Zootaxa 5179 (1): 001–061
https://www.mapress.com/zt/

Monograph

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5179.1.1
http://zoobank.org/urn:lsid:zoobank.org:pub:70366A84-EBDE-427D-B525-09E5A2D81EB5

ZOOTAXA

5179

Integrative revision of the *Lygodactylus madagascariensis* group reveals an unexpected diversity of little brown geckos in Madagascar's rainforest

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Magnolia Press
Auckland, New Zealand

Accepted by M. Heinicke: 7 Jul. 2022; published: 1 Sept. 2022

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(*Zootaxa* 5179)

61 pp.; 30 cm.

1 Sept. 2022

ISBN 978-1-77688-580-0 (paperback)

ISBN 978-1-77688-581-7 (Online edition)

FIRST PUBLISHED IN 2022 BY

Magnolia Press

P.O. Box 41-383

Auckland 1041

New Zealand

e-mail: magnolia@mapress.com

https://www.mapress.com/zt

ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

Table of Contents

Abstract

The *Lygodactylus madagascariensis* species group, constituting the subgenus *Domerguella*, currently contains five valid species of inconspicuous dwarf geckos from Madagascar's humid forests, but at least 18 deep genetic lineages have been revealed by recent molecular studies. Given the high morphological similarity of these lineages, taxonomic resolution of this astonishing diversity requires efforts to correctly delimit species, as well as assigning the available nomina to the species-level lineages identified. We here combine DNA sequences of one mitochondrial and two nuclear-encoded gene fragments with morphometric measurements and scale counts, and report evidence for a species status of most of the previously identified lineages. In particular, we rely on sympatric and often even syntopic occurrence of several of these lineages without evidence for genetic admixture, and consistent with subtle morphological differences. Furthermore, the very high divergences of 7.4–23.8% pairwise distances in the relatively conserved mitochondrial 16S rRNA gene, combined with a lack of haplotype sharing in the nuclear-encoded genes and differences in scale counts convinced us that most of the other, allopatrically distributed lineages also represent distinct species. We elevate *L. madagascariensis petteri* to species level and formally name eight new species: *L. salvi* **sp. nov.**, a species from the Sambirano region in northern Madagascar, previously called *L.* sp. 8; *L. tantsaha* **sp. nov.** (*L.* sp. 10), a species occurring sympatrically with *L. madagascariensis* and *L. petteri* on Montagne d'Ambre in far northern Madagascar; *L. roellae* **sp. nov.** (*L.* sp. 17), a species characterized by a striped coloration in all known specimens, from northern Madagascar; *L. winki* **sp. nov.** (*L.* sp. 18), an unstriped species from northern Madagascar but belonging to a subclade mostly distributed in the eastern rainforests of the island; *L. ulli* **sp. nov.** (*L.* sp. 21), a species from the same subclade as *L. winki* but known only from the Marojejy Massif in the North East; *L. fritzi* **sp. nov.** (*L.* sp. 11), a further species of this subclade from coastal lowlands in the Northern Central East; *L. hodikazo* **sp. nov.** (*L.* sp. 23) known from a single specimen collected at the Tsingy de Bemaraha and therefore the only *Domerguella* species known from the West region of Madagascar; and *L. hapei* **sp. nov.** (*L.* sp. 26), an enigmatic species from the Sambirano region characterized by a striped pattern on the throat that is otherwise unknown in the subgenus. Three additional deep mitochondrial lineages of *Domerguella* were identified in our analysis, but could not be further analyzed due to the lack or scarcity of voucher specimens. More field work and collection of voucher specimens is needed to understand their status. Furthermore, the taxonomy of the *Domerguella* subclade occurring in eastern Madagascar, with three described species (*L. guibei*, *L. miops, L. fritzi*), two synonyms (*L. septemtuberculatus, Microscalabotes spinulifer*) and at least two further deep genetic lineages co-occurring in a relatively small area, requires further revisionary work, possibly aided by target-enrichment sequencing of the respective name-bearing types.

Key words: Squamata, Gekkonidae, *Domerguella*, dwarf geckos, cryptic species, integrative taxonomy

