Article

Taxonomizing a truly morphologically cryptic complex of dwarf geckos from Madagascar: molecular evidence for new species-level lineages within the *Lygodactylus tolampyae* complex

MIGUEL VENCES[1,*], MALTE MULTZSCH[1], MILENA ZERBE[1], SVEN GIPPNER[1], FRANCO ANDREONE[2], ANGELICA CROTTINI[3,4,5], FRANK GLAW[6], JÖRN KÖHLER[7], SANDRATRA RAKOTOMANGA[8], SOLOHERY RASAMISON[8] & ACHILLE P. RASELIMANANA[8,9]

[1]*Zoologisches Institut, Technische Universität Braunschweig, Mendelssohnstr. 4, 38106 Braunschweig, Germany.*
✉ *m.multzsch@tu-braunschweig.de;* 🔘 *https://orcid.org/0000-0002-7189-0755*
✉ *milenazerbe@outlook.com;* 🔘 *https://orcid.org/0009-0008-4995-9243*
✉ *s.gippner@tu-braunschweig.de;* 🔘 *https://orcid.org/0000-0003-2621-1001*
[2]*Museo Regionale di Scienze Naturali, Via G. Giolitti, 36, 10123 Torino, Italy.*
✉ *franco.andreone@regione.piemonte.it;* 🔘 *https://orcid.org/0000-0001-9809-5818*
[3]*CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, 4485-661 Vairão, Portugal.*
[4]*Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, 4099-002 Porto, Portugal.*
[5]*BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, 4485-661 Vairão, Portugal.*
✉ *tiliquait@yahoo.it;* 🔘 *https://orcid.org/0000-0002-8505-3050*
[6]*Zoologische Staatssammlung München (ZSM-SNSB), Münchhausenstr. 21, 81247 München, Germany.*
✉ *glaw@snsb.de;* 🔘 *https://orcid.org/0000-0003-4072-8111*
[7]*Hessisches Landesmuseum Darmstadt, Friedensplatz 1, 64283 Darmstadt, Germany.*
✉ *joern.koehler@hlmd.de;* 🔘 *https://orcid.org/0000-0002-5250-2542*
[8]*Mention Zoologie et Biodiversité Animale, Université d'Antananarivo, BP 906, Antananarivo, 101 Madagascar.*
✉ *sandratrapro@gmail.com;* 🔘 *https://orcid.org/0009-0005-1825-9226*
✉ *soloherivelona@gmail.com;* 🔘 *https://orcid.org/0000-0002-8415-962X*
[9]*Association Vahatra, Lot V A 38 LBA Ter Ambohidempona Tsiadana, BP 3972, Antananarivo, 101 Madagascar.*
✉ *raselimananaachille@gmail.com;* 🔘 *https://orcid.org/0000-0003-1610-7307*
*Corresponding author. ✉ *m.vences@tu-braunschweig.de;* 🔘 *https://orcid.org/0000-0003-0747-0817*

Abstract

The *Lygodactylus tolampyae* complex includes several deep genetic lineages of small diurnal geckos from the West and North West of Madagascar whose taxonomy is largely unsolved. We sequenced DNA fragments of one mitochondrial and four nuclear-encoded genes for up to 70 samples across the entire known range of these geckos. We find as many as 11 mitochondrial lineages differentiated by >4% pairwise distances in the 16S rRNA gene fragment, with >9% pairwise distance for the majority of lineage comparisons. Many of these lineages were concordantly differentiated in all of the nuclear-encoded genes without any haplotype sharing, despite the syntopic occurrence of some of them. We therefore hypothesize that the complex contains seven candidate species, but a comprehensive taxonomic resolution is complicated by various hindrances. These include incomplete sampling, with two lineages each known only from a single specimen, and one further lineage with no voucher specimens available for examination. Further hurdles are the probably lost holotype of *L. tolampyae* and its imprecise type locality, as well as the apparent lack of any morphological differentiation between the majority of the genetic lineages. Based on a survey of historical literature and the travel routes of the original collector, A. Grandidier, we conclude that the provenance of the holotype of *L. tolampyae* is likely in the wider Morondava area in the West and assign the sole candidate species from this area to this name. We then proceed to describe three species that represent separate genetic lineages for all markers studied: *Lygodactylus morii* **sp. nov.**, a species common in Ankarafantsika National Park and several nearby sites in the North West; *L. herilalai* **sp. nov.**, a species occurring in close syntopy with *L. morii* in Ankarafantsika without any signal of genetic admixture; and *L. schwitzeri* **sp. nov.** from Sahamalaza Peninsula in the North West. This leaves three more lineages without a name and with the need to gather additional samples, two from Namoroka National Park and one from other sites in the North West. We confirm the *L. tolampyae* complex to be an apparently rare example of truly cryptic reptile species in Madagascar, where even detailed

morphological examination does not reveal morphological differences among lineages that are clearly evolutionarily independent and require recognition as distinct species due to their co-occurrence without admixture.

Introduction

Cryptic species are usually defined as genetically distinct species-level lineages that are morphologically very similar to each other or indistinguishable (e.g., Saéz & Lozano 2005), but sometimes more generally as two or more distinct species that are classified as a single species (Bickford *et al.* 2007). Beyond terminological questions, it is clear that the actual degree of reduced phenotypic disparity in cryptic species requires testing (Struck & Cerca 2019) and that some species considered morphologically similar can in fact be distinguished once their morphology is reassessed in light of the genetic evidence (e.g., Korshunova *et al.* 2019). One such group are dwarf geckos of the genus *Lygodactylus*, which encompass a puzzling diversity of species as it has recently been documented by Gippner *et al.* (2021). In a recent revision of the Madagascar-endemic subgenus *Domerguella*, the conventional characters typically used to differentiate *Lygodactylus* species, such as numbers of postmental scales, scansors under teeth, labials, or precloacal pores, failed to diagnose the majority of species whereas the inclusion of additional, time-consuming longitudinal counts of dorsal and ventral scales enabled Vences *et al.* (2022) to establish morphological diagnoses of eight new species. Also in African *Lygodactylus* species complexes (e.g., Marques *et al.* 2020; Lobón-Rovira *et al.* 2023) careful morphological comparisons typically revealed diagnostic differences between species. However, as discussed by Glaw *et al.* (2021) for Malagasy treefrogs of the genus *Boophis*, some lineages might be genuinely "cryptic" in that even with sophisticated methods and detailed analyses, a clear-cut morphological delimitation is impossible.

Next to *Domerguella*, the analysis of Gippner *et al.* (2021) pointed to a second group of dwarf geckos in Madagascar that contains a substantial amount of genetic variation: The *Lygodactylus tolampyae* complex, a species complex within the *L. verticillatus* group (clade B of Gippner e*t al.* 2021), was found to consist of four deeply divergent genetic lineages that these authors named as *L. tolampyae, L.* sp. 14 aff. *tolampyae*, *L.* sp. 15 aff. *tolampyae*, and *L.* sp. 25 aff. *tolampyae*. However, the morphology of these lineages remained unassessed and no in-depth analysis of the distribution and ecology of these geckos has been carried out so far.

Lygodactylus tolampyae was described as *Hemidactylus tolampyae* Grandidier, 1872 based on the holotype specimen MNHN 7636. In the original description, the type locality was given as "Forêts de la côte ouest". Subsequent accounts (e.g., Mocquard 1909, Angel 1942) did not provide any additional information on collecting circumstances, locality, or year of collection. Grandidier travelled extensively in the wider Morondava region in 1869 and 1870 (Monnier 2017), but he also carried out a voyage to the North West of Madagascar: according to Grandidier (1893), he travelled "de Mojanga à Antananarivo, en longeant la vallée du Betsiboka" ("Mojanga" probably referring to the current Mahajanga), and according to Monnier (2017), this voyage took place in 1869, although the respective maps in Grandidier (1893) illustrate a voyage from Ambatotokana to Marovoay in 1869, which may correspond to the same trip. However, apparently no new reptile species descriptions originated from material collected during this trip in the North West. Grandidier (1872) did not describe any other reptile species with *verbatim* the same type locality as *L. tolampyae*, but several other species were described from western Madagascar: *Furcifer antimena* ("Côte occidentale de Madagascar"), *F. labordi* ("Côte occidentale de Madagascar"), *Madascincus mouroundavae* ("Mouroundava" = Morondava), *Madatyphlops arenarius* ("Mouroundava" = Morondava), *Euprepes sakalava* (junior synonym of *Trachylepis elegans*; from "Malaimbandy pays des Sakalaves", a locality wrongly attributed to the gerrhosaurid *Zonosaurus aeneus* in the past: see Brygoo 1985a,b; Vences *et al.* 1996). Malaimbandy is located in the central West (E of Morondava) as well, and therefore, Grandidier's (1872) work did not report on any species or specimen from the North West of Madagascar. It can therefore be concluded that an origin of the holotype of *L. tolampyae* from the central west coast, likely from the wider Morondava region, is most plausible.

Here, we undertake a comprehensive analysis of all samples and voucher specimens of the *Lygodactylus tolampyae* complex available to us at this time, integrating both molecular and morphological data. Our goal is to provide an initial taxonomic revision of this species complex, which required dealing with species-level lineages that turned out to partly occur in sympatry without genetic admixture but could not be diagnosed by any meristic or morphometric character.

Materials and methods

Sampling

Specimens were collected opportunistically in the wild between 2000 and 2022, especially during the night when sleeping individuals can be easily spotted at the outermost parts of small twigs, leaves or small branches. Voucher specimens were euthanized using injection of an overdose of the anesthetic MS222, ketamine, or saturated solution of chlorotone, or by application of lidocaine cream in the oral cavity. Tissue samples, usually leg muscle or a part of an autotomized tail, were preserved in 99% ethanol or EDTA buffer, and specimens fixed in 95% ethanol or 3% formalin, and subsequently preserved in 80% ethanol after removing formalin solution by rinsing with water. From some individuals, small autotomized tail tips were preserved as tissue samples, and individuals were subsequently released. The field numbers ACZC, APR, FAZC, FGMV, FGZC, MVTIS, and ZCMV correspond to the field series of Angelica Crottini, Achille P. Raselimanana, Franco Andreone, Frank Glaw, and Miguel Vences, respectively.

Morphology was examined mainly from genotyped voucher specimens deposited in the herpetological collections of the Zoologische Staatssammlung München (ZSM), Museo Regionale di Scienze Naturali di Torino (MRSN), and the Mention Zoologie et Biodiversité Animale of the University of Antananarivo (UADBA). Comparative material was studied from the collections of the Muséum National d'Histoire Naturelle, Paris (MNHN), Naturmuseum Senckenberg, Frankfurt am Main (SMF). Specimens in the UADBA collection are in many cases not provided with final catalogue numbers due to lack of curatorial resources, but are identifiable by their field number tags; we therefore report these specimens as UADBA-APR (for specimens with APR field numbers) and UADBA-ZCMV (for specimens with ZCMV field numbers). A few scale counts were taken from photos of individuals that were released after sampling.

Molecular methods

The molecular data set used in this study is based on the *Lygodactylus* DNA sequences compiled by Gippner *et al.* (2021) but expanded with sequences of numerous additional markers and a substantial number of new samples to achieve a reliable species delimitation in the *L. tolampyae* complex.

DNA was extracted using a standard salt-extraction protocol (Bruford *et al.* 1992). We base our analysis on one mitochondrial marker, a fragment of the 16S rRNA gene (16S), and four nuclear-encoded markers: fragments of the genes for oocyte maturation mos (CMOS), recombination-activating gene 1 (RAG1; two separate non-overlapping fragments named B and V), prolactin receptor (PRLR) and leucine-rich repeat and WD repeat-containing protein (KIAA1239). Amplifications were carried out using standard and nested polymerase chain reactions (PCRs). Primers and cycling conditions are listed in Supplementary Tables S1 and S2 (available from Zenodo repository: DOI: 10.5281/zenodo.8208843). Reaction mixes contained 1 µl template DNA, 0.25 µl of 10 µM dNTPs, 0.3 µl of each 10 µM Primer, 2.5 µl Colorless 5x GoTaq Reaction Buffer, and 0.1 µl GoTaq G2 DNA Polymerase (5 U/µl) in a total volume of 12.5 µl. Nucleotide debris was removed by adding 2.4 µl ExoSAP to 8 µl PCR product (Bell 2008).

Sequencing of purified PCR products was conducted on capillary sequencers by LGC Biosearch Technologies in Berlin, Germany. CodonCode Aligner 6.0.2 (CodonCode Corporation) was utilized to verify sequence quality of chromatograms and stretches of poor read quality were removed. New sequences were submitted to GenBank (accession numbers: PP456881–PP457119 and PP466876–PP466900). A table with all sequences used and their accession numbers, as well as the tree files and alignments, are available from the Zenodo repository (DOI: 10.5281/zenodo.8208843).

Phylogenetic analyses and allele sharing

DNA sequences were aligned using the Muscle option in MEGA7 (Kumar *et al.* 2016). A Maximum Likelihood tree of all available 16S sequences of the *L. tolampyae* complex was reconstructed in RaxML (Stamatakis 2014) using raxmlGUI v. 2.0 (Edler *et al.* 2020), under a General Time Reversible model (GTR+G) based on the Bayesian Information Criterion from a model testing analysis performed in MEGA7, and testing node support with 500

