useful to verify its bioacoustic differentiation from related species. Second, the area around Andasibe (including sites such as Maromizaha and Vohidrazana) is easy to access and exceptionally species-rich (Vieites et al. 2009), and characterized by co-occurrence of several lineages of *Spinomantis* of uncertain status. For instance, new collections and call recordings of *S. peraccae* and *S.* sp. Ca13 in this area would allow one to conclusively determine their possible morphological and bioacoustic differentiation and clarify the possible status of the latter as a distinct species. Similarly, in the same area, sympatric occurrence of *S. fimbriatus* and *S.* sp. Ca09 is known (Fig. 3), incentivizing a focus on collecting new material from these lineages there. Third, the Tsaratanana Massif is difficult to access but harbors a high richness especially of lineages of the *peraccae* clade, and new material from this massif will be needed to clarify the status and distribution of *S. nussbaumi, S.* sp. Ca05, and *S.* sp. Ca10. In addition, new collections in the Masoala Peninsula will be instrumental to clarify the status of *S.* sp. Ca03 in the *peraccae* clade, and new collections in Ranomafana National Park are needed to clarify the taxonomy of *S.* sp. Ca02 in the *aglavei* clade.

The *Spinomantis* example illustrates the enormous amount of yet unexplored amphibian diversity in Madagascar, and the need of further field exploration, including the collection of voucher specimens and of bioacoustic data, to complete the herpetofaunal inventory of the island.

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Supplementary data

The following data are available online:

Supplementary documents. Full distance matrix: https://doi.org/10.5281/zenodo.18020638.