Introduction

The reptiles of Madagascar, as the island's entire fauna and flora, are characterized by high species diversity, high proportion of island-endemic species and radiations, and a striking number of range-restricted species. Although distribution, ecology, reproduction, and taxonomy of several reptile groups have been studied more intensively than those of other animal groups, the majority of taxa are still incompletely known. This is also reflected by a lack of taxonomic information, indicated by numerous deep genetic lineages still not revised and scientifically named (Nagy *et al.* 2012). These candidate species are relatively evenly distributed across all main clades of Malagasy reptiles, and consequently, many recent taxonomic papers revised and named single or a limited number of new species, for instance in geckos (e.g., Glaw *et al.* 2010, 2014, 2018; Jono *et al.* 2015; Crottini *et al.* 2011, 2015; Köhler *et al.* 2019; Ratsoavina *et al.* 2011, 2015, 2017, 2019a,b, 2020; Miralles *et al.* 2021). In some groups of geckos and other squamates, the amount of cryptic genetic variation detected was so enormous that long-term efforts integrating multiple lines of evidence—including genetics, external morphology, osteology, and genital morphology, as well as new targeted fieldwork to collect fresh tissue samples and voucher specimens—were necessary to circumscribe species, assign historical types, and eventually describe multiple new species in a series of papers: e.g., chameleons of the *Calumma nasutum* group or leaf-tailed geckos of the *Uroplatus ebenaui* group, where initial diversity was detected by DNA barcoding (Gehring *et al.* 2012; Ratsoavina *et al.* 2013) and species subsequently named and described over several years (Ratsoavina *et al.* 2015, 2017, 2019a,b, 2020; Prötzel *et al.* 2017, 2018, 2020).

One group of Malagasy reptiles with a disproportionately high number of candidate species is the genus *Lygodactylus* Gray, 1864. These dwarf day geckos consist of 71 currently described species across Africa, Madagascar, and parts of South America (Gippner *et al.* 2021). In Madagascar, 22 species are currently known (Puente *et al.* 2009; Uetz *et al.* 2021). These species were most recently reviewed by Puente *et al.* (2009) on the basis of morphology, and organized into four major species groups based on gross morphology. Recent genetic work by Gippner *et al.* (2021) led to a partial rearrangement of species groups, and suggested that these four Malagasy clades do not form a single monophyletic radiation, but rather are the result of complex biogeographic patterns that involved several trans-oceanic dispersal events.

Gippner *et al.* (2021) also revealed that there is an exceptionally high number of unnamed deep genetic lineages in *Lygodactylus*. Most of these belong to a single species group: the arboreal, predominantly rainforest-dwelling *L. madagascariensis* species group, considered as subgenus *Domerguella* Pasteur, 1964. This clade, which is sister to the rest of the genus *Lygodactylus*, contains eight available names (five valid species, one subspecies, and two current synonyms), but at least 18 very deep genetic lineages. The clade is therefore in need of major taxonomic revisions. However, this is far from simple. Work on the taxonomy of *Lygodactylus* geckos is notoriously challenging (Puente *et al.* 2005, 2009). They are difficult to capture, highly active, diminutive lizards (snout–vent length < 40 mm) covered in minute scales, with highly variable and often cryptic coloration. Several key characters for species determination are difficult to assess in living specimens, and only visible under a strong hand lens or dissecting microscope. Even hemipenial features, often useful in species determination among squamates (e.g. Prötzel *et al.* 2015, 2017) do not appear to show distinctive interspecific differences between many species (Puente *et al.* 2009). Thus, an integrative approach drawing on congruence among multiple lines of evidence is necessary in order to resolve the taxonomy of this species group.

Here, we take such an integrative approach in a "first pass" at this group. We address the identity of the available names, and describe the eight new species for which material is currently available to us. Additional specimens will be needed to address the remaining lineages, and only by further sampling across the rainforests of Madagascar will it be possible to fully understand the distribution, origin, and evolution of the high diversity of these cryptic but charming little geckos.

Materials and methods

Molecular methods

The comprehensive database of 1,764 *Lygodactylus* nucleic acid sequences compiled by Gippner *et al.* (2021) provides the molecular basis of this study. The data set consists of 13 genetic markers, five of which are mitochondrial (16S, ND2, ND4, CYTB, COI) and eight nuclear (RAG1, RAG2, CMOS, PDC, POMC, ACM4, BDNF, and

MXRA5). Sampling strategy, laboratory methods and assembly of the 13-marker dataset is adapted from Gippner *et al.* (2021). For the present study, we updated this database by filling the gaps with newly generated sequences especially of supposed *Domerguella* specimens.

Newly sequenced material of *Lygodactylus* specimens were collected in Madagascar between 2000 and 2018 and preserved in 99% ethanol. A standard salt-extraction protocol (Bruford *et al.* 1992) was used for DNA isolation from the collected tissue samples. Amplification of fragments of the mitochondrial genes 16S, ND2, and ND4, as well as RAG1 (two different fragments marked with (V) for Vences and (B) for Bauer; see Gippner *et al.* 2021), CMOS, PDC, and BDNF were conducted 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.6687543). 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. 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: ON798426–ON798467 and ON809114–ON809320). 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.6687543).