thorough bootstrap replicates. Pairwise genetic distances were calculated from the 16S alignment using TaxI2 (Vences *et al.* 2021), based on an alignment from which sequences with large numbers of missing data were removed (except for two divergent lineages for which only one sequence each was available, and these were maintained despite large stretches of missing data in the beginning; see Results). Species partitions were inferred using ASAP (Puillandre *et al.* 2021), and the favored ASAP partition was subsequently compared for concordance with differentiation in the nuclear genes. Diagnostic positions in the 16S rRNA alignment (given relative to the full 16S rRNA gene sequence of *Phelsuma guimbeaui*; accession number AB661664: Kumazawa *et al.* 2014) were determined using MolD (Fedosov *et al.* 2022) as implemented in iTaxoTools (Vences *et al.* 2021); for the MolD analysis, only sequences of lineages assigned to *L. tolampyae* and the three new species described herein were included, as for most other lineages only single and sometimes short sequences were available.
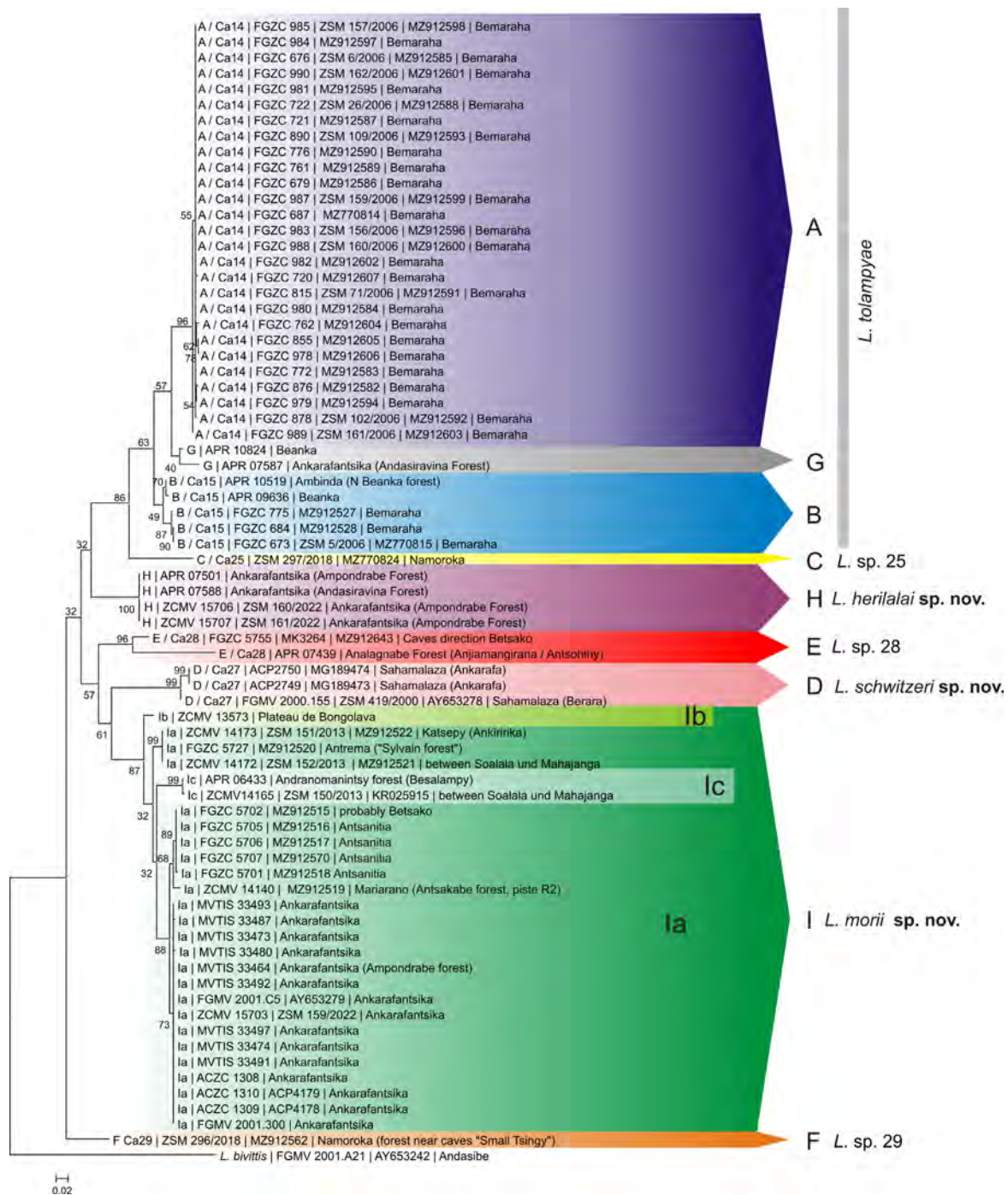
FIGURE 1. Maximum Likelihood tree calculated from DNA sequences of the mitochondrial 16S rRNA gene (alignment length: 517 bp) for 70 samples of the *L. tolampyae* complex. A sample of *L. bivittis* was used as outgroup. Numbers are bootstrap support values in percent (500 replicates). Clades are defined on the basis of an analysis with ASAP.
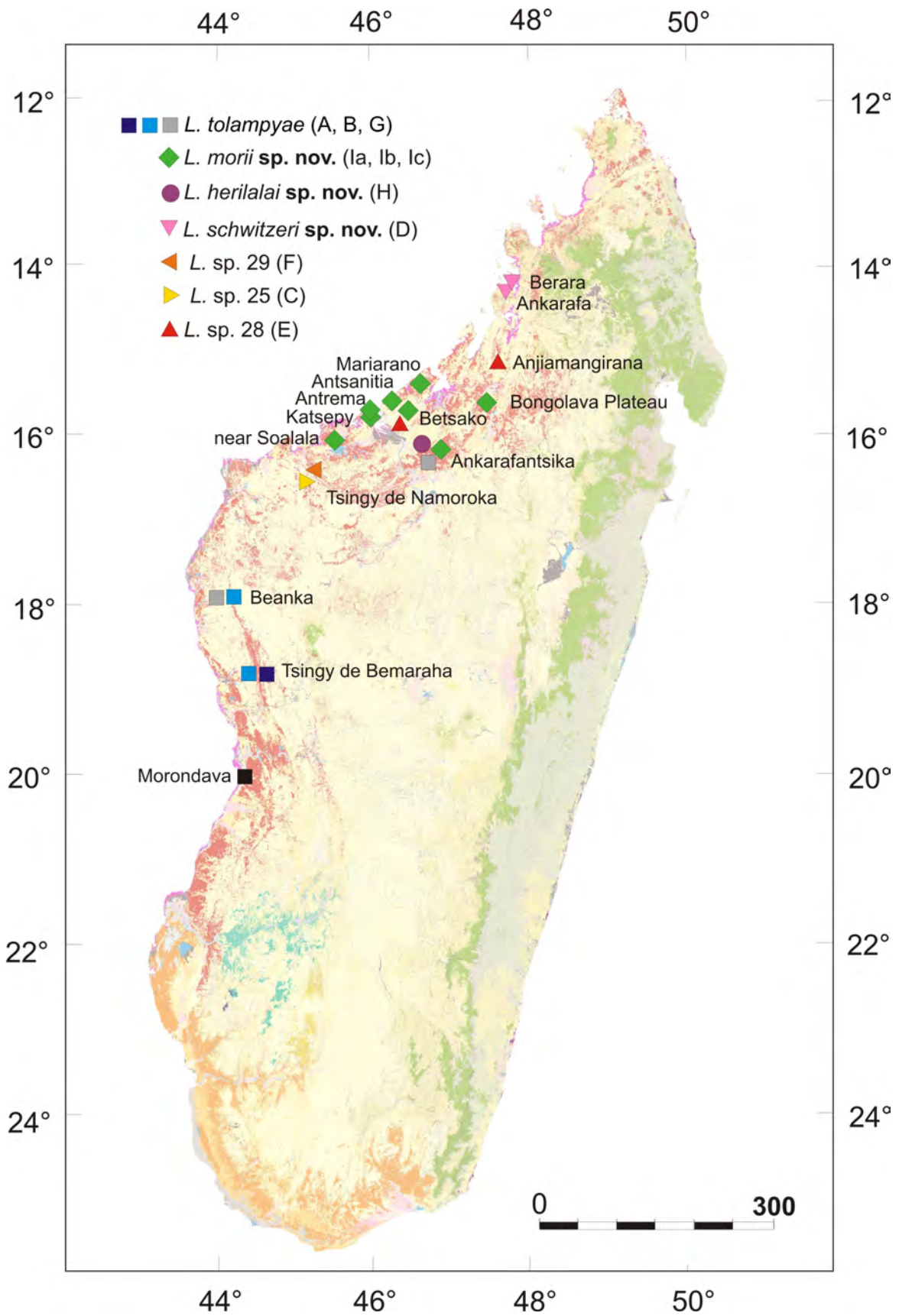
FIGURE 2. Map of Madagascar with genetically confirmed sampling localities of the *Lygodactylus tolampyae* complex. Colours correspond to those used for mitochondrial lineages. The black square marks the town Morondava from which no samples were analyzed; it is likely that the type locality of *L. tolampyae* is located in the wider Morondava area.
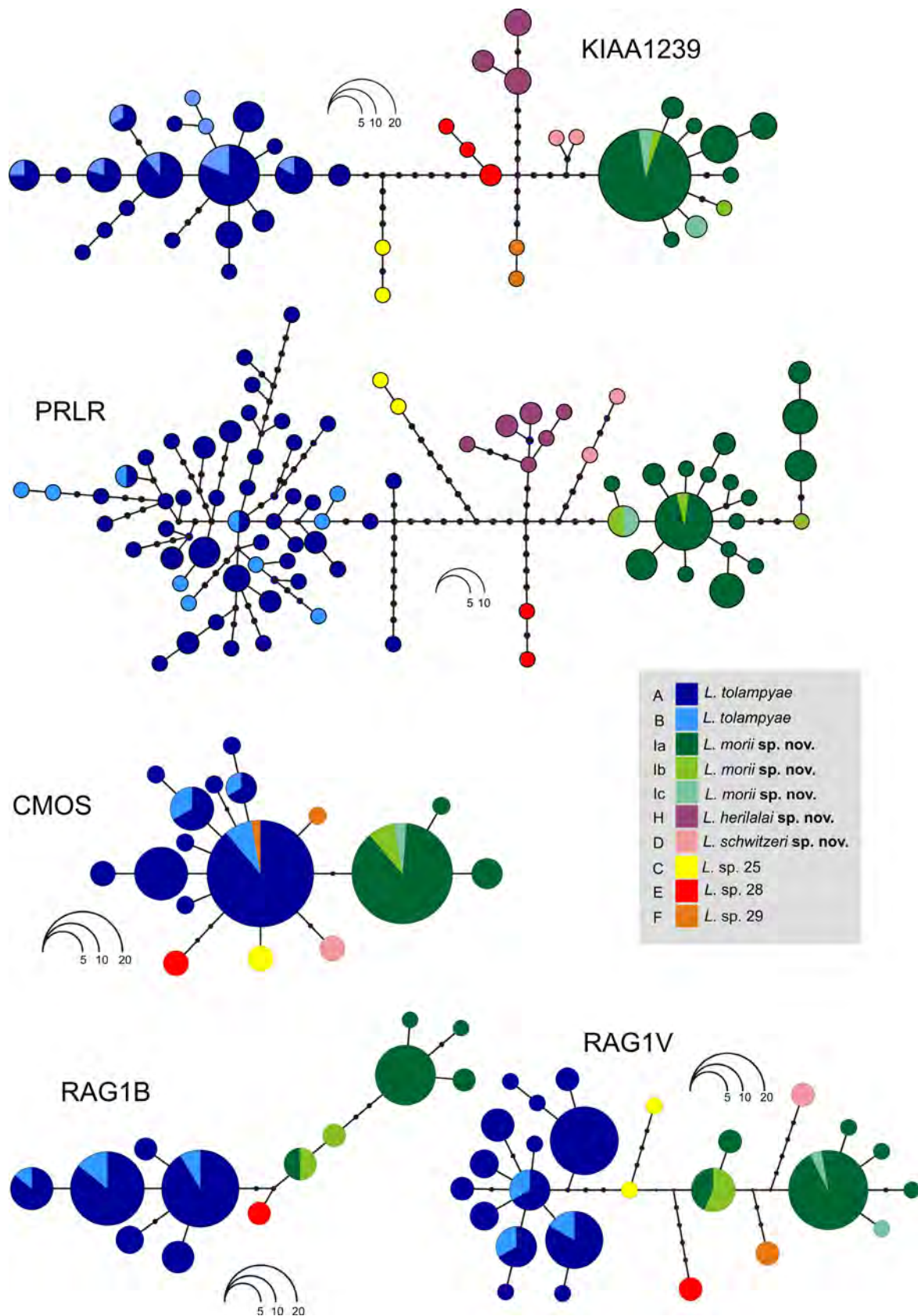
FIGURE 3. Haplotype networks calculated from phased sequences of five nuclear-encoded protein-coding gene fragments (including two non-overlapping fragments of the RAG1 gene analyzed separately) for samples of the *L. tolampyae* complex. Based on alignments of 834 bp for 68 samples (KIAA1239), 466 bp for 65 samples (PRLR), 318 bp for 51 samples (CMOS), 307 bp for 43 samples (RAG1-B), and 818 bp for 52 samples (RAG1-V). Colours correspond to those used for mitochondrial lineages of the respective samples.

We chose to graphically represent the relationship among alleles (haplotypes) of the nuclear-encoded genes separately as haplotype networks. For this, alleles were inferred from the sequences with heterozygous positions (double peaks) using the PHASE algorithm (Stephens *et al.* 2001) implemented in the software DnaSP (Version 5.10.3; Librado & Rozas 2009). The phased sequences were then used to reconstruct Maximum Likelihood trees with the Jukes-Cantor substitution model with uniform rates in MEGA7 (Kumar *et al.* 2016). We chose this simple model to avoid overparametrization. These trees were then used together with the respective alignments as input for Haploviewer (written by G. B. Ewing; http://www.cibiv.at/~greg/haploviewer), a software that implements the methodological approach of Salzburger *et al.* (2011).

Morphological characters

We largely followed the selection of morphological characters assessed to be informative in another subgroup of Malagasy *Lygodactylus* by Vences *et al.* (2022). The following morphometric measurements were taken to the nearest 0.1 mm with a caliper: snout–vent length (SVL); tail length (TAL), measured from cloaca to tip of tail; head width (HW), measured at the broadest part of the head; hind limb length (HIL), measured from the hind limb insertion to the tip of the longest toe (claw excluded); eye diameter (ED); snout tip to ear distance (SED). In addition, for the comparison of two closely related species that we suspected differed in head shape, we measured for a subset of well-preserved individuals snout-tympanum distance (STD; from snout tip to center of tympanum), and head height (HH; from ventral limit of the lower jaw to upper limit of the center of the supraocular bulge). Meristic data included: number of precloacal pores in males (PCL); number of postmental scales (PM); number of post-postmental scales (PPM); number of supralabial scales (SUPL); number of infralabial scales (INFL); number of internasal scales (IN); number of dorsal scales along the body (LCDS), from the first scale after the internasals to the first scale row or whorl of the tail; longitudinal count of the number of ventral scales (LCVS), from the mental scale to the cloaca; presence and size of spiny tubercles at the tail base (STT): 0 not visible, 1 small, 2 medium-sized, 3 large-sized. Furthermore, the following additional characters were assessed/verified in each specimen: number of subdigital lamellae on the fourth toe (FtoeL), from the tip of the toe to the first undivided lamellae on fourth toe; presence of tail whorls (WHORL); number of dorsolateral tubercles between limbs (NDT); number of scales in each dorsolateral tubercle (NSDT); presence of miniaturized series of vertebral scales, as characteristic for *L. expectatus* (mVertS); granular or keeled shape of dorsal scales (DS); presence of first finger (Ffin); presence of a claw on first finger (CFFin); divided, semi-divided, or undivided mental scale (MS); extent of posterior contact between mental and first infralabial scale (PMS); symmetry of postmental scales (SPMS). Statistical tests (non-parametric Mann-Whitney U-tests) for selected pairwise comparisons of potentially diagnostic variables were carried out in Jamovi v. 2.3.28 (The Jamovi project 2023).

Hemipenial structures were not examined, as only a few voucher specimens with everted hemipenes were available.

Species delineation and associated terminology

Species delineation herein follows the general lineage concept (de Queiroz 1998, 2007), but demanding a "soft" biological species criterion to be fulfilled: reproductive isolation, i.e., restricted gene flow among lineages (as e.g., Speybroeck *et al.* 2020). As a proxy for ascertaining this condition, we apply a genealogical concordance species criterion (Avise & Ball 1990) between mitochondrial and nuclear loci, especially in populations occurring in sympatry or close geographical proximity (see also Avise & Wollenberg 1997), along with concordance between genetic and morphological evidence (Padial *et al.* 2010). We here use the term "lineage" to refer to genealogical lineages at or below the species level, and "clade" to refer to monophyletic groups with reference to a phylogenetic tree. We refer to geographic regions of Madagascar as originally defined by Boumans *et al.* (2007) primarily on the basis of major river basins, not on bioclimatic or biogeographical grounds: North, Sambirano, North East, North West, Northern Central East, West, Central, Southern Central East, South East, and South. These regions are consistently written in upper case. Some other general geographical descriptions, such as "central highlands" or "east coast", do not refer to well-defined regions and just indicate general geographical position; they are consistently written in lower case. We furthermore followed Brown *et al.* (2016) in defining 'northern Madagascar' as an area roughly delimited by a diagonal spanning from 15.5°S on the east coast to ca. 15.0°S on the west coast.

Results

Molecular differentiation in the *L. tolampyae* complex

The 16S alignment contained 70 ingroup sequences plus one outgroup sequence (*L. bivittis*) for a total of 517 bp. A Maximum Likelihood tree calculated under the best-fitting GTR+G model (Fig. 1) revealed substantial genetic variation across samples of the *L. tolampyae* complex, with several lineages newly identified in addition to the four deep lineages already recovered by Gippner *et al.* (2021). To subdivide the high amount of genetic variation encountered in a more objective way, we relied on the preferred species partition suggested by ASAP, based on the lowest ASAP score of 3.5, which contained 12 ingroup subsets. In one case two individuals were clustered by ASAP at separate places of the guide tree and thus assigned to two different subsets but placed in a monophyletic group in the ML tree (lineage E, see below), and thus we group them together in one subset. We thus consider a total of 11 subsets which we here name with capital letters A–H and Ia, Ib and Ic. Of these subsets, A–F correspond to the candidate species identified by Gippner *et al.* (2021) as *Lygodactylus* sp. 14, 15, 25, 27, 28, and 29, respectively; G–H correspond to two lineages newly discovered in the present study; and Ia–Ic correspond to samples falling into the definition of *L. tolampyae* in Gippner *et al.* (2021).