Phylogenetic analyses and allele sharing

Sequence alignment for each marker was conducted with MAFFT Version 7.450 by selecting the automatic option for alignment strategy (Katoh & Standley 2013). Aligned sequences were manually checked and trimmed in MEGA 7. A Maximum Likelihood tree of all *Domerguella* 16S sequences was reconstructed by using the RAxML-HPC2 (8.2.12) tool implemented in CIPRES (Miller et al. 2010; Stamatakis 2014). A General Time Reversible model (GTR) set as model of evolution was applied based on the Bayesian Information Criterion from a model testing analysis performed in MEGA 7 (Kumar *et al.* 2016). The number of bootstrap replications for branch evaluation was set to 1000. With the same alignment and substitution model, a phylogenetic reconstruction using Bayesian inference (BI) was performed with MrBayes version 3.2.7a implemented in CIPRES (Ronquist *et al.* 2012). Two parallel runs with four MCMC chains and a sampling of every 10,000th generation were set with a total of 10 million generations. The default burn-in of 25% of trees was used.

In addition, one representative sequence from each lineage of the reconstructed 16S tree was selected and subsequently transferred into the interleaved Nexus file already used by Gippner *et al.* (2021), where the composition and sequence length of the concatenated supermatrix is described. After exclusion of unalignable hypervariable regions the final concatenated sequence for each taxon consists of 10,141 bp. For the partition scheme and selection of the best fitting model of molecular evolution, see Gippner *et al.* (2021). MrBayes version 3.2.7a implemented in CIPRES was applied for Bayesian inference (BI) (Ronquist *et al.* 2012). Four MCMC chains in two parallel runs were set with sampling of every 10,000th generation in a total of 30 million generations. The default burn-in of 25% of trees was used. With the same final concatenated dataset, a maximum likelihood analysis was performed with the RAxML-HPC2 (8.2.12) tool implemented in CIPRES (Stamatakis 2014). The maximum likelihood partitioning scheme was adopted from Gippner *et al.* (2021). Node support was assessed with 1000 bootstrap replicates.

We chose to graphically represent the relationship among alleles (haplotypes) of two different nuclear-encoded genes as haplotype networks. For this, alleles were inferred from RAG1 and CMOS 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 overparameterization. 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

Morphology was examined from genotyped voucher specimens and types. Specimens were examined from the herpetological collections of the Zoologische Staatssammlung München (ZSM), Mention Zoologie et Biodiversité Animale of the University of Antananarivo (UADBA), Muséum National d'Histoire Naturelle, Paris (MNHN), Natural

History Museum, London (BMNH), and Naturmuseum Senckenberg, Frankfurt am Main (SMF). We examined in all individuals a series of characters known to be taxonomically informative in Malagasy *Lygodactylus* (Puente *et al.* 2009), plus a few other traits that we observed to be characteristic for some *Domerguella* lineages. 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; hindlimb length (HIL), measured from the hindlimb insertion to the tip of the longest toe; 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 head length, snout-tympanum distance (STD; from snout tip to center of tympanum) and head height (HH; from ventral limit of 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 postpostmental 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 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 tail base (STT): 0 not visible, 1 small, 2 medium-sized, 3 large-sized. Furthermore also the following additional characters were assessed/verified in each specimen: dorsal ground color (DGC); dorsal color pattern (DCP); ventral color (VC); presence of dorsolateral markings as characteristic for *L. expectatus* (DLM); presence of distinct and regular broad crossbanding on tail, as characteristic for *L. rarus* (CBC); 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 shape of mental scale (MS); posterior contact between mental and first infralabial scale (PMS); symmetry of postmental scales (SPMS).

We did not examine hemipenial structures in the present study. Species of *Domerguella* differ from other Malagasy *Lygodactylus* by their lack of hemipenial serrated ridges with pointed papillae, short pedicel, and poorly defined lobes (Rösler 2000a; Puente *et al.* 2009). Possible differences among species might exist, but to reliably distinguish distinct character states from artefacts caused by different preservation, by seasonal effects, or by incomplete eversion, modern approaches such as micro-CT scanning will be necessary beyond simple visual examination in these small squamates.

Species delineation and associated terminology

We delineate species following the general lineage concept (de Queiroz 1998, 2007), but in general 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. To describe occurrence of lineages, we use geographic regions of Madagascar as originally defined by Boumans *et al.* (2007) which were delimited 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

Analysis of the complete set of 16S rRNA sequences for 199 ingroup samples (alignment length 537 bp; Fig. 1) confirmed the main deeply divergent lineages already identified and discussed in Gippner *et al.* (2021). In that study, these lineages were defined with the aid of a species delimitation analysis using the program ASAP (Puillandre *et al.* 2021), which we therefore did not repeat here. Species partition inferred by ASAP retrieved, for the partition with best (smallest) ASAP score, a total of 18 species-level lineages of *Domerguella* within this dataset, corresponding to the nominal species *L. expectatus, L. guibei, L. madagascariensis, L. miops, L. rarus* as defined herein, plus 13 additional lineages. Of these 13 lineages, we will go on to formally name eight as new species, revalidate a former subspecies name for another one, leave three taxonomically unresolved due to the lack of voucher specimens, and consider one as deep conspecific lineage of *L. guibei* (see also Fig. 1). Minimum interspecific divergences (uncorrected p-distances) between species-level lineages in the 16S rRNA gene fragment ranged from 7.4% (between *L. guibei* and *L. miop*s) to 23.8% (between *L. rarus* and *L.* sp. 24). Only eight comparisons had distances below 10%: *L. guibei* to *L. miops* (7.4%), *L. guibei* to *L.* sp. 11 (9.8%), *L. guibei* to *L.* sp. 18 (8.8%), *L. miops* to *L.* sp. 11 (9.0%), *L. madagascariensis* to *L. petteri* (9.0%), *L. madagascariensis* to *L.* sp. 23 (8.4%), *L. petteri* to *L.* sp. 23 (9.3%), and *L.* sp. 11 to *L.* sp. 19 (8.5%).

Comparison of allocation of individuals to mitochondrial lineages with their differentiation in two fragments of nuclear-encoded genes revealed a lack of haplotype sharing among most of them (Fig. 2). In the RAG1 fragment dataset (101 individuals sequenced for 784 bp), haplotype sharing was only detected between *L. madagascariensis* from localities outside Montagne d'Ambre and *L. petteri*, while haplotypes of *L.* sp. 23 were mixed with those of *L. madagascariensis,* although without sharing specific haplotypes. *Lygodactylus madagascariensis* from Montagne d'Ambre had a distinct set of unique haplotypes. In the CMOS fragment dataset (102 individuals sequenced for 376 bp), all *L. madagascariensis* and *L. petteri* haplotypes were separate, but haplotype sharing was observed between *L. expectatus* and *L. rarus*, between *L. guibei* and *L.* sp. 18, between *L.* sp. 8 and *L.* sp. 17, and between *L.* sp. 20 and *L.* sp. 21.

The Bayesian analysis of the multigene dataset (10,141 bp) for 18 ingroup samples representing all species and candidate species of the *L. madagascariensis* group (= *Domerguella*), plus three outgroups, produced a tree in which all but two nodes had maximum support (Posterior Probability = 1.0; Fig. 3). This phylogenetic hypothesis was fully in agreement with that of Gippner *et al.* (2021) but with higher support of one node (the one of the clade containing *L.* sp. 24, *L.* sp. 26, and *L.* sp. 10), probably due to the additional sequences added to reduce the amount of missing data of the supermatrix in Gippner *et al.* (2021). To maintain consistency with Gippner *et al.* (2021) where the *L. madagascariensis* group was named clade A, we here label the main subclades within the group revealed by the multigene analysis as A1 to A5, for convenience of discussing their phylogeny, morphological differentiation, and biogeography. We found subclade A1, containing two species endemic to the northern Ankarana Massif, to be sister to all remaining species of the *L. madagascariensis* group. The next basal-most node in the group separates subclade A2, containing three candidate species from the North and Sambirano regions, from the remaining species. Sublades A3 and A4 are sister to each other and contain *L. madagascariensis, L. petteri,* and several candidate species, all restricted to northern and western Madagascar; together, A3+A4 are sister to A5, the subclade that contains the lineages occurring in the South East, Southern Central East, and Northern Central East of Madagascar, plus a few candidate species with ranges in northern Madagascar (Fig. 4).

Morphological differentiation

A full table with all original measurements, character states, and counts is provided as Supplementary Information in the Zenodo repository under DOI 10.5281/zenodo.6687543.

The most taxonomically relevant characters and measurements are reported in Table 1. The individuals examined almost invariably showed the defining character states of the *L. madagascariensis* group as compared to other *Lygodactylus*, i.e., first finger small but present, claw on first finger absent, mental shield semi-divided with two post-mentals (the only exceptions being one individual of *L. madagascariensis*, and one individual of *L.* sp. 21, with three postmentals); further by granular dorsal scales; three lamellae under fourth toe (except one individual of *L.* sp. 21 with four lamellae); tail whorls absent.