Genetic divergences among samples were high. Uncorrected pairwise distances for 16S (summarized in Table 1) were >9% for the majority of comparisons between ASAP-defined lineages, with the following exceptions: 4.3–6.4 for comparisons between lineages A, B, and G, and 3.6–6.5 between lineages Ia, Ib and Ic. Very high values were observed comparing lineage E and, especially, lineage C with the others. The highest value of 17.8% characterized a comparison between lineage C and D. This almost certainly can be explained by an inflation of distance values in all comparisons of lineages C as well as lineage E due to an overrepresentation of hypervariable 16S stretches in the respective comparisons due to large stretches of missing data in the single sequences available for these two lineages. Although some of the lineages were geographically restricted, sympatry and even close syntopy between several of them was noted (Fig. 2).

The haplotype networks of the five nuclear gene fragments CMOS (alignment length 318 bp, sequences of 51 samples included), RAG1-B (307 bp, 43 samples), RAG1-V (818 bp, 52 samples), PRLR (466 bp, 65 samples), and KIAA1239 (834 bp, 68 samples) largely coincided in that most lineages identified from the mitochondrial data lacked haplotype sharing and formed coherent separate phylogroups (Fig. 3).

Lineages A and B together were represented by multiple individuals in all haplotype networks; especially for lineage A, numerous sequences were available. In all cases, A+B samples formed a distinct haplogroup separated from all other lineages and shared haplotypes in all gene fragments. No nuclear-encoded sequences were available for lineage G (related to A+B based on mitochondrial data). Lineages C, D and F were represented in the nuclear DNA dataset by only single samples each, but these had alleles separate from all other lineages in every network (except RAG1-B, where these lineages were not represented). Lineage E, also represented by 1–2 samples only, had unique haplotypes in CMOS (not included in the network because the sequence was shorter than most others, but it differed by three mutations), RAG1-B, RAG1-V, PRLR, and KIAA1239. Lineage G, newly identified in this study, was represented by only two samples which could not be sequenced for any of the nuclear gene fragments, and its nuclear DNA divergence thus remains unstudied. Lineage H, also newly identified in this study, was included only in the PRLR and KIAA1239 haplotype networks and formed a distinct haplogroup in both, differing by numerous mutations from all other included samples. Finally, lineage Ia was represented by multiple individuals in all networks and formed a cluster that, in all cases, was distinctly separate from lineages A–F. For lineages Ib and Ic, only a few sequences were available; we detected haplotype sharing between Ib/Ic and Ia in all networks where these lineages were included.

Morphological differentiation in the *L. tolampyae* complex

A comparison of morphological characters revealed extremely few indications for differentiation among the genetic lineages of the *L. tolampyae* complex. For a selection of measurements and scale counts, see Table 2; a table with all data taken is available from the Zenodo repository (DOI 10.5281/zenodo.8208843).

TABLE 1. Uncorrected pairwise distances between and within ASAP-determined lineages of the *Lygodactylus tolampyae* complex (mean with minimum and maximum in parentheses) calculated from DNA sequences of the 16S rRNA gene fragment sequenced.

	A	B	C	D	E	F	G	H	Ia	Ib	Ic
A (*L. tolampyae*)	0.3 (0.0–1.0)										
B (*L. tolampyae*)	5.7 (5.0–6.4)	1.0 (0.0–1.6)									
C (*L.* sp. 25)	12.8 (12.5–13.3)	10.8 (10.7–11.0)	NA								
D (*L. schwitzeri* **sp. nov.**)	14.0 (13.9–14.5)	14.3 (13.7–14.7)	17.8 (17.8–17.8)	0.8 (0.0–1.3)							
E (*L.* sp. 28)	13.6 (13.3–14.0)	12.2 (12.0–12.3)	17.0 (17.0–17.0)	11.6 (11.6–11.6)	NA						
F (*L.* sp. 29)	12.6 (12.1–13.0)	10.4 (9.7–11.1)	9.8 (9.8–9.8)	10.8 (10.8–10.8)	9.9 (9.9–9.9)	NA					
G (*L. tolampyae*)	5.2 (4.3–6.2)	4.9 (4.5–5.8)	11.6 (11.3–11.9)	14.8 (14.3–15.2)	12.6 (12.3–12.9)	11.1 (10.6–11.6)	3.0 (3.0–3.0)				
H (*L. herilalai* **sp. nov.**)	13.8 (13.1–15.0)	11.7 (11.1–12.9)	13.7 (13.7–13.7)	13.3 (12.9–13.4)	12.6 (12.3–13.4)	10.3 (10.3–10.3)	11.7 (10.8–12.9)	0.1 (0.0–0.2)			
Ia (*L. morii* **sp. nov.**)	13.0 (12.1–14.5)	12.6 (11.4–14.3)	15.5 (13.8–16.1)	12.0 (11.6–13.1)	10.6 (10.1–11.6)	10.3 (9.5–10.4)	12.8 (11.8–14.3)	11.4 (10.1–12.5)	1.7 (0.0–4.4)		
Ib (*L. morii* **sp. nov.**)	12.7 (12.5–13.1)	11.7 (11.6–12.0)	15.8 (15.8–15.8)	10.3 (10.3–10.3)	11.0 (11.0–11.0)	9.0 (9.0–9.0)	12.4 (12.2–12.6)	11.5 (11.2–12.3)	4.9 (3.6–5.5)	NA	
Ic (*L. morii* **sp. nov.**)	13.6 (12.9–14.6)	12.9 (12.2–13.7)	14.9 (14.9–14.9)	12.3 (11.8–12.8)	12.4 (12.0–12.8)	9.4 (9.4–9.4)	13.1 (11.9–14.2)	12.1 (11.3–12.9)	5.6 (4.8–6.5)	5.9 (5.7–6.1)	0.2 (0.2–0.2)

TABLE 2. Selected morphometric and meristic data for voucher specimens of *Lygodactylus tolampyae* lineages examined for this study. All morphometric measurements (SVL, TAL, HIL, HW, ED, and SED) are in mm. Abbreviations are those described in the Materials and Methods section; additional abbreviations and symbols are as follows: NA, not assessed or not applicable; * specimen not genotyped; ** tail broken or incomplete; *** tail regenerated. HT, holotype; PT, paratype; LT, lectotype. For a full set of measurements and counts, see table in the Zenodo repository (DOI: 10.5281/zenodo.8208843).

Specimen voucher	16S clade	Field number	Locality	Type status	Sex	SVL	TAL	HIL	HW	ED	SED	PPM	INFL	SUPL	IN	PCL	LCDS	LCVS
L. tolampyae																		
SMF 8948 (*tuberifer*)	*	NA	Menabé	LT	M	32.2	35.1***?	15.1	5.6	2.4	8.0	5–6	7	8	2?	6–7	224	103
ZSM 5/2006	B	FGZC 673	Bemaraha		F	31.2	30.9	16.1	5.9	2.0	7.7	5	5–6	6–7	2	0	230	105
ZSM 6/2006	A	FGZC 676	Bemaraha		F	30.2	37.7**	14.5	6.1	2.0	7.8	6	7	8	2	0	232	103
ZSM 26/2006	A	FGZC 722	Bemaraha		M	27.8	3.4**	13.9	5.7	1.9	7.3	5	6	7	2	8	233	104
ZSM 70/2006	*	FGZC 814	Bemaraha		F	32.2	10.2**	15.0	5.8	1.8	7.7	5	6	7	2	0	230	111
ZSM 71/2006	A	FGZC 815	Bemaraha		F	29.0	30.2***	13.0	5.6	1.9	7.5	4	6	7	3	0	234	107
ZSM 102/2006	A	FGZC 878	Bemaraha		F	31.9	28.2***	13.8	5.9	1.9	7.6	5	6	7	2	0	232	100
ZSM 109/2006	A	FGZC 890	Bemaraha		F	31.3	35.4	16.1	6.6	1.6	7.7	5	5–6	6	2	0	222	104
ZSM 156/2006	A	FGZC 983	Bemaraha		F	27.4	31.8	12.9	5.1	1.6	7.0	5	6	8	2	0	228	105
ZSM 158/2006	*	FGZC 986	Bemaraha		M	27.1	33.4**	12.8	5.7	2.0	7.4	5	6	8	1	7	229	103
ZSM 159/2006	A	FGZC 987	Bemaraha		F	30.1	22.7**	14.4	5.5	1.7	7.8	5	5	7	2	0	204	105
ZSM 160/2006	A	FGZC 988	Bemaraha		F	30.3	33.7	14.9	5.7	1.8	7.4	5	6	6	2	0	239	107
ZSM 161/2006	A	FGZC 989	Bemaraha		M	27.6	15.8**	13.3	5.4	1.8	7.1	6	6	6	2	7	221	93
ZSM 162/2006	A	FGZC 990	Bemaraha		F	29.0	31.7	14.1	5.7	1.9	7.4	5	6	6	2	0	241	115
UADBA-APR 7587	G	NA	Ankarafantsika (Andasiravina)		F	27.2	**	NA	5.3	1.8	7.5	5	7	7	1–2	0	NA	94
L. morii **sp. nov.**																		
ZSM 501/2001	Ia	FGMV 2001.300	Ankarafantsika (Ampijoroa)	HT	M	29.4	4.3**	15.3	5.5	2.1	7.7	7	6	8	2	7	245	102
ZSM 152/2013	Ia	ZCMV 14172	Katsepy, Ankiririka	PT	M	28.7	31.8	12.8	5.7	1.9	7.2	3–5	6	6–7	1	6	261	103
ZSM 151/2013	Ia	ZCMV 14173	between Soalala and Mahajanga	PT	F	32.8	30.6	14.1	5.7	2.0	7.6	5	6	7	2	0	256	105
ZSM 224/2018	Ia	FGZC 5701	Antsanitia	PT	F	28.7	3.4**	12.6	5.4	2.0	7.5	6	5	7	1	0	232	110
ZSM 225/2018	Ia	FGZC 5705	Antsanitia	PT	F	31.6	28.3**	14.1	5.9	2.1	8.0	6	7	8	1	0	269	121
ZSM 226/2018	Ia	FGZC 5706	Antsanitia	PT	F	29.5	30.5**	14.8	5.6	1.9	7.5	5	6	7–8	1	0	253	107
ZSM 159/2022	Ia	ZCMV 15703	Ankarafantsika (Ampijoroa)	PT	M	NA	NA	NA	NA	NA	NA	5	7	7	2?	6	247	104

......Continued on the next page

TABLE 2. (Continued)

Specimen voucher	16S clade	Field number	Locality	Type status	Sex	SVL	TAL	HIL	HW	ED	SED	PPM	INFL	SUPL	IN	PCL	LCDS	LCVS
UADBA-ZCMV 15704	Ia	ZCMV 15704	Ankarafantsika (Ampijoroa)	PT	F	NA	NA	NA	NA	NA	NA	5	NA	NA	2	0	237	98
UADBA-ZCMV 15705	Ia	ZCMV 15705	Ankarafantsika (Ampijoroa)	PT	F	NA	NA	NA	NA	NA	NA	5	NA	NA	1	0	225	100
ZSM 227/2018	Ia	FGZC 5727	Antrema ("Sylvain forest")	PT	F	30.2	33.0	17.7	5.6	2.0	8.2	6	6	7	1	0	260	112
ZSM 491/2001	*	NA	Ankarafantsika		F	32.1	14.3***	14.7	5.9	1.9	7.9	5	7	8	2	0	247	101
ZSM 502/2001	*	FGMV 2001.301	Ankarafantsika (Ampijoroa)		M	28.2	5.1**	14.9	5.4	2.0	7.2	6	6	8	1	6	243	104
ZSM 503/2001	*	FGMV 2001.305	Ankarafantsika (Ampijoroa)		F	31.8	31.6	14.4	5.8	2.1	7.7	5	7	8	2	0	234	102
ZSM 150/2013	Ic	ZCMV 14165	between Soalala and Mahajanga		M	29.4	32.5	15.1	5.9	2.0	7.6	3–5	5	6	2	6	262	104
MVTIS 33401 / 33473	Ia	NA	Ankarafantsika (Ampijoroa)		F	NA	NA	NA	NA	NA	NA	5	NA	NA	2	0	237	94
MVTIS 33402 / 33488	Ia	NA	Ankarafantsika (Ampijoroa)		M	NA	NA	NA	NA	NA	NA	5	NA	NA	2	6	241	99
MVTIS 33403 / 33491	Ia	NA	Ankarafantsika (Ampijoroa)		M	NA	NA	NA	NA	NA	NA	5	NA	NA	2	6	242	99
MVTIS 33404 / 33493	Ia	NA	Ankarafantsika (Ampijoroa)		F	NA	NA	NA	NA	NA	NA	5	NA	NA	2?	0	231	105
MVTIS 33405 / 33487	Ia	NA	Ankarafantsika (Ampijoroa)		M	NA	NA	NA	NA	NA	NA	5	NA	NA	1	6	246	96
MVTIS 33406 / 33492	Ia	NA	Ankarafantsika (Ampijoroa)		M	NA	NA	NA	NA	NA	NA	5	NA	NA	2?	6–7	239	93
MVTIS 33407 / 33497	Ia	NA	Ankarafantsika (Ampijoroa)		F	NA	NA	NA	NA	NA	NA	6	7	8	1?	0	245	103
MVTIS 33408 / 33480	Ia	NA	Ankarafantsika (Ampijoroa)		M?	NA	NA	NA	NA	NA	NA	5	NA	NA	1	6?	256	98

L. schwitzeri **sp. nov.**

TABLE 2. (Continued)

Specimen voucher	16S clade	Field number	Locality	Type status	Sex	SVL	TAL	HIL	HW	ED	SED	PPM	INFL	SUPL	IN	PCL	LCDS	LCVS
ZSM 419/2000	D	FGMV 2000.155	Berara (Anabohazo)	HT	F	28.1	2.8**	15.1	5.4	1.8	7.1	5	7	8	2	0	240	102
MRSN R1913	*	FAZC 10496	Sahamalaza, Berara	PT	M	30.6	33.0**	16.3	6.0	2.0	7.6	5	7	8	NA	6	271	111
MRSN R1914	*	FAZC 10498	Sahamalaza, Berara	PT	M	29.9	34.3**	14.8	6.4	2.2	7.9	5	6	7	2–3	6?	252	117
MRSN R1915	*	FAZC 10499	Sahamalaza, Berara	PT	M	26.3	11.6**	13.8	5.2	1.7	7.2	6	7	8	NA	6	258	113
MRSN R1916	*	FAZC 10501	Sahamalaza	PT	M	27.3	29.7	14.1	5.7	1.3	7.6	5			NA	6	267	112
MRSN R1917	*	FAZC 10503	Sahamalaza, Berara	PT	F	30.7	28.4	15.8	5.6	1.7	7.7	5	7	8	NA	0	254	110
MRSN R1918	*	FAZC 10504	Sahamalaza	PT	F	29.7	23.2**	14.3	5.2	1.4	7.6	5	NA	NA	NA	0	241	107
MRSN R1921	*	NA	Sahamalaza, Berara	PT	M	28.0	27.3**	14.2	5.9	1.7	7.9	5	6	7	NA	6	252	102
MRSN R1922	*	NA	Sahamalaza, Berara	PT	F	29.9	27.1**	14.0	5.0	1.5	6.7	5	6	7	NA	0	255	103
L. herilalai **sp. nov.**																		
ZSM 161/2022	H	ZCMV 15707	Ankarafantsika (Ampondrabe)	HT	F	31.0	31.6	13.7	5.9	1.9	7.9	5	6	7	1	0	243	98
ZSM 160/2022	H	ZCMV 15706	Ankarafantsika (Ampondrabe)	PT	M	NA	NA	NA	NA	NA	NA	5	NA	NA	1?	6	229	105
UADBA-APR 7501	H	NA	Ankarafantsika (Ampondrabe)	PT	M	24.4	**	NA	5.0	1.9	6.5	5	7	9	1–2	6?	NA	103
UADBA-APR 7588	H	NA	Ankarafantsika (Andasiravina)	PT	M	31.0	**	NA	5.8	2.4	8.4	5	7	9	1–2	6	262	106
L. sp. 25																		
ZSM 297/2018	C	NA	Namoroka		F	29.4	32.7	18.6	4.9	1.5	7.3	5	6	6	3	0	238	115
L. sp. 29																		
ZSM 296/2018	F	NA	Namoroka		F	17.8	18.8	9.1	3.8	1.1	5.3	5	6–7	6–7	2	0	224	104

Colour pattern (Fig. 4–10) showed a rather large variation within lineages, without obvious differences between lineages in dorsal or ventral colour. According to photos in life, specimens of lineage A+B had reddish-copper colour in the inner part of the iris (Fig. 4) which was less distinct in photos of individuals of the other lineages (Fig. 5–8), but it is unknown to what extent this might represent a true diagnostic character.