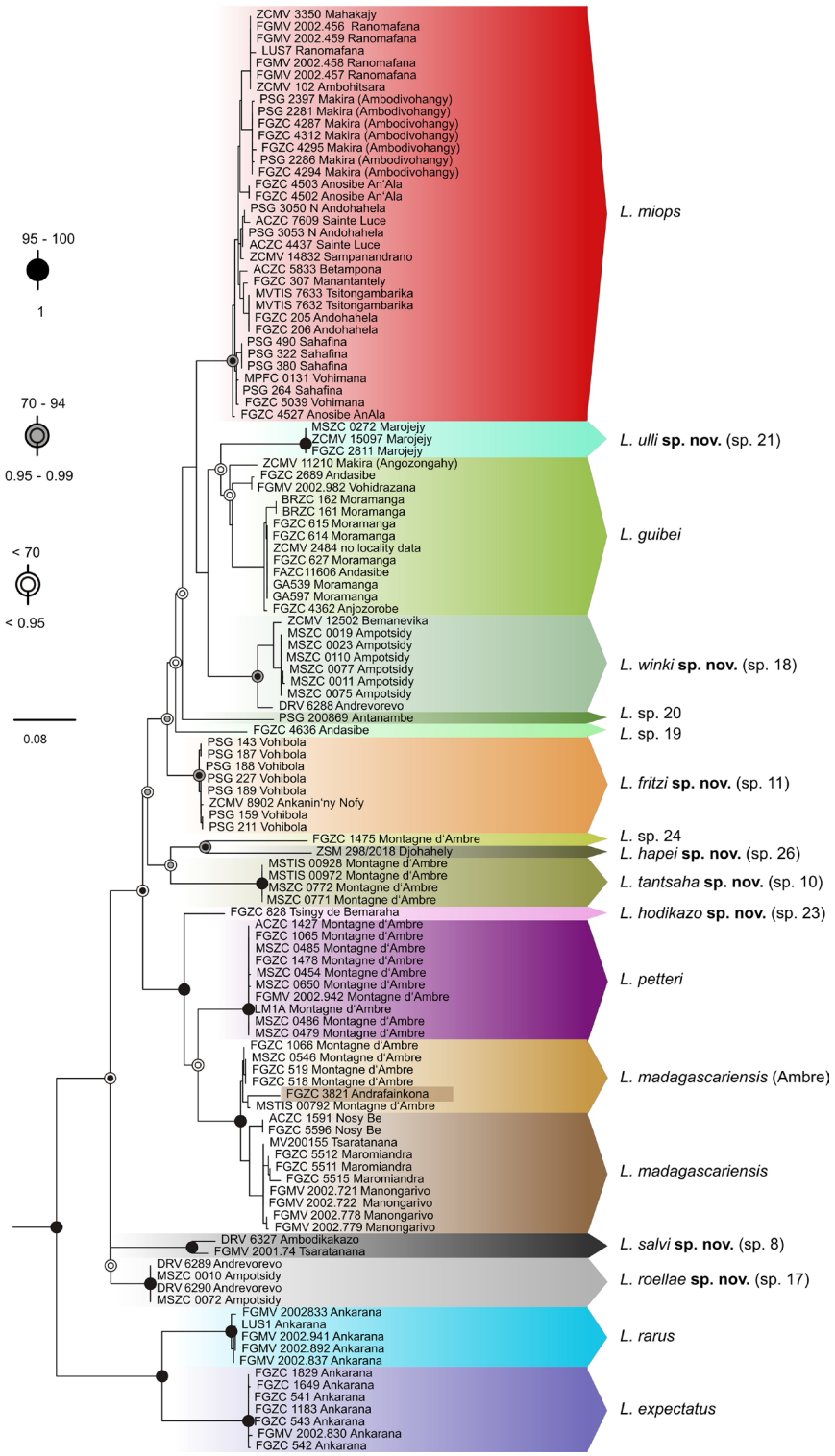

FIGURE 1. Majority-rule consensus tree from a Maximum likelihood analysis based on 537 bp of the mitochondrial 16S rRNA gene, for all available samples of the *Lygodactylus madagascariensis* group. Outer circles of different color mark categories of bootstrap branch support as indicated, inner circles of different color mark categories of Posterior Probability support from a separate Bayesian analysis. Missing circles on the backbone of clade A5 indicate different topology in the ML and BI analysis. Colors correspond to species-level lineages delimited by the ASAP partition with lowest ASAP score, with two exceptions: (i) *L. madagascariensis* samples from Montagne d'Ambre are shown as different clusters to better illustrate its co-occurrence with other lineages at this site, as well as patterns of allele sharing in the nuclear encoded genes (Fig. 2); (ii) the three uppermost samples of *L. guibei* were defined by ASAP as separate lineage but are here considered as conspecific with *L. guibei* in a preliminary way.

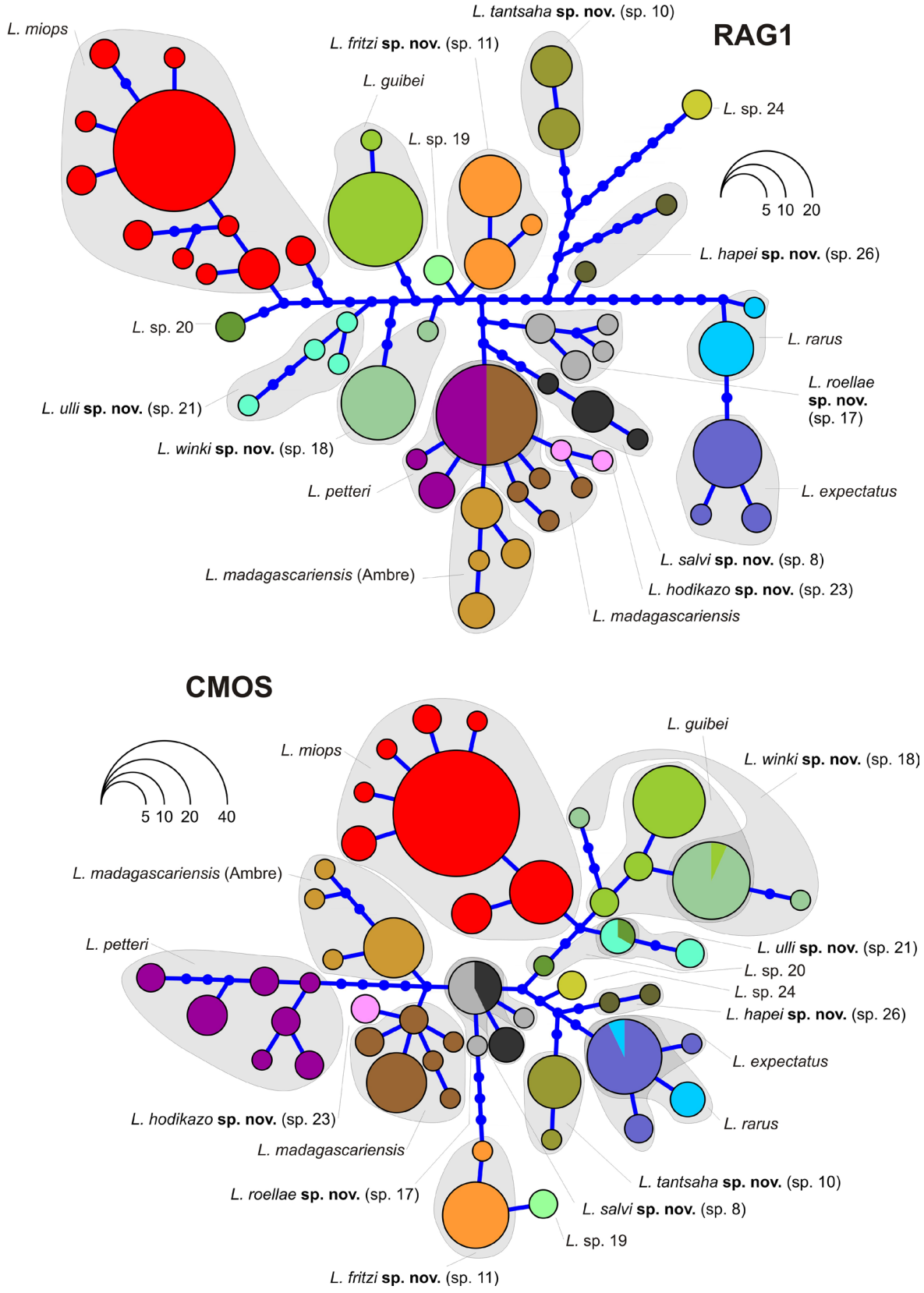

FIGURE 2. Haplotype networks constructed from partial sequences of the nuclear-encoded genes for RAG1 (784 bp) and CMOS (376 bp) for species of the *Lygodactylus madagascariensis* group. Small blue dots represent additional mutational steps or unsampled haplotypes. Colors match those of allocation of individuals to species-level lineages inferred from the 16S dataset and represented in the mtDNA tree (Fig. 1). The networks were constructed from phased sequences and each individual is therefore included twice in each network (circle size proportional to the total number of haplotype sequences).