All individuals examined from all lineages had the combination of character states deemed to be diagnostic for *L. tolampyae*: granular (non-keeled) dorsal scales, tail without whorls, males with 6 (rarely 7–8) precloacal pores, first finger present (typically with a claw), three subdigital lamellae on fourth toe, semi-divided mental scale, three symmetric postmentals (Fig. 11), 4–6 post-postmentals, 6–7 infralabials, 6–9 supralabials (Fig. 12), dorsolateral tubercles (between limbs) usually absent, but exceptionally up to 6 such tubercles visible. The variation observed in these characters was found within every lineage for which a sufficient number of specimens was measured. Possible differences between clades were: a claw on the first finger was visible on all individuals examined except for 5 out of 13 individuals of lineage A+B, possibly indicating a tendency in that lineage towards claw reduction (although it cannot be excluded that the claw was lost during climbing in these specimens); posterior contact between the mental scale and the first infralabial scale was assessed as broad in 11 out of 14 specimens of lineage A (and in the only two available individuals of lineages B, C, and F), but as intermediate between broad and narrow in at least half of the specimens in lineages D, H, and I; the number of internasal scales was 2–3 in almost all individuals of lineages A+B, C, and F, but only a single internasal scale was recorded in 9 out of 19 specimens of lineage I. Lastly, despite overlap in values, a tendency towards low longitudinal counts of dorsal scales was detected in lineages A+B, C, and F (204–241), while this number appears to be overall higher in lineages D (240–271), I (225–269), and possibly also H (229–262). Differences in the number of dorsals were statistically significant in several pairwise comparisons with sufficiently large sample sizes (see Diagnoses below). Despite a high within-lineage variation, the longitudinal count of ventral scales might also be somewhat higher in lineage D (102–117) than in lineage I, where values <100 were recorded from 7 out of 19 specimens. Due to low sample sizes and lack of data for several genetic lineages, we did not carry out a comprehensive statistical analysis of morphometric and meristic intra- and inter-lineage differences; such analyses will be presented in a forthcoming study that will include additional material from ongoing field surveys.

Identity of *Lygodactylus tolampyae* (Grandidier, 1872)

The holotype specimen of *Hemidactylus tolampyae* Grandidier, 1872 (MNHN 7636) unfortunately appears to be missing from the MNHN collection and is likely to be lost. According to the MNHN catalogue and online database, it has not been found since an inventory of the collection in 1983. This agrees with Brygoo (1990), who stated that the specimen had not been found during a search in 1983 and mentioned that the presence of the type had been reported by Angel (1942) and Guibé (1954).

Furthermore, reliable information on the holotype is relatively scarce. Only little morphological information (not even body size) is given by Grandidier (1872) in the original description. Mocquard (1895) only mentions the type but provides no further relevant information. Mocquard (1909) provides the first detailed description: *"Queue non distinctement annelée. Ecailles médianes sous-caudales agrandies et formant une série régulière. Narine ouverte au-dessus de la suture entre la rostrale et la première supéro-labiale. 3 écailles entre les naso-rostrales. Mentonnière presque complètement tripartite, la partie médiane bordée en arrière par 3 postmentonnières. 6 pores préanaux."*

This description is highly informative regarding the identity of *L. tolampyae* as it probably is based (also) on examination of the holotype (apparently only one further individual assigned to the species was available in the Paris museum at that time: MNHN 1899.344 from "Environs de Suberbieville, Boeny" in the North West), and thus confirms that (very probably) the holotype was characterized by several key character states that are currently seen to be typical for this species: (i) a non-verticillated tail (= without whorls); (ii) a mental scale semi-divided by a suture; and (iii) three postmental scales. Unfortunately, the description does not mention the broad contact of the posterior projection of the mental scale with the first infralabial scale, which is considered to be diagnostic for *L. tolampyae* (Puente *et al.* 2009). However, the data allow us to exclude conspecificity of the *L. tolampyae* holotype with other species commonly occurring in the West and South West of Madagascar (*L. verticillatus*: tail with distinct whorls; *L. tuberosus, L. pictus*: two post-mentals). Angel (1942) provides a more detailed morphological account from which it becomes clear that he examined among various individuals also the holotype: *"Queue aussi longue,*

…, fortement gonflée a la bàse, se rétrécissant brusquement aussitôt, au moins chez l'exemplaire type qui est un male." This author thus provides information on the male sex of the holotype, as well as on its size: 56 mm total length and 28 mm tail length (thus 28 mm SVL and 28 mm TAL). Subsequent morphological accounts of the species by Pasteur (1965) and Puente *et al.* (2009) did not provide further information on the holotype.

In summary, the available information confirms (i) that the name *L. tolampyae* has been correctly attributed to the complex of *Lygodactylus* lineages occurring in the West and North West of Madagascar which are characterized by absence of tail whorls, semi-divided mental and three postmentals, and (ii) that the presumably lost *L. tolampyae* holotype most likely originated from the West of Madagascar and more specifically from the wider Morondava region. Consequently, the *nomen* is best applied to the clade containing the mitochondrial lineages A and B ("*L.* sp. 14 and 15 aff. *tolampyae*" according to Gippner *et al.* 2021), which are the only lineages of the complex occurring in this region, according to our data.

Identity of *Lygodactylus tuberifer* Boettger, 1913

Lygodactylus tuberifer is currently considered a junior synonym of *L. tolampyae* (e.g., Uetz *et al.* 2023), and therefore it might be an earlier available name for a species-level lineage in the *L. tolampyae* complex. This *nomen* has a convoluted history. It was coined by Boettger (1913) based on three explicitly listed specimens: one adult female from "Menabé, W. Mad." and two adult females from "Tsimanampetso, SW. Mad.", with the numbers "(coll. Senckenberg No. 4160,4 b)", but in the original description, there is also a mention of one or several male specimens that would bear 5 or 7 femoral pores. Mertens (1922), in his type catalogue of the collections of the Senckenberg Museum in Frankfurt, Germany, listed the specimen SMF 4160,4a from Menabé as type of the species (without any mention of other syntypes however), thus implicitly designating this specimen as lectotype. Pasteur (1965) criticized this choice because the lectotype specimen was the only one in the heterogeneous type series that did not correspond to the species that previously had been considered as *L. tuberifer* but instead was *L. tolampyae*. Mertens (1965) responded to this criticism by providing a rationale for the choice of the lectotype (which had been renumbered as SMF 8948) and also clarified that the specimen was a male, not a female, as suggested by Boettger (1913). Mertens (1965) then proceeded to describe *L. tuberosus* to provide a name for the species to which the paralectotypes of *L. tuberifer* from Tsimanampetsotsa belong. Therefore, SMF 5949 is concurrently a paralectotype of *L. tuberifer* and the holotype of *L. tuberosus* Mertens, 1965; and SMF 8950–8952 are concurrently paralectotypes of *L. tuberifer* and paratypes of *L. tuberosus*.

The origin of the *L. tuberifer* holotype from the Menabé region in the West suggests that it probably belongs to the same evolutionary lineage as the holotype of *L. tolampyae* (thus, mitochondrial lineage A+B). This hypothesis is further supported by the scale counts of the specimen: with longitudinal counts of 225 dorsal and 103 ventral scales, it fits the comparatively lower values for dorsals and higher values for ventrals that we observed in individuals of lineage A+B from the Tsingy de Bemaraha, a locality not far from Menabé.

Taxonomic conclusions

Our data provide conclusive evidence for multiple species-level lineages currently being hidden in the *L. tolampyae* complex. ASAP identified a total of 11–12 deeply divergent mitochondrial lineages within the complex, several of which occurred in close geographic proximity or even syntopy.

In a few cases, these lineages were characterized by widespread allele sharing in nuclear-encoded genes. This applies to the syntopic lineages A and B from the Tsingy de Bemaraha and Beanka, which we therefore regard as conspecific. Also, lineages Ib and Ic, at least in some nuclear-encoded genes, share alleles with lineage Ia; we provisionally consider these three lineages (Ia, Ib, and Ic) as conspecific, but this hypothesis requires further testing given the small amount of material available for Ib and Ic. No nuclear data are available for lineage G, but based on comparatively low genetic divergences in 16S, we consider this lineage provisionally conspecific with A+B.

In contrast, most other lineages were reciprocally monophyletic in the mitochondrial tree and formed distinct haplotype groups in the nuclear haplotype networks, without any haplotype sharing. Most importantly, such full concordance between differences in mitochondrial DNA and in several putatively unlinked nuclear markers was observed in several cases in syntopy: between lineages H and I at Ankarafantsika, and between lineages C and F at

Namoroka; or at close geographic proximity, such as clade E with one sample from near Betsako occurring just a few kilometers away from individuals of clade I at Antsanitia. This clearly suggests strong reproductive isolation among these lineages and, thus, the existence of multiple, partly syntopic species in the *L. tolampyae* complex.

However, strikingly, morphological differences between these species-level lineages were weak, if not absent. Our data suggest that the southernmost occurring lineage A+B (and perhaps also lineages C and F) differs from lineages D, H, and I by some faint differences in scalation, especially a lower longitudinal count of dorsal scales. On the other hand, no morphological differences were detected between the syntopic lineages H and I, despite their strong and consistent genetic divergence, qualifying them as truly cryptic species.

A full taxonomic revision of the *L. tolampyae* complex is out of reach with the current data, especially due to the scarcity or lack of voucher specimens from several lineages. However, initial conclusions are possible with the data at hand: (1) Only one genetic species-level lineage (A+B) was collected from areas in the West corresponding to the imprecise type locality of *L. tolampyae* (west coast forests; probably corresponding to the wider Morondava area), and we therefore consider this lineage to correspond to *L. tolampyae* sensu stricto. (2) Based on the provenance and morphology of the lectotype, we confirm *L. tuberifer* as a junior synonym of *L. tolampyae* sensu stricto and conclude that no earlier name is available for any of the lineages of the *L. tolampyae* complex from the North West of Madagascar. (3) The various lineages from the North West differ from *L. tolampyae* sensu stricto by genetics and weakly by morphology, and correspond to multiple distinct species based on syntopic occurrence without admixture. We here formally name three of these lineages (D, H, and I) as new species and leave lineages C, F, and E for future study.

Taxonomy

Lygodactylus tolampyae (Grandidier, 1872)
Original name. *Hemidactylus tolampyae* Grandidier, 1872
(Fig. 4, 11, 12)

Remark. Gippner *et al.* (2021) named the mitochondrial lineages comprised in this species as *L.* sp. 14 aff. *tolampyae* A and *L.* sp. 15 aff. *tolampyae* B.

Holotype. MNHN 7636, male, from "Forêts de la côte ouest", Madagascar, according to the original description. Probably originating from the wider Morondava area. Specimen probably lost. No paratypes.

Junior synonym. Lygodactylus tuberifer Boettger, 1913; Lectotype of *L. tuberifer*: SMF 8948 (originally numbered SMF 4160,4a) from "Menabé, W. Mad." according to the original description. Paralectotypes of *L. tuberifer*: SMF 5949 and SMF 8950–8952 (which are not conspecific with the lectotype of *L. tuberifer* and are concurrently holotype and paratypes of another valid species, *L. tuberosus*; see above).

Diagnosis. As justified in the Identity section above, we consider the name-bearing types of both *nomina*, *L. tolampyae* and *L. tuberifer*, as corresponding to the genetic lineage A+B, which is the only one detected by our surveys in the supposed areas of provenance of the respective types. *L. tolampyae* can be distinguished from all other Malagasy *Lygodactylus* not belonging to the *L. tolampyae* complex by a mental scale semi-divided by a suture, broad contact of the posterior projection of the mental scale with the first infralabial scale, and three postmental scales. Furthermore, it is characterized by the absence of whorls on the tail (original tail), and a typical look of the head with relatively large eyes. For a distinction of newly described species in the *L. tolampyae* complex, see species accounts below. For variation in color pattern, see Fig. 4.

Distribution. *L. tolampyae*, as redefined here, is primarily known from the West region of Madagascar, corresponding to the most likely provenance of the holotype. Genotyped samples of lineage A+B originate from (1) Tsingy de Bemaraha, (2) Beanka, and (3) north of Beanka, all located in the West region associated with dry deciduous forest. In addition, one sample of lineage G, most likely also assignable to *L. tolampyae,* originated from Ankarafantsika National Park in the North West, but this sample requires further study as, so far, it has not been sequenced for nuclear-encoded genes.

Natural history. At Tsingy de Bemaraha the species was collected at five out of 10 study sites (Bora *et al*. 2010). Individuals were observed being active during daytime within forest habitat (Fig. 13), mainly on bushes and smaller trees up to at least 2.5 m in height (see also Bora *et al*. 2010). In some instances, individuals were also found

being active in the leaf litter, but we did not encounter the species on rock surfaces. At night, individuals were seen sleeping on leaves or smaller twigs, mainly between 0.5 and 1.6 m above the ground. One female (ZSM 6/2006; Fig. 4), collected in mid of March 2006, contained two large eggs.

FIGURE 4. Individuals of *Lygodactylus tolampyae* from Tsingy de Bemaraha National Park, all photographed in 2006. The upper three individuals are not unambiguously assignable to voucher specimens but correspond to samples included in the mitochondrial tree (Fig. 1) and grouped in lineage A+B; the lowermost picture shows the female ZSM 6/2006 (FGZC 676).

Lygodactylus morii sp. nov.
(Fig. 5–7, 10–12)

Remark. This species corresponds to populations previously considered as *L. tolampyae* sensu stricto by Gippner *et al.* (2021).

Holotype. ZSM 501/2001 (field number FGMV = MV 2001.300), adult male (Fig. 5, 10), collected by M. Vences, D.R. Vieites, G. Garcia, V. Raherisoa, and A. Rasoamamonjinirina, near Ampijoroa, Ankarafantsika National Park, Madagascar (approximate geographical coordinates 16.3°S, 46.82°E), on 22 February 2001.

Paratypes. A total of nine specimens (only genotyped individuals included in paratype series). ZSM 151/2013 (ZCMV 14173), one female, collected by F. Ratsoavina, J. Erens, and E. Rajeriarison, between Soalala and Mahajanga (at geographical coordinates 16.05298°S, 45.81034°E, 8 m a.s.l.), on 3 January 2013; ZSM 152/2013 (ZCMV 14172), one male, collected by F. Ratsoavina, J. Erens, and E. Rajeriarison at Katsepy (Ankiririka; 15.71289°S, 46.21650°E, 18 m a.s.l.), on 4 January 2013; ZSM 224/2018 (FGZC 5701), ZSM 225/2018 (FGZC 5705) and ZSM 226/2018 (FGZC 5706), three females, collected by F. Glaw, D. Prötzel, N.A. Raharinoro, R.N. Ravelojaona, A. Razafimanantsoa, J. Forster, K. Glaw, T. Glaw, and C. Zanotelli at Antsanitia (15.567710°S, 46.423104°E, ca. 10 m a.s.l.), on 28 March 2018; ZSM 227/2018 (FGZC 5727), female, collected by F. Glaw, D. Prötzel, N.A. Raharinoro, R.N. Ravelojaona, A. Razafimanantsoa, J. Forster, K. Glaw, T. Glaw, and C. Zanotelli at Antrema (15.716604°S, 46.216802°E, 90 m a.s.l.), on 31 March 2018; ZSM 159/2022 (ZCMV 15703), UADBA-ZCMV 15704, UADBA-ZCMV 15705, one male and two females, collected by M. Vences, S. Rakotomanga, S. Rasamison, and P. Galán near Ampijoroa, Ankarafantsika National Park (approximate geographical coordinates 16.3°S, 46.82°E), on 12 November 2022.

Referred additional material. ZSM 150/2013 (ZCMV 14165), male, collected by F. Ratsoavina, J. Erens, and E. Rajeriarison between Soalala and Mahajanga (at geographical coordinates 16.05298°S, 45.81034°E, 8 m a.s.l.), on 3 January 2013 (not included in paratype series as it belongs to genetic lineage Ic). ZSM 491/2001, ZSM 502/2001, ZSM 503/2001, one male and two females, collected in February 2001 by M. Vences, D.R. Vieites, G. Garcia, V. Raherisoa, and A. Rasoamamonjinirina, near Ampijoroa, Ankarafantsika National Park (not included in paratype series as species assignment not confirmed by molecular data).

FIGURE 5. Male holotype of *Lygodactylus morii* **sp. nov.**, ZSM 501/2001 (FGMV 2001.300) from Ampijoroa, Ankarafantsika National Park, in life, photographed in February 2001.
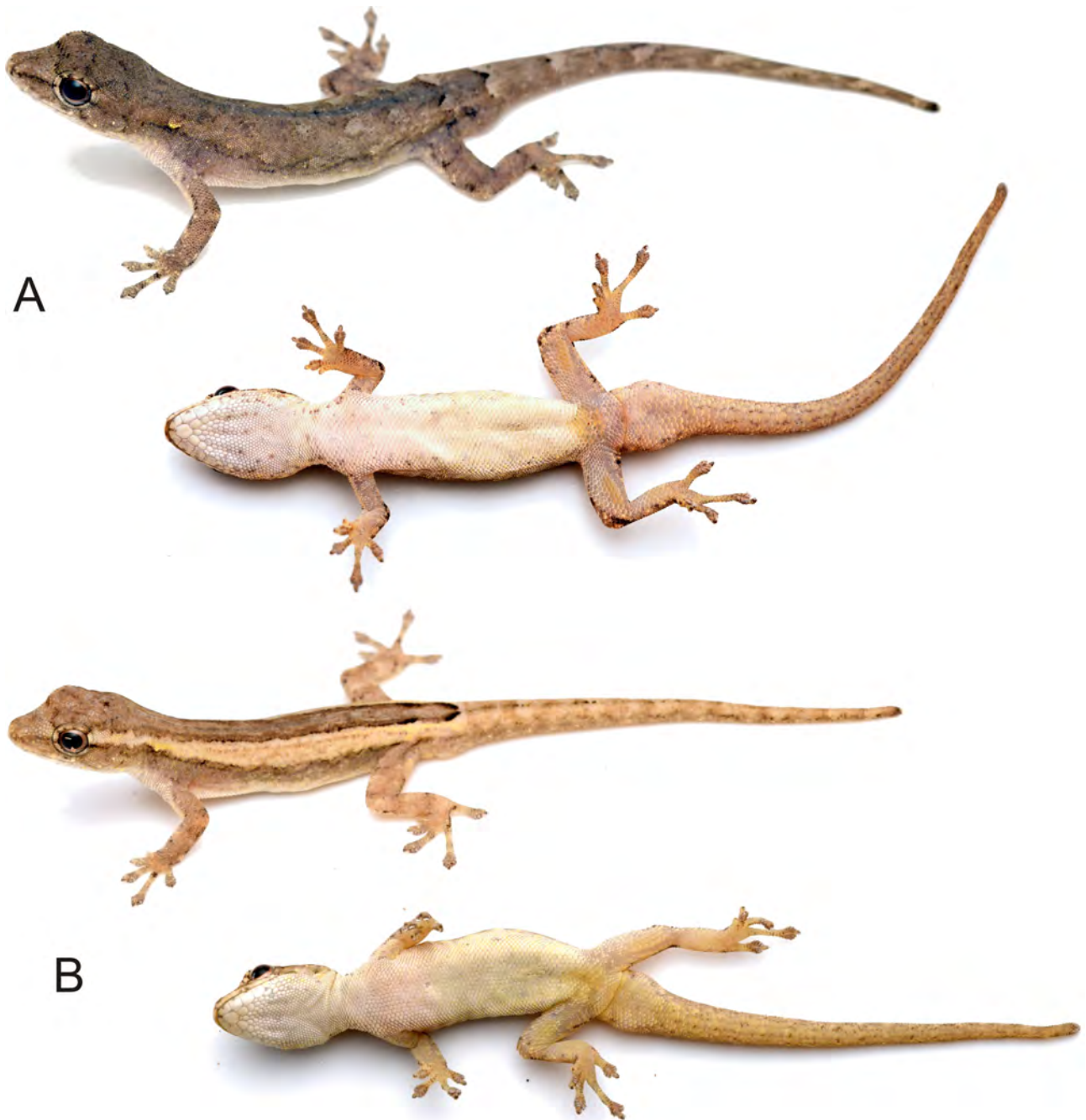
FIGURE 6. Individuals of *Lygodactylus morii* **sp. nov.** from near Ampijoroa (Ankarafantsika National Park) in life, photographed in November 2022. A. specimen with sample number MVTIS 33402/33488 (not collected). B. paratype ZSM 159/2022 (ZCMV 15703).

Diagnosis. *L. morii* **sp. nov.** is characterized as member of the *L. tolampyae* complex (and thereby distinguishable from all other Malagasy *Lygodactylus* not belonging to the complex) by combination of a mental scale semi-divided by a suture, broad contact of the posterior projection of the mental scale with the first infralabial scale, and three postmental scales; furthermore, it is characterized by the absence of whorls on the tail, and a typical look of the head with relatively large eyes. It is distinguished from *L. tolampyae* sensu stricto (as defined herein; mitochondrial lineages A+B and possibly G) by significantly higher mean counts of dorsal scales despite widely overlapping ranges (mean 246 vs. 229; ranges 225–269 vs. 204–241; Mann-Whitney U-test P<0.001), and possibly by a tendency towards broader posterior contact between the mental scale and the first infralabial scale, and by fewer (1 vs. 2–3) internasal scales in the majority of specimens. From a molecular perspective, the new species is characterized by

numerous diagnostic nucleotide positions in the mitochondrial 16S rRNA gene: MolD identified a robust diagnostic nucleotide combination of an 'A' in the site 1072, 'C' in the site 1091, and 'G' in the site 1108 (positions relative to the full 16S rRNA gene of *Phelsuma guimbeaui*).

FIGURE 7. Four individuals of *Lygodactylus morii* **sp. nov.** photographed in November 2022 at different sites near Ampijoroa (Ankarafantsika National Park) in life, resting at night on terminal twigs of trees as is typical for the *L. tolampyae* complex. Individuals not individually assignable to sample or voucher specimen numbers, but corresponding to sequences included in Fig. 1.

Description of the holotype. Adult male, hemipenes everted, in moderate state of preservation, left hind limb removed as tissue source for molecular analysis, tail missing. SVL 29.4 mm, TAL 4.3 mm (as the tail is mutilated); for other measurements, see Table 2. Body broader than head, possibly due to a flattened preservation state. The

distance from the tip of the snout to the anterior border of the eye (3.7 mm) is less than the anterior interorbital distance (4.2 mm), and greater than the distance between the eye and ear opening (2.5 mm). Snout covered with granular scales larger than those on the dorsum. Nostril surrounded by five scales: rostral, first supralabial, one postnasal and two supranasals. The mental scale is semi-divided; contact between posterior projection of mental scale and first infralabial scale is roughly 40% of the infralabial scale length; three symmetrical postmental scales, followed by seven post-postmentals; six infralabial scales; eight supralabial scales; two internasal scales; dorsal scales granular; dorsum with small, homogeneous, granular, and unkeeled scales of similar size to those on trunk, no distinct size difference of scales on limbs; 245 dorsal scales longitudinally along the body; 102 ventral scales between mental and cloaca; venter with larger homogeneous smooth scales; first finger present, small, but bearing a claw; three pairs of subdigital lamellae on the fourth toe; no dorsolateral tubercles; seven preanal pores; no observable lateral spines at the base of the tail.

Based on the available photograph (Fig. 5), *in life*, the holotype displayed a brownish colouration with darker regions on the dorsum and limbs. Above the spinal cord was a repeated darker pattern that continued on the tail. After each instance of the pattern, there was a spot of lighter colouration next to the middle stripe. The flanks were also darker in colour. The legs appeared to be lightly striped with a dark stripe followed by a lighter brownish region. The darker stripe at the flank continued on the head and transforms into a thin stripe, crossing the eye and ending shortly before the nostrils. The greyish colour visible in the picture was probably the result of a skin shedding, which just happened or was about to happen soon. The ventral side appeared to be whitish. In the throat region there were three visible tubercles of one scale each. After 22 years in ethanol (Fig. 10), the specimen is overall darkened in colouration with the darker region still discernible from the lighter regions. The particular dorsal pattern, however, is not visible, except for the base of the tail and the limbs. Between the eyes is a whitish stripe, bordered by thin, darker stripes. The ventral side is whitish in colouration, with dark brown and light brown spots on the underside throat. The bluish spot between the limbs is probably coming from the organs, visible through the skin.

Variation. Similar to other Malagasy *Lygodactylus*, *L. morii* **sp. nov.** also has a striped colour morph that, according to our observations in the field, is rare; among at least 20 individuals seen in the wild in the Ankarafantsika/ Ampijoroa area, only one striped individual was found (male paratype ZSM 159/2022; see Fig. 6B); it is characterized by a light brown to beige dorsolateral stripe that starts behind the eye and becomes gradually broader towards midbody, then narrows again; the stripes on either side of the body fuse on the tail and make up an overall light brown colour of the tail. The ventral side is usually uniformly white, especially on the throat, which can have a few scattered black spots in some individuals; this sparse spotting may extend onto the chest. The underside of the tail and especially the area of the precloacal pores can have a yellowish colour. The tail base is swollen in males due to the presence of hemipenes, but no lateral tail base tubercles are visible (as they would be characteristic for some species of the subgenus *Domerguella*). Males appear to be smaller than females (SVL 28.2–29.4 vs. 28.7–32.8; see Table 2). For variations of other morphometric and scalation characters, see Table 2.

Etymology. We dedicate this species to Akira Mori, Kyoto University, in recognition of his contributions to reptile biology and especially his leading role in the study of reptiles in Ankarafantsika National Park. The species epithet is a noun in the genitive case.

Natural history. This is a very common species in Ankarafantsika National Park (Fig. 13) and apparently also occurs in other dry deciduous forests in the region, close to the North West coast. At Ankarafantsika, individuals were observed active during the day on relatively thin tree trunks at low perch heights of 1–2 m, but were mostly observed at night, sleeping on thin terminal twigs (Fig. 7), in agreement with observations in Mori *et al.* (2006). These authors recorded activity in the dry season but stated that individuals were more easily found during the rainy season.

Distribution. According to current data, reliably genotyped specimens of mitochondrial lineage Ia are known from (1) the type locality, Ankarafantsika National Park (including Ampijoroa, Ampondrabe forest, and unspecified sites outside of the protected area), (2) Antsakabe forest (Mariarano), (3) Antsanitia, (4) probably Betsako, (5) Katsepy (Ankiririka), (6) an unnamed place between Soalala and Mahajanga, and (7) Antrema. Furthermore, the only sample of lineage Ib was collected at (8) Bongolava Plateau, and a sample of Ic was collected from Besalampy (Andranomanintsy Forest).

Lygodactylus herilalai **sp. nov.**
(Fig. 8, 10–12)

Remark. This species does not correspond to a previously identified genetic lineage or candidate species and was newly discovered in the present study.

Holotype. ZSM 161/2022 (ZCMV 15707), adult female (Fig. 8, 10), collected by S. Rakotomanga and S. Rasamison at Ampondrabe forest, Ankarafantsika National Park, Madagascar (geographical coordinates 16.3343°S, 46.8987°E, 223 m a.s.l.), on 13 November 2022.

Paratypes. Three specimens: ZSM 160/2022 (ZCMV 15706), male, with same collection data as holotype; UADBA-APR 7501, male, collected by A.P. Raselimanana at Ampondrabe forest, Ankarafantsika National Park (16.325°S, 46.923°E, 270 m a.s.l.), on 2 December 2006; UADBA-APR 7588, male, collected by A.P. Raselimanana at Andasiravina forest, Ankarafantsika National Park (16.303°S, 46.930°E, 150 m a.s.l.), on 12 December 2006.

Diagnosis. *L. herilalai* **sp. nov.** is characterized as a member of the *L. tolampyae* complex (and thereby distinguishable from all other Malagasy *Lygodactylus* not belonging to the complex) by combination of a mental scale semi-divided by a suture, broad contact of the posterior projection of the mental scale with the first infralabial scale, and three postmental scales; furthermore, characterized by absence of whorls on the tail, and a typical look of the head with relatively large eyes. According to the limited data available, it appears to be distinguished from *L. tolampyae* sensu stricto (as defined herein; mitochondrial lineages A+B and possibly G) by higher mean and maximum counts of dorsal scales despite wide range overlap (mean 245 vs. 229; ranges 229–262 vs. 204–241; not statistically tested due to low sample size of n=3 in *L. herilalai* **sp. nov.**), possibly by a tendency towards broader posterior contact between mental scale and first infralabial scale, and by fewer (1 vs. 2–3) internasal scales in a high proportion of individuals. The new species is most similar morphologically to the syntopic *L. morii*, with no differentiating morphological characters known; however, the two species differ strongly in mitochondrial and nuclear DNA sequences. The new species can be differentiated from *L. morii* and all other lineages in the *L. tolampyae* complex by numerous diagnostic nucleotide positions in the mitochondrial 16S rRNA gene: MolD identified a robust diagnostic nucleotide combination of a 'C' in the site 959, 'A' in the site 1017, 'T' in the site 1042 (positions relative to the full 16S rRNA gene of *Phelsuma guimbeaui*).

Description of the holotype. Adult female, in good state of preservation, left forelimb removed as tissue source for molecular analysis. SVL 31.0 mm, TAL 31.6 mm; for other measurements, see Table 2. Body broader than head. The distance from the tip of the snout to the anterior border of the eye (4.0 mm) is equal to the anterior interorbital distance (4.0 mm), and greater than the distance between the eye and ear opening (2.9 mm). Snout covered with granular scales larger than those on the dorsum. Nostril surrounded by five scales: rostral, first supralabial, one postnasal and two supranasals. The mental scale is semi-divided; contact between posterior projection of mental scale and first infralabial scale is roughly 30% of the infralabial scale length; three symmetrical postmental scales, followed by five post-postmentals; six infralabial scales; seven supralabial scales; one internasal scale; granular dorsal scales; dorsum with small, homogeneous, granular, and unkeeled scales of similar size to those on trunk, no distinct scale size difference on limbs; 243 dorsal scales longitudinally along the body; 98 ventral scales between mental and cloaca; venter with larger homogeneous smooth scales; first finger present, small, but bearing a claw; three pairs of subdigital lamellae on the fourth toe; six not very distinct dorsolateral tubercles, each consisting of one to three scales; tail without whorls; no observable lateral spines at the base of the tail.