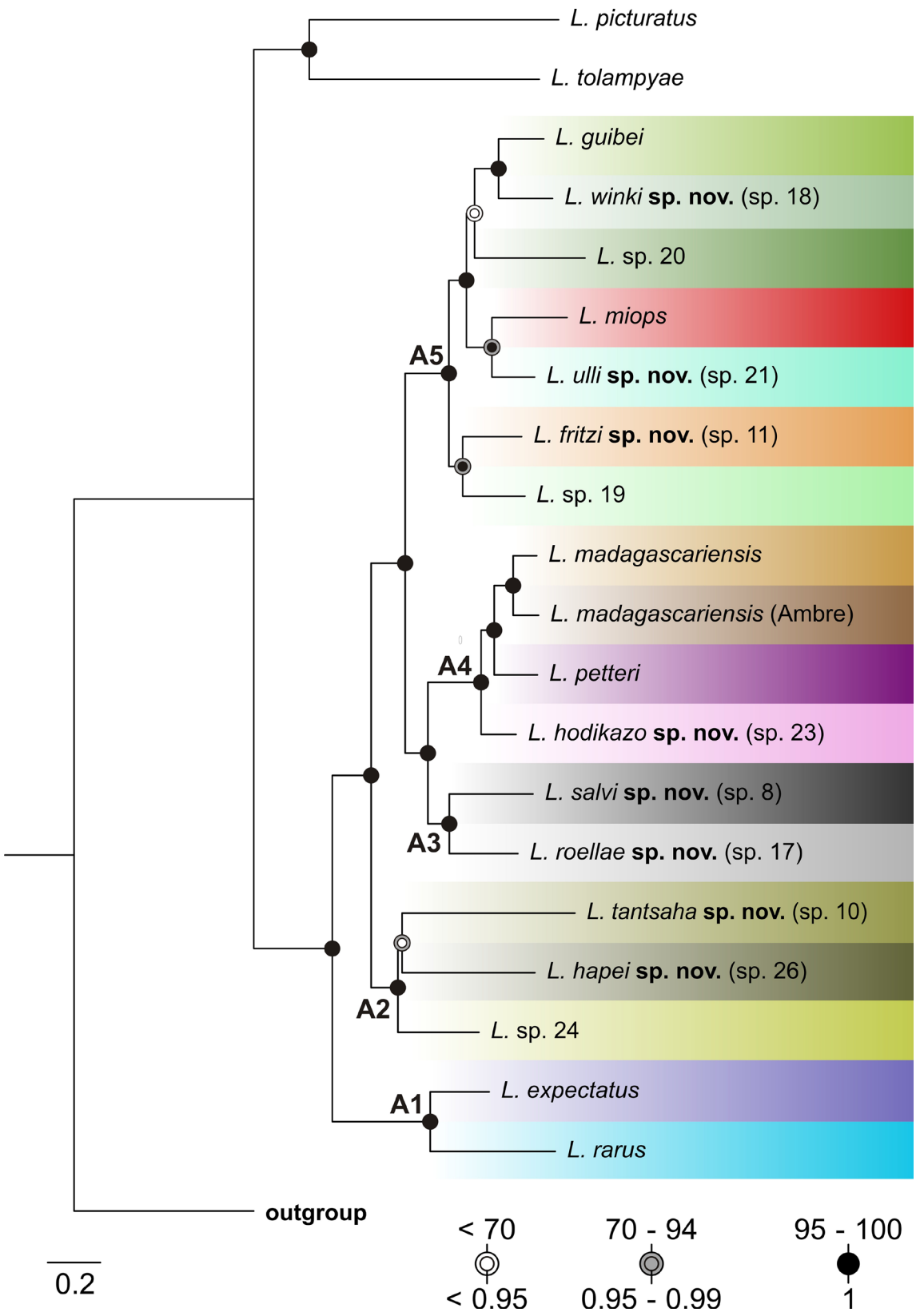

FIGURE 3. Majority-rule consensus tree from a partitioned maximum likelihood analysis of a multigene dataset of 10,141 bp of fragments of five mitochondrial and eight nuclear markers for all species and candidate species in the *Lygodactylus madagascariensis* group. Lineages are colored to match the 16S tree and haplotype networks (Figs. 1–2). A1 to A5 are ad-hoc defined major subclades as discussed in the text. Outer circles of different color mark categories of bootstrap branch support as indicated, inner circles of different color mark categories of Posterior Probability support from a separate partitioned Bayesian analysis.

A detailed comparison of specimens informed by their initial molecular assignment revealed a series of characters (scale counts, skin tubercles, color pattern, body shape) that constituted differences among lineages. We here summarize the most informative differences, which will be documented in further detail in the species accounts and diagnoses below.

The two species included in A1 were morphologically distinct, *L. rarus* due to its long-legged body shape and regularly banded tail and *L. expectatus* due to its enlarged dorsolateral scales compared to miniaturized vertebral scales (resulting in low longitudinal dorsal scale counts if the miniaturized vertebral scales were not taken into account), although we did not identify a shared morphological character state that would enable allocation of the two species together to a clade based on morphology alone.

Several species in the *Domerguella* subclades A2, A4, and especially A3 were characterized by a distinct longitudinally striped pattern in some or all individuals, which in Madagascar was previously only known from an unrelated species (*L. bivittis*): *L.* sp. 8 and *L.* sp. 17 (A3), *L.* sp. 24 (A2). Phenotypes with less distinctly expressed striped pattern were also observed among specimens assignable to *L. petteri* (A4) and *L. miops* (A5), and one specimen tentatively assigned to *L. guibei* (A5).