Based on available photographs (Fig. 8), *in life* the holotype specimen displayed a brownish to grayish colouration on the dorsum and limbs. Above the spinal cord was a darker stripe, paired with a repeating pattern of lighter spots slowly fading to a darker colour on each side. The spots unified into a single spot on the tailbase, from where the pattern was weakened in colouration. On the head were some yellowish scales. On the neck and between the limbs were yellowish tubercles. The limbs were vaguely patterned with stripes of lighter and darker colouration at the same strength as the dorsum. The ventral side was whitish with a darker colouration on the legs and tail, and without a pattern (Fig. 8). After 6 months in ethanol (Fig. 10), the specimen is overall darkened in colouration with the pattern still clearly visible. The yellow spots and tubercles are more whitish. The ventral side lost its white-pinkish colour for a more white-yellowish colouration and a few slightly darker spots appeared in the throat area.

Etymology. The name is a patronym for Herilala Jean Aimé Rudolph Randriamahazo, Malagasy field herpetologist and conservation biologist, in recognition for his contributions to our understanding of the ecology of various reptile species in Ankarafantsika National Park, and to the conservation of Malagasy amphibians and reptiles. The species epithet is a noun in the genitive case.

FIGURE 8. Female holotype of *Lygodactylus herilalai* **sp. nov.**, ZSM 161/2022 (ZCMV 15707) from Ampondrabe, Ankarafantsika National Park, in life, photographed November 2022.

Variation. For variation in morphometric and scalation characters, see Table 2. Body size ranged between 24.4–31.0 mm in males, vs. 31.0 in the female holotype.

Natural history. Individuals in Ampondrabe Forest (Fig. 13) were found active during the day on tree trunks in November 2022. UADBA-APR 7501 was collected at 20:00 h, roosting at the extremity of a tiny branch at 1.5 m above the forest floor, in dry deciduous forest with sandy soil. UADBA-APR 7588 was found at 19:00 h roosting at the extremity of a small branch in vertical position with the head in the direction of the extremity of the support (upside-down) in semi-deciduous forest. It was quite common in the forest, mostly on tree trunks below 1.5 m, and when disturbed, they would descend the trunk to hide under loose bark, underneath the roots, or in fallen dry leaves among leaf litter.

Distribution. The species has so far only been found in two sites within Ankarafantsika National Park: (1) Ampondrabe forest and (2) Andasiravina forest.

Lygodactylus schwitzeri **sp. nov.**
(Fig. 9–12)

Remark. This species corresponds to the candidate species *L.* sp. 27 aff. *tolampyae* D of Gippner *et al.* (2021).

Holotype. ZSM 419/2000 (FGMV 2000.155), female (Fig. 9–10), collected by F. Andreone, J.E. Randrinirina, and M. Vences at Berara Forest (Ambonihazo; 14.310°S, 47.915°E, 170 m a.s.l.), Sahamalaza Peninsula, Madagascar, on 18 February 2000.

Paratypes. Eight specimens: MRSN R1913–1918 and 1921–1922, five males and three females (see Table 2), with same collection data as holotype. These specimens were not genotyped but are included in the paratype series because (1) they agree with the holotype in morphological features, (2) were collected at the same site, and (3) only one lineage of the *L. tolampyae* complex was found at Sahamalaza.
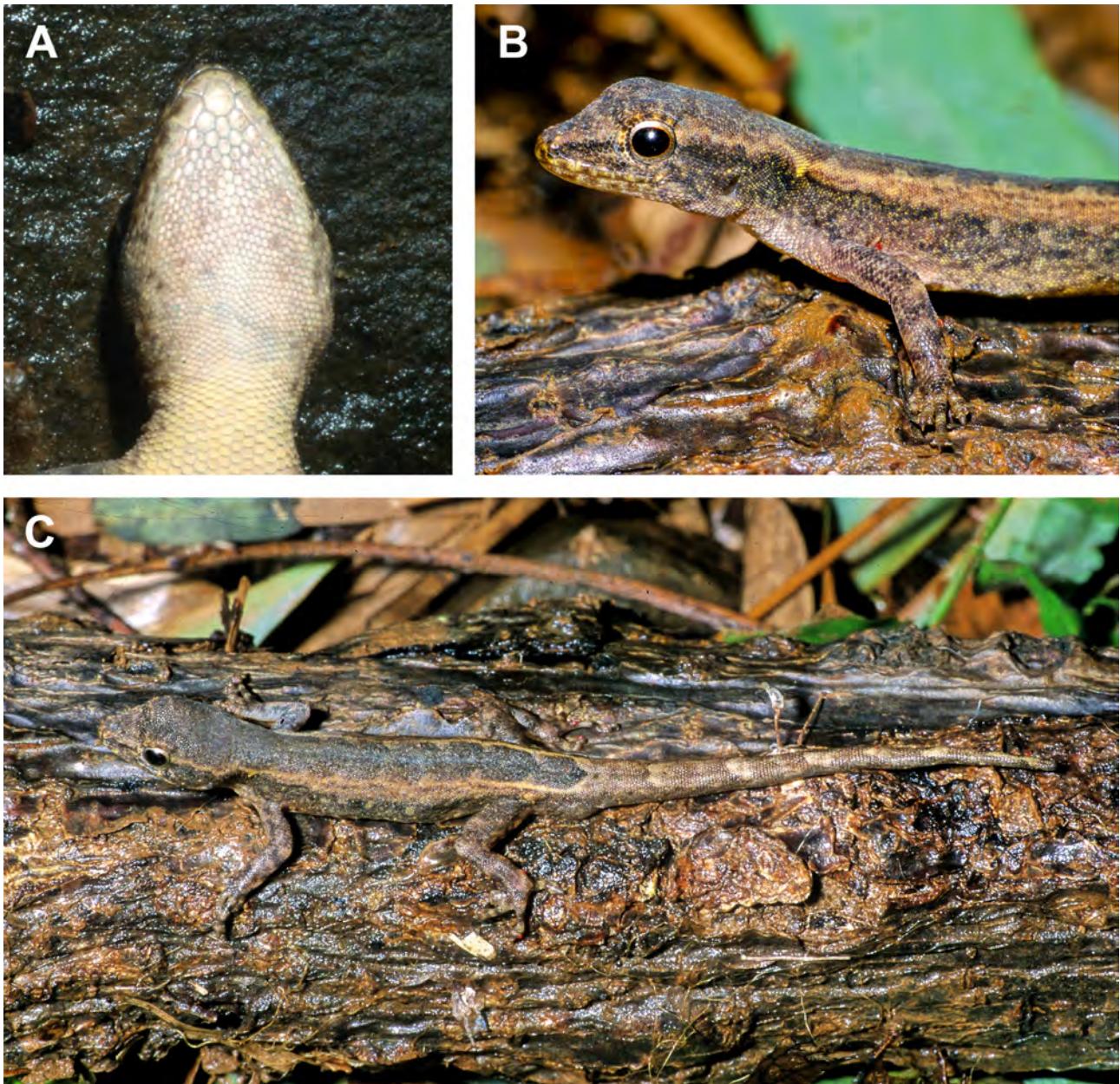
FIGURE 9. Female holotype of *Lygodactylus schwitzeri* **sp. nov.**, ZSM 419/2000 (FGMV 2000.155), from Berara Forest, Sahamalaza, in life, photographed in February 2000.

Diagnosis. L. schwitzeri **sp. nov.** is characterized as a member of the *L. tolampyae* complex (and thereby distinguishable from all other Malagasy *Lygodactylus* not belonging to the complex) by combination of a mental scale semi-divided by a suture, broad contact of the posterior projection of the mental scale with the first infralabial scale, and three postmental scales; furthermore, characterized by absence of whorls on the tail, and a typical look of the head with relatively large eyes. The new species differs from *L. tolampyae* sensu stricto (as defined herein; mitochondrial lineages A+B and possibly G) by higher maximum and mean counts of dorsal scales despite overlap of ranges (mean 254 vs. 229; ranges 240–271 vs. 204–241; U-test, P<0.001), and possibly by a tendency towards broader posterior contact between mental scale and first infralabial scale in a high proportion of specimens. From *L. morii* and *L. herilalai* the new species cannot be clearly diagnosed morphologically. From a molecular perspective, the new species is characterized by numerous diagnostic nucleotide positions in the mitochondrial 16S rRNA gene: MolD identified a robust diagnostic nucleotide combination of a 'T' in the site 967, 'T' in the site 992, 'C' in the site 1001 (positions relative to the full 16S rRNA gene of *Phelsuma guimbeaui*).
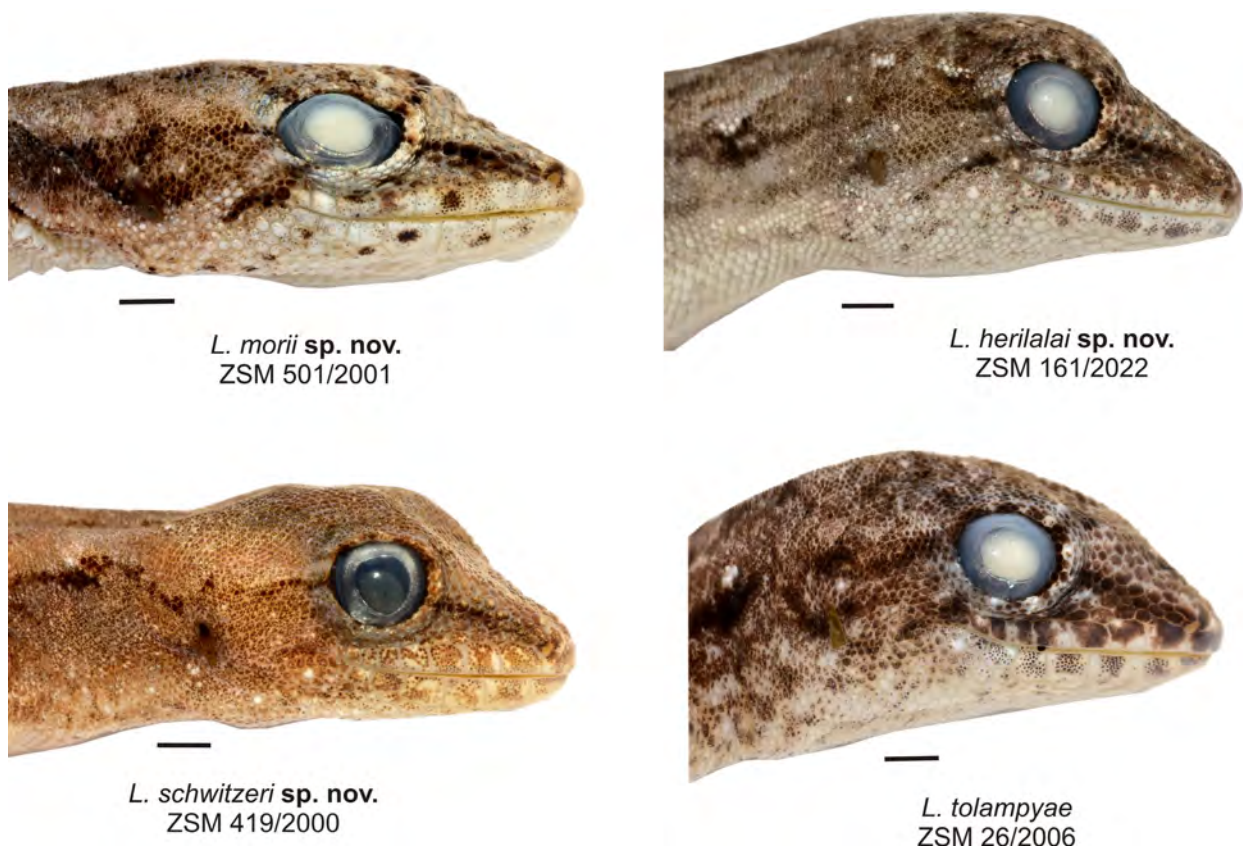
FIGURE 10. Preserved holotypes of the three new species of the *Lygodactylus tolampyae* complex described herein, photographed in May 2023.

Description of the holotype. Female, in good state of preservation, tail missing. SVL 28.1 mm, TAL 2.8 mm (broken and missing); for other measurements, see Table 2. Head and body have approximately the same width. The distance from the tip of the snout to the anterior border of the eye (3.7 mm) is larger than the anterior interorbital distance (3.6 mm), and greater than the distance between the eye and ear opening (2.8 mm). Snout covered with granular scales slightly larger than those on the dorsum. Nostril surrounded by 5 scales: rostral, first supralabial, one postnasal and two supranasals. The mental scale is semi-divided; contact between posterior projection of mental scale and first infralabial scale is around 30% of the infralabial scale length; three symmetrical postmental scales, followed by five postpostmentals; seven infralabial scales; eight supralabial scales; two internasal scales; granular dorsal scales; dorsum with small, homogeneous, granular, and unkeeled scales of similar size to those on trunk, slightly larger on limbs; 240 dorsal scales longitudinally along the body; 102 ventral scales between mental and
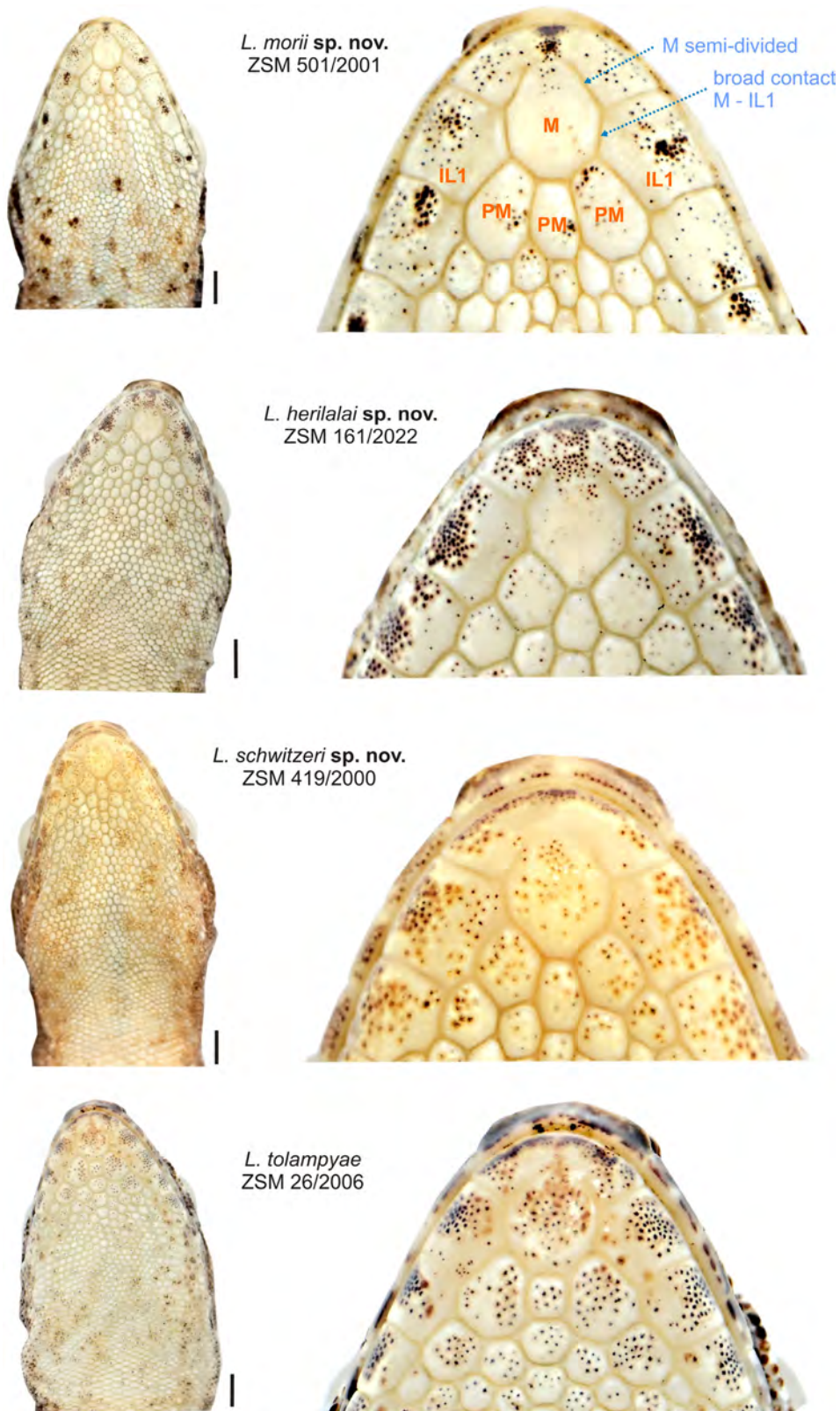
FIGURE 11. Ventral views of the heads of the holotypes of the three new species of *Lygodactylus* described herein, and one representative specimen of *L. tolampyae*. The images on the right show the mental region magnified and strongly sharpened to improve visibility of sutures between scales. For the holotype of *L. morii* **sp. nov.**, the typical arrangement of scales in the mental region in this species complex is labelled: M, mental scales (semi-divided by incomplete sutures), PM, post-mentals (typically three), IL1, first infralabial (which maintains a broad contact with the mental). Scale bars (referring to the images on the left) represent 1 mm.

FIGURE 12. Lateral views of the heads of the holotypes of the three new species of *Lygodactylus* described herein, and one representative specimen of *L. tolampyae.* The scale bar represents 1 mm.

cloaca; venter with larger homogeneous smooth scales; first finger present, small, but bearing a claw; three pairs of subdigital lamellae on the fourth toe; no dorsolateral tubercles; no observable lateral spines at the base of the tail.

After 23 years of preservation in ethanol (Fig. 10), the specimen is brownish in colouration with a broad dark middorsal stripe above. This stripe appears to continue in an interrupted pattern on the tail, which cannot be described as it is missing. On the head is a darker spot, from which the dark stripe appears to start. The limbs are patternless. Each side of the neck has a whitish tubercle consisting of one scale. The ventral side is mostly whitish, with a few light brown spots on the throat. A dark blueish spot is probably not integument colouration but organs visible through the skin. The underside of the hind limbs is spotted with light-brown colour around the knees. *In life* (Fig. 9), colouration was quite similar but more contrasting, with distinct light brown dorsolateral stripes.

Variation. For variation in morphometric and scalation characters, see Table 2. Body size ranged between 26.3–30.6 mm in males and 28.1–30.7 mm in females.

Etymology. The species epithet is a patronym for Christoph Schwitzer, in recognition for his contribution to lemur research and nature conservation in Madagascar, specifically in the Sahamalaza Peninsula. The species epithet is a noun in the genitive case.

Natural history. Very poorly known. The species inhabits transitional forest (Fig. 13). This is a quite common species in the Anabohazo Forest in Sahamalaza. Three individuals were found roosting at night at the extremities of leaves and stems at about 1.5–2 m above the forest floor of a narrow valley forest along a dried temporary stream in dry semi-deciduous forest. During the day, one individual was found active on tree trunk at 0.8 m on slope in dry semi-deciduous forest in the same area.

Distribution. According to available molecular data, the species is known from two sites on the Sahamalaza Peninsula: (1) Ambonihazo (Berara Forest) and (2) Ankarafa. Penny *et al.* (2017) further report a record of the *L. tolampyae* complex, probably referring to this species from (3) Analavory. However, this forest fragment has been entirely destroyed by uncontrolled burning in 2004 (Penny *et al*. 2016).

FIGURE 13. Habitat of species of the *Lygodactylus tolampyae* complex. A. Dry deciduous forest at Ampijoroa (Ankarafantsika) where *L. morii* **sp. nov.** occurs in high densities. B. View of remains of dry deciduous Ampondrabe forest (habitat of *L. morii* **sp. nov.** and *L. herilalai* **sp. nov.**) with large areas of forest destroyed by fire in the foreground. C, D. Transitional forest on Sahamalaza Peninsula, habitat of *L. schwitzeri* **sp. nov.** E. Forest in the Tsingy de Bemaraha, habitat of *L. tolampyae*. All photos by the authors except A by P. Galán.

Discussion

This study revealed unexpected species diversity within a complex of dwarf geckos in the West and North West of Madagascar. In general, *Lygodactylus* geckos in Madagascar, as in other parts of their range, have long been neglected in taxonomic revisions, also because only subtle morphological differences exist between most species and field identification is often not readily possible (Pasteur 1965; Puente *et al.* 2009; Vences *et al.* 2022). Molecular data (Puente *et al.* 2005; Nagy *et al.* 2012; Mezzasalma *et al.* 2017; Gippner *et al.* 2021; Vences *et al.* 2022) have confirmed the majority of the morphological species delimitations of Angel (1942), Pasteur (1962, 1964, 1965, 1967a, 1967b) and Pasteur & Blanc (1967, 1973), but also uncovered a substantial amount of additional molecular variation, indicative of an incomplete species inventory of *Lygodactylus*. Within *Lygodactylus*, Vences *et al.* (2022) formally named a series of candidate species of the subgenus *Domerguella* initially defined by Gippner *et al.* (2021), after demonstrating concordance between high mitochondrial divergences, the absence of haplotype sharing in two nuclear-encoded genes, and weak but consistent morphological differentiation. In their *Domerguella* revision, Vences *et al.* (2022) emphasized the importance of two arguments to assess the species status of their new species: (i) the syntopic occurrence of some species apparently without nuclear genomic admixture and under maintenance of morphological differences; and (ii) the morphologically most similar species not being each other's sister taxa. The situation in the *L. tolampyae* complex adds a layer of complexity to this species delimitation rationale because the morphological differentiation among genetic lineages is extremely low or absent, especially between the two species confirmed to occur syntopically at Ankarafantsika. For this reason, we doubled the number of nuclear-encoded genes studied compared to Vences *et al.* (2022) and (except for the short and conserved CMOS fragment) found a fully concordant signal for the main evolutionary lineages, which convinced us to herein formally name them as distinct species despite the scarcity or absence of morphological differentiation.

Along with several other authors (e.g., Jörger & Schrödl 2013; Delić *et al.* 2017; Fišer *et al.* 2018), we here advocate describing and formally naming species even if they qualify as truly cryptic, i.e., morphologically not distinguishable even upon detailed examination. This especially applies if these species occur in syntopy without admixture, providing a clear indication for the biological species criterion being fulfilled. Recognizing these species and providing them with a scientific name facilitates their study in an evolutionary framework and their inclusion in conservation management (Delić *et al.* 2017). For the *L. tolampyae* complex, the natural and life history of all included lineages is almost completely unknown to date, and our study emphasizes the importance of conducting in-depth studies of these and other Malagasy reptiles. This especially applies to species such as *L. morii* and *L. herilalai*, whose occurrence in syntopy may either reflect ongoing, dynamic competition processes or differentiation of ecological niches.

Our study highlights the importance of the North West region (as defined by Boumans *et al.* 2007 based on river catchments outlined by Wilmé *et al.* 2006) of Madagascar as an apparent center of species diversity and endemism of geckos in the *L. tolampyae* complex: in this area, three nominal species (*L. herilalai, L. morii*, and *L. schwitzeri*) occur, along with a further deep mitochondrial lineage (E) that remains unstudied due to the lack of voucher specimens. Furthermore, if the presence of clade G in Ankarafantsika and its close relationships to *L. tolampyae* sensu stricto is confirmed, *L. tolampyae* would also occur in this area. On the contrary, in the West region, only *L. tolampyae* sensu stricto was recorded by our genetic screening of the complex (Fig. 1), plus two lineages (C and F) from the Tsingy de Namoroka at the northern edge of the West region. A high genetic fragmentation and possible presence of new microendemic species in the North West is also apparent in ground chameleons of the genus *Brookesia* (Glaw *et al.* 2022). Spatial analyses (Brown *et al.* 2016) have highlighted the importance of northern Madagascar (not including most of the North West region) as center of endemism of reptiles, but did not reveal a large amount of microendemism in the North West or an important turnover between the North West and the West. We hypothesize that this is due to the insufficient taxonomic resolution of the distribution records used by Brown *et al.* (2016) combined with incomplete sampling, and call for intensified fieldwork and genetic screening of reptile populations in the remaining natural habitat in the North West of Madagascar. As already stated by Vences *et al.* (2022), the occurrence of syntopic cryptic species of *Lygodactylus* (as with *L. herilalai* and *L. morii* in Ankarafantsika; and lineages C and F at Namoroka) exemplifies that sampling and genetic screening of multiple individuals might be necessary to detect the presence of species, especially if these are more localized and rarer than their cryptic siblings, as in the case of *L. herilalai*.

All species of the *L. tolampyae* complex occur in dry or transitional forest that is under high anthropogenic pressure. Many forests in the North West and West of Madagascar have suffered from rampant destruction through slash-and-burn agriculture over the past years (e.g., Waeber *et al.* 2015; Vieilledent *et al.* 2020; Rafanoharana *et al.* 2021; Suzzi-Simmons 2023), including those within Ankarafantsika National Park (Carver 2021). The remaining forests in the Sahamalaza Peninsula are similarly threatened (e.g., Schwitzer *et al.* 2013; Seiler *et al.* 2013; Hending *et al.* 2023). All of these remaining dry forest blocks are surrounded by woodland savanna and grassland, which are regularly burned, reducing the forest edges progressively. On the other hand, trees in the canyons of the karstic limestone massifs of Tsingy de Bemaraha National Park might be slightly more protected by the terrain's topography as well as the rare narrow gallery forests. At present, the IUCN Red List classifies *L. tolampyae* as Least Concern (Vences 2011), and this classification can probably be maintained for *L. tolampyae,* as redefined herein. Also, *Lygodactylus morii* is very common in Ankarafantsika National Park, including the most protected parcels around Ampijoroa, and was also found at other forest fragments outside the park, so the species might qualify to be classified as Least Concern (or perhaps Near Threatened). However, *L. herilalai* is only known from two sections of Ankarafantsika NP that, according to our observations, are subject to heavy degradation (fire and forest resource exploitation), and we suggest classifying this species as Endangered, based on criteria B1ab(iii), similar to other Ankarafantsika endemics such as *Voeltzkowia yamagishii* (see Randriamahazo & Vences 2011), i.e., due to the known extent of occurrence estimated to be less than 100 km^2 and estimates indicating that the range is severely fragmented, with continuing decline in area, extent, and/or quality of habitat. Finally, *L. schwitzeri* is so far known only from the Sahamalaza Peninsula, and along with the classification of other amphibians and reptiles with a similar distribution pattern (e.g., *Boophis ankarafensis*, *Cophyla berara*, *Pseudoacontias menamainty*), a classification as Endangered or as Critically Endangered might be adequate, again under criteria B1ab(iii). In general, more intensive surveys (including exhaustive genetic screening) of *Lygodactylus* populations in the West and North West are needed for more reliable conservation assessments and for a future exhaustive revision of this complex that should particularly address the status of lineages C, E, and F, whose status we could not address herein due to the scarcity or lack of voucher specimens available for examination.

Acknowledgments

References

Angel, F. (1942) Les lézards de Madagascar. *Mémoires de l'Académie Malgache*, 36, 1–139.

Avise, J.C. & Ball, R.M. (1990) Principles of genealogical concordance in species concepts and biological taxonomy. *In*: Futuyma, D. & Antonovics, J. (Eds.), *Oxford Surveys in Evolutionary Biology*. Oxford University Press, Oxford, pp. 45–67. https://doi.org/10.1073/pnas.94.15.7748

Avise, J. & Wollenberg, K. (1997) Phylogenetics and the origin of species. *Proceedings of the National Academy of Sciences of the United States of America*, 94, 7748–7755. https://doi.org/10.1073/pnas.94.15.7748

Bell, J. (2008) A simple way to treat PCR products prior to sequencing using ExoSAP-IT. *Biotechniques*, 44, 834. https://doi.org/10.2144/000112890

Bickford, D., Lohman, D.J., Sodhi, N.S., Ng, P.K., Meier, R., Winker, K., Ingram, K.K. & Das, I. (2007) Cryptic species as a

window on diversity and conservation. *Trends in Ecology & Evolution*, 22,148–155.
https://doi.org/10.1016/j.tree.2006.11.004

Boettger, O. (1913) Reptilien und Amphibien von Madagascar, den Inseln und dem Festland Ostafrikas. *In*: Voeltzkow, A. (Ed.), *Reise in Ostafrika in den Jahren 1903-1905. Wissenschaftliche Ergebnisse. Vol. 3. Systematische Arbeiten*. Schweizerbart' sche Verlagsbuchhandlung, Nägele und Sproesser, Stuttgart, pp. 269–375.

Bora, P., Randrianantoandro, J.C., Randrianavelona, R., Hantalalaina, E.F., Andriantsimanarilafy, R.R., Rakotondravony, D., Ramilijaona, O.R., Vences, M., Jenkins, R.K.B., Glaw, F. & Köhler, J. (2010) Amphibians and reptiles of the Tsingy de Bemaraha Plateau, Western Madagascar: Checklist, biogeography and conservation. *Herpetological Conservation and Biology*, 5, 111–125.

Boumans, L., Vieites, D.R., Glaw, F. & Vences, M. (2007) Geographical patterns of deep mitochondrial differentiation in widespread Malagasy reptiles. *Molecular Phylogenetics and Evolution*, 45, 822–839.
https://doi.org/10.1016/j.ympev.2007.05.028

Brown, J.L., Sillero, N., Glaw, F., Bora, P., Vieites, D.R. & Vences, M. (2016) Spatial biodiversity patterns of Madagascar's amphibians and reptiles. *PLoS ONE*, 11, e0144076.
https://doi.org/10.1371/journal.pone.0144076

Bruford, M.W., Hanotte, O., Brookfield, J.F.Y. & Burke, T. (1992) Single-locus and multilocus DNA fingerprint. *In*: Hoelzel, A.R. (Ed.), *Molecular Genetic Analysis of Populations: A Practical Approach*. IRL Press, Oxford, pp. 225–270.

Brygoo, E.R. (1985a) Les Gerrhosaurinae de Madagascar, Sauria (Cordylidae). *Mémoire du Muséum National d'Histoire Naturelle*, Nouvelle Série, Série A, Zoologie, 134, 1–65.

Brygoo, E.R. (1985b) Les types de Cordylidés et de Dibamidés (Reptiles, Sauriens) du Muséum national d'Histoire naturelle, Catalogue critique. *Bulletin du Muséum National d'Histoire Naturelle, Paris*, 4e Série 7A (1), 249–265.
https://doi.org/10.5962/p.285886

Brygoo, E.R. (1990) Les types de Gekkonidés (Reptiles, Sauriens) du Muséum national d'Histoire naturelle. Catalogue critique. *Bulletin Museum National d'Histoire Naturelle*, Série 4, Section A (Zoologie, Biologie Écologie Animale), 3–4 (Supplement), 19–141.
https://doi.org/10.5962/p.289594

Carver, E. (2021) 'Unprecedented' Fires in Madagascar National Park Threaten Livelihoods and Lemurs. Mongabay. Available from: https://news.mongabay.com/2021/12/fires-in-madagascar-national-park-threaten-livelihoods-and-lemurs/ (accessed 29 April 2024)

Delić, T., Trontelj, P., Rendoš, M. & Fišer, C. (2017) The importance of naming cryptic species and the conservation of endemic subterranean amphipods. *Scientific Reports*, 7 (1), 3391.
https://doi.org/10.1038/s41598-017-02938-z

de Queiroz, K. (1998) The general lineage concept of species, species criteria, and the process of speciation. *In*: Howard, D.J. & Berlocher, S.H. (Eds.), *Endless Forms. Species and Speciation*. Oxford University Press, Oxford, pp. 49–89.

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

Edler, D., Klein, J., Antonelli, A. & Silvestro, D. (2020) raxmlGUI 2.0: A graphical interface and toolkit for phylogenetic analyses using RAxML. *Methods in Ecology and Evolution*, 12, 373–377.
https://doi.org/10.1111/2041-210X.13512

Fedosov, A., Achaz, G., Gontchar, A. & Puillandre, N. (2022) Mold, a novel software to compile accurate and reliable DNA diagnoses for taxonomic descriptions. *Molecular Ecology Resources*, 22, 2038–2053.
https://doi.org/10.1111/1755-0998.13590

Fišer, C., Robinson, C.T. & Malard, F. (2018) Cryptic species as a window into the paradigm shift of the species concept. *Molecular Ecology*, 27, 613–635.
https://doi.org/10.1111/mec.14486

Gippner, S., Travers, S.L., Scherz, M.D., Colston, T.J., Lyra, M.L., Mohan, A.V., Multzsch, M., Nielsen, S.V., Rancilhac, L., Glaw, F., Bauer, A.M. & Vences, M. (2021) A comprehensive phylogeny of dwarf geckos of the genus *Lygodactylus*, with insights into their systematics and morphological variation. *Molecular Phylogenetics and Evolution*, 165, 107311.
https://doi.org/10.1016/j.ympev.2021.107311

Glaw, F., Köhler, J., Crottini, A., Gehring, P.-S., Prötzel, D., Randriamanana, L., Andreone, F. & Vences, M. (2021) An additional level of cryptic diversity: A new green-coloured Malagasy treefrog of the *Boophis luteus* species group. *Salamandra*, 57, 295–308.

Glaw, F., Raharinoro, N.A., Ravelojaona, R.N., Prötzel, D. & Vences, M. (2022) New records of threatened leaf chameleons highlight unexpected genetic diversity of the *Brookesia decaryi/B. bonsi* species complex in western Madagascar. *Der Zoologische Garten*, 90, 71–80.

Grandidier, A. (1872) Quelque reptiles nouveaux découverts à Madagascar en 1870. *Annales des Sciences Naturelles*, Zoologie, Séries 5, 15, 6–11.

Grandidier, A. (1893) Les voyageurs français à Madagascar pendant les trente dernières années. *Bulletin de la Société Géographie, Paris*, 14, 289–300.

Guibé, J. (1954) *Catalogue des Types de Lézards du Muséum national d'Histoire naturelle*. Imprimérie Colas, Bayeux, 120 pp.

Hending, D., Randrianarison, H., Andriamavosoloarisoa, N.N.M., Ranohatra-Hending, C., Holderied, M., McCabe, G. & Cotton,

S. (2023) Forest fragmentation and its associated edge-effects reduce tree species diversity, size, and structural diversity in Madagascar's transitional forests. *Biodiversity Conservation*, 32, 3329–3353. https://doi.org/10.1007/s10531-023-02657-0

Jörger, K.M. & Schrödl, M. (2013) How to describe a cryptic species? Practical challenges of molecular taxonomy. *Frontiers in Zoology*, 10, 59. https://doi.org/10.1186/1742-9994-10-59

Korshunova, T., Picton, B., Furfaro, G., Mariottini, P., Pontes, M., Prkić, J., Fletcher, K., Malmberg, K., Lundin, K. & Martynov, A. (2019) Multilevel fine-scale diversity challenges the 'cryptic species' concept. *Scientific Reports*, 9 (1), 6732. https://doi.org/10.1038/s41598-019-42297-5

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

Kumazawa, Y., Miura, S., Yamada, C. & Hashiguchi, Y. (2014) Gene rearrangements in gekkonid mitochondrial genomes with shuffling, loss, and reassignment of tRNA genes. *BMC Genomics*, 15, 930. https://doi.org/10.1186/1471-2164-15-930

Librado, P. & Rozas, J. (2009) DnaSP. Version 5. A software for comprehensive analysis of DNA polymorphism data. *Bioinformatics*, 25, 1451–1452. https://doi.org/10.1093/bioinformatics/btp187

Lobón-Rovira, J., Bauer, A.M., Vaz Pinto, P., Trape, J.F., Conradie, W., Kusamba, C., Júlio, T., Cael, G., Stanley, E.L., Hughes, D.F., Behangana, M., Masudi, F.M., Pauwels, O.S.G. & Greenbaum, E. (2023) Integrative revision of the *Lygodactylus gutturalis* (Bocage, 1873) complex unveils extensive cryptic diversity and traces its evolutionary history. *Zoological Journal of the Linnean Society*, 201, 447–492. https://doi.org/10.1093/zoolinnean/zlad123

Marques, M.P., Ceríaco, L.M.P., Buehler, M.D., Bandeira, S.A., Janota, J.M. & Bauer, A.M. (2020) A revision of the dwarf geckos, genus *Lygodactylus* (Squamata: Gekkonidae), from Angola, with description of three new species. *Zootaxa*, 4853 (3), 301–352. https://doi.org/10.11646/zootaxa.4853.3.1

Mertens, R. (1922) Verzeichnis der Typen in der herpetologischen Sammlung des senckenbergischen Museums. *Senckenbergiana*, 4, 162–183.

Mertens, R. (1965) Über *Lygodactylus tuberifer* und seinen Lectotypus. *Senckenbergiana biologica*, 46, 467–469.

Mezzasalma, M., Andreone, F., Aprea, G., Glaw, F., Odierna, G. & Guarino, F.M. (2017) Molecular phylogeny, biogeography and chromosome evolution of Malagasy dwarf geckos of the genus *Lygodactylus* (Squamata, Gekkonidae). *Zoologica Scripta*, 46 (1), 42–54. https://doi.org/10.1111/zsc.12188

Mocquard, F. (1895) Sur les Reptiles recueillis à Madagascar de 1867 à 1885 par M. Grandidier. *Bulletin De la Société Philomathique Paris*, 8e Série, 7 (3), 93–111.

Mocquard, F. (1909) Synopsis des familles, genres et espèces des Reptiles écailleux et des Batraciens de Madagascar. *Nouveaux Archives du Muséum National d'Histoire Naturelle, Paris*, 5e Série 1, 108. https://doi.org/10.5962/bhl.title.11837

Monnier, J.E. (2017) *Profession explorateur: Alfred Grandidier 1836–1921*. Presses Universitaires de Rennes, Rennes, 257 pp. https://doi.org/10.4000/books.pur.161596

Mori, A., Ikeuchi, I. & Hasegawa, M. (2006) Herpetofauna of Ampijoroa, Ankarafantsika Strict Nature Reserve, a dry forest in northwestern Madagascar. *Herpetological Natural History*, 10 (1), 31–60.

Nagy, Z.T., Sonet, G., Glaw, F. & Vences, M. (2012) First large-scale DNA barcoding assessment of reptiles in the biodiversity hotspot of Madagascar, based on newly designed COI primers. *PLoS ONE*, 7 (3), e34506. https://doi.org/10.1371/journal.pone.0034506

Padial, J.M., Miralles, A., De la Riva, I. & Vences, M. (2010) The integrative future of taxonomy. *Frontiers in Zoology*, 7, e16. https://doi.org/10.1186/1742-9994-7-16

Pasteur, G. (1962) Notes préliminaires sur les lygodactyles (Gekkonidés). III Diagnose de *Millotisaurus* gen. nov., de Madagascar. *Société des Sciences Naturelles et Physiques du Maroc*, *Comptes Rendus des Séances Mensuelles*, 3, 65–66.

Pasteur, G. (1964) Notes préliminaires sur les lygodactyles (Gekkonidés). IV Diagnoses de quelques formes africaines et malgaches. *Bulletin du Muséum National d'Histoire Naturelle*, 36, 311–314.

Pasteur, G. (1965) Recherches sur l'évolution des lygodactyles, lézards afro-malgaches actuels. *Travaux de l'Institut scientifique chérifien*, *Série Zoologique*, 29, 1–132.

Pasteur, G. (1967a) Note préliminaire sur les geckos du genre *Lygodactylus* rapportés par Charles Blanc du Mont Ibity (Madagascar). *Bulletin du Muséum National d'Histoire Naturelle*, 39, 439–443.

Pasteur, G. (1967b) Redécouverte d'un genre de sauriens malgache: *Microscalabotes* (Gekkonidés). *Annales de la Faculté des Sciences de l'Université de Madagascar*, 5, 75–78.

Pasteur, G. & Blanc, C.P. (1967) Les lézards du sous-genre malgache de lygodactyles *Domerguella* (Gekkonidés). *Bulletin de la Société Zoologique de France*, 92, 583–597.

Pasteur, G. & Blanc, C.P. (1973) Nouvelles études sur les lygodactyles (Sauriens Gekkonidés). I. Données récentes sur

Domerguella et sur ses rapports avec la Phytogéographie malgache. *Bulletin de la Société Zoologique de France*, 98, 165–174.

Penny, G.S., Andreone, F., Crottini, A., Holderied, M.W., Rosa, G.M. & Schwitzer, C. (2016) *The amphibians of the Sahamalaza Peninsula, northwest Madagascar—actions for their conservation*. Bristol Zoological Society, Bristol, 34 pp. [ISBN: 978-1-5262-0040-2]

Penny, S.G., Crottini, A., Andreone, F., Bellati, A., Rakotozafy, L.M.S., Holderied, M.W., Schwitzer, C. & Rosa, G.M. (2017) Combining old and new evidence to increase the known biodiversity value of the Sahamalaza Peninsula, Northwest Madagascar. *Contributions to Zoology*, 86, 273–296.
https://doi.org/10.1163/18759866-08604002

Puente, M., Glaw, F., Vieites, D.R. & Vences, M. (2009) Review of the systematics, morphology and distribution of Malagasy dwarf geckos, genera *Lygodactylus* and *Microscalabotes* (Squamata: Gekkonidae). *Zootaxa*, 2103 (1), 1–76.
https://doi.org/10.11646/zootaxa.2103.1.1

Puente, M., Thomas, M. & Vences, M. (2005) Phylogeny and biogeography of Malagasy dwarf geckos, *Lygodactylus* Gray, 1864: Preliminary data from mitochondrial DNA sequences (Squamata: Gekkonidae). *In*: Huber, B.A. & Lampe, K.H. (Eds.), African Biodiversity: Molecules, Organisms, Ecosystems. *Proceedings of the 5th International Symposium of the Tropical Biology,* Museum Koenig Springer, Bonn, pp. 229–235.
https://doi.org/10.1007/0-387-24320-8_21

Puillandre, N., Brouillet, S. & Achaz, G. (2021) ASAP: assemble species by automatic partitioning. *Molecular Ecology Resources*, 21, 609–620.
https://doi.org/10.1111/1755-0998.13281

Rafanoharana, S.C., Andrianambinina, F.O.D., Rasamuel, H.A., Rakotoarijaona, M.A., Ganzhorn, J.U., Waeber, P.O. & Wilmé, L. (2021) Exemplifying stratified deforestation in four protected areas in Madagascar. *Forests*, 12, 1143.
https://doi.org/10.3390/f12091143

Randriamahazo, H. & Vences, M. (2011) *Sirenoscincus yamagishi. The IUCN Red List of Threatened Species*, 2011, e.T172949A6946762.
https://doi.org/10.2305/IUCN.UK.2011-2.RLTS.T172949A6946762.en

Saéz, A.G. & Lozano, E. (2005) Body doubles. *Nature*, 433, 111.
https://doi.org/10.1038/433111a

Salzburger, W., Ewing, G.B. & Von Haeseler, A. (2011) The performance of phylogenetic algorithms in estimating haplotype genealogies with migration. *Molecular Ecology*, 20, 1952–1963.
https://doi.org/10.1111/j.1365-294X.2011.05066.x

Schwitzer, C., Mittermeier, R.A., Davies, N., Johnson, S., Ratsimbazafy, J., Razafindramanana, J., Louis Jr., E.E. & Rajaobelina, S. (Eds.) (2013) *Lemurs of Madagascar: A Strategy for Their Conservation 2013–2016*. IUCN SSC Primate Specialist Group, Bristol Conservation and Science Foundation, and Conservation International, Bristol, 185 pp.

Seiler, M., Holderied, M. & Schwitzer, C. (2013) Effects of habitat alteration on resting behaviour of the Sahamalaza sportive lemur in North West Madagascar. *In*: Marsh, L.K. & Chapman, C.A. (Eds.), *Primates in Fragments*. Springer, New York, New York, pp. 259–271.
https://doi.org/10.1007/978-1-4614-8839-2_18

Speybroeck, J., Beukema, W., Dufresnes, C., Fritz, U., Jablonski, D., Lymberakis, P., Martinez-Solano, I., Razzettis, E., Vamberger, M., Vences, M., Vörös, J. & Crochet, P.-A. (2020) Species list of the European herpetofauna—2020 update by the Taxonomic Committee of the Societas Europaea Herpetologica. *Amphibia-Reptilia*, 41, 139–189.
https://doi.org/10.1163/15685381-bja10010

Stamatakis, A. (2014) RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30, 1312–1313.
https://doi.org/10.1093/bioinformatics/btu033

Stephens, M., Smith, N.J. & Donnelly, P. (2001) A new statistical method for haplotype reconstruction from population data. *American Journal of Human Genetics*, 68, 978–989.
https://doi.org/10.1086/319501

Struck, T.H. & Cerca, J. (2019) Cryptic species and their evolutionary significance. *Encyclopedia of Life Sciences.* [published online]
https://doi.org/10.1002/9780470015902.a0028292

Suzzi-Simmons, A. (2023) Status of deforestation of Madagascar. *Global Ecology and Conservation*, 42, e02389.
https://doi.org/10.1016/j.gecco.2023.e02389

The Jamovi project (2023) jamovi. Version 2.3. Computer Software. Available from: https://www.jamovi.org (accessed 29 April 2024)

Uetz, P., Freed, P, Aguilar, R. & Hošek, J. (Eds.) (2023) The Reptile Database. Available from: http://www.reptile-database.org (accessed 3 August 2023)

Vences, M. (2011) *Lygodactylus tolampyae. The IUCN Red List of Threatened Species*, 2011, e.T172945A6946218.
https://doi.org/10.2305/IUCN.UK.2011-2.RLTS.T172945A6946218.en

Vences, M., Müller-Jung, J., Glaw, F. & Böhme, W. (1996) Review of the *Zonosaurus aeneus* species group, with resurrection of *Zonosaurus subunicolor* (Boettger 1881) (Reptilia: Squamata: Gerrhosauridae). *Senckenbergiana biologica*, 76 (1/2),

47–59.

Vences, M., Miralles, A., Brouillet, S., Ducasse, J., Fedosov, A., Kharchev, V., Kostadinov, I., Kumari, S., Patmanidis, S., Scherz, M.D., Puillandre, N. & Renner, S.S. (2021) iTaxoTools 0.1: Kickstarting a specimen-based software toolkit for taxonomists. *Megataxa*, 6 (2),77–92.
https://doi.org/10.11646/megataxa.6.2.1

Vences, M., Multzsch, M., Gippner, S., Miralles, A., Crottini, A., Gehring, P.-S., Rakotoarison, A., Ratsoavina, F.M., Glaw, F. & Scherz, M.D. (2022) Integrative revision of the *Lygodactylus madagascariensis* group reveals an unexpected diversity of little brown geckos in Madagascar's rainforest. *Zootaxa*, 5179 (1), 1–61.
https://doi.org/10.11646/zootaxa.5179.1.1

Vieilledent, G., Nourtier, M., Grinand, C., Pedrono, M., Clausen, A., Rabetrano, T., Rakotoarijaona, J.R., Rakotoarivelo, B., Rakotomalala, F.A., Rakotomalala, L., Razafimpahanana, A., Ralison, J.R. & Achard, F. (2020) It's not just poverty: Unregulated global market and bad governance explain unceasing deforestation in Western Madagascar. *bioRxiv*, 2020.07.30.229104.
https://doi.org/10.1101/2020.07.30.229104

Waeber, P.O., Wilmé, L., Ramamonjisoa, C., Garcia, C., Rakotomalala, D., Rabemananjara, Z.H., Kull, C.A., Ganzhorn, J.U. & Sorg, J.P. (2015). Dry forests in Madagascar: Neglected and under pressure. *International Forestry Review*, 17 (S2), 127–148.
https://doi.org/10.1505/146554815815834822

Wilmé, L., Goodman, S.M. & Ganzhorn, J.U. (2006) Biogeographic evolution of Madagascar's microendemic biota. *Science*, 312 (5776), 1063–1065.
https://doi.org/10.1126/science.1122806