The presence of dermal spine-like tubercles on the body has been used to coin two species-level nomina in the *L. madagascariensis* group (*septemtuberculatus, spinulifer*; see below), but according to our data, the presence of these small spines along body and tail is rather variable within and among species. However, several species and candidate species in subclade A5 (especially *L. guibei*) are characterized by lateral tubercles at the tail base, present in both sexes but particularly prominent in males (Fig. 5), which constitutes a distinct difference to several other species where these tubercles are entirely lacking or rudimentary, even in adult males with well-developed hemipenes (Fig. 5A–C).

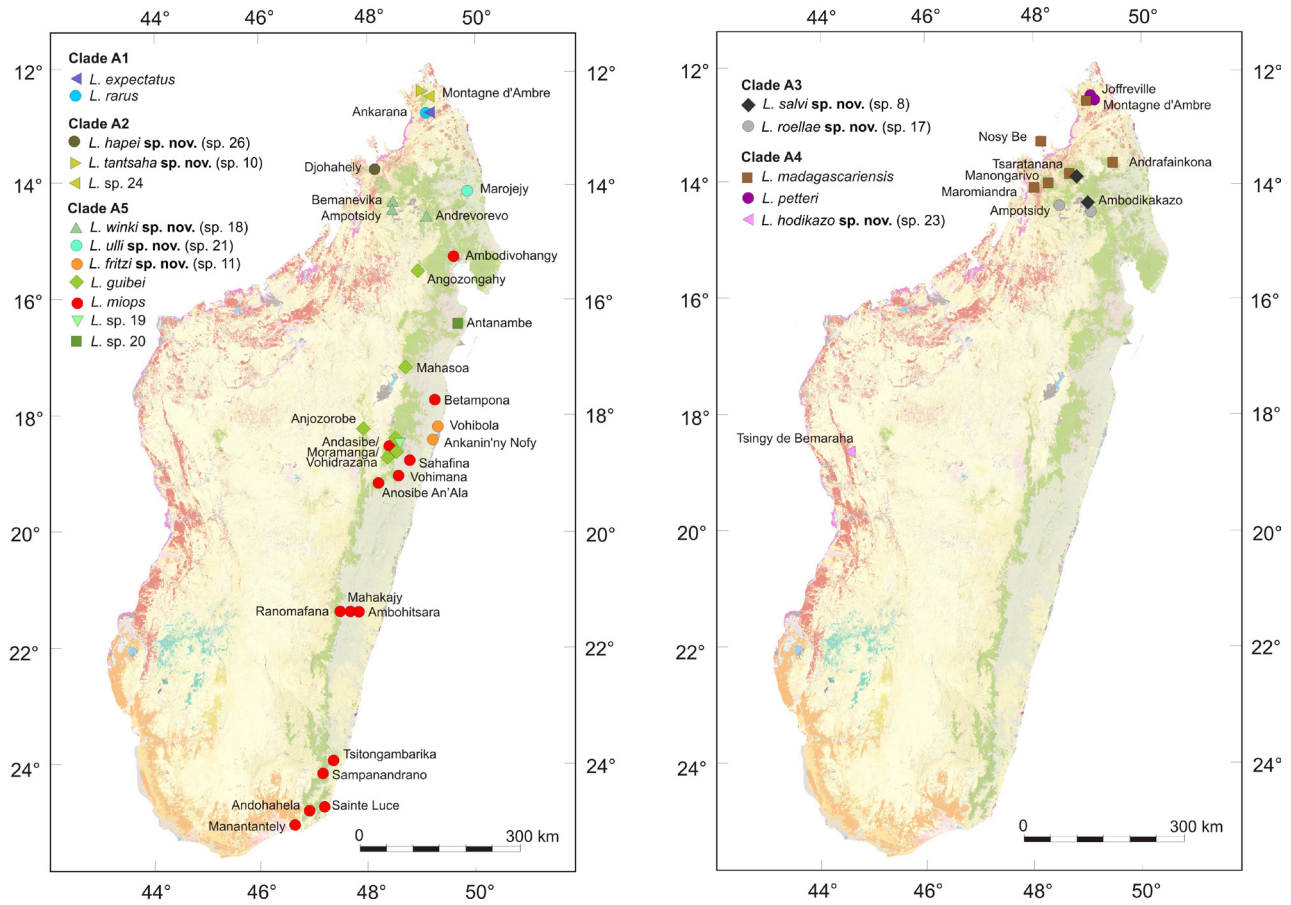

FIGURE 4. Maps showing the distribution of species and candidate species of the *Lygodactylus madagascariensis* group (= subgenus *Domerguella*), as verified by molecular data presented herein. Basemap shows vegetation across Madagascar from the Madagascar Vegetation Mapping Project (Moat & Smith 2007; formerly available at www.vegmad.org). Vegetation is colored as follows: green, humid forest (rainforest); red, western dry deciduous forest; bluish, western subhumid forest; orange, south western dry spiny forest-thicket; yellow, tapia forest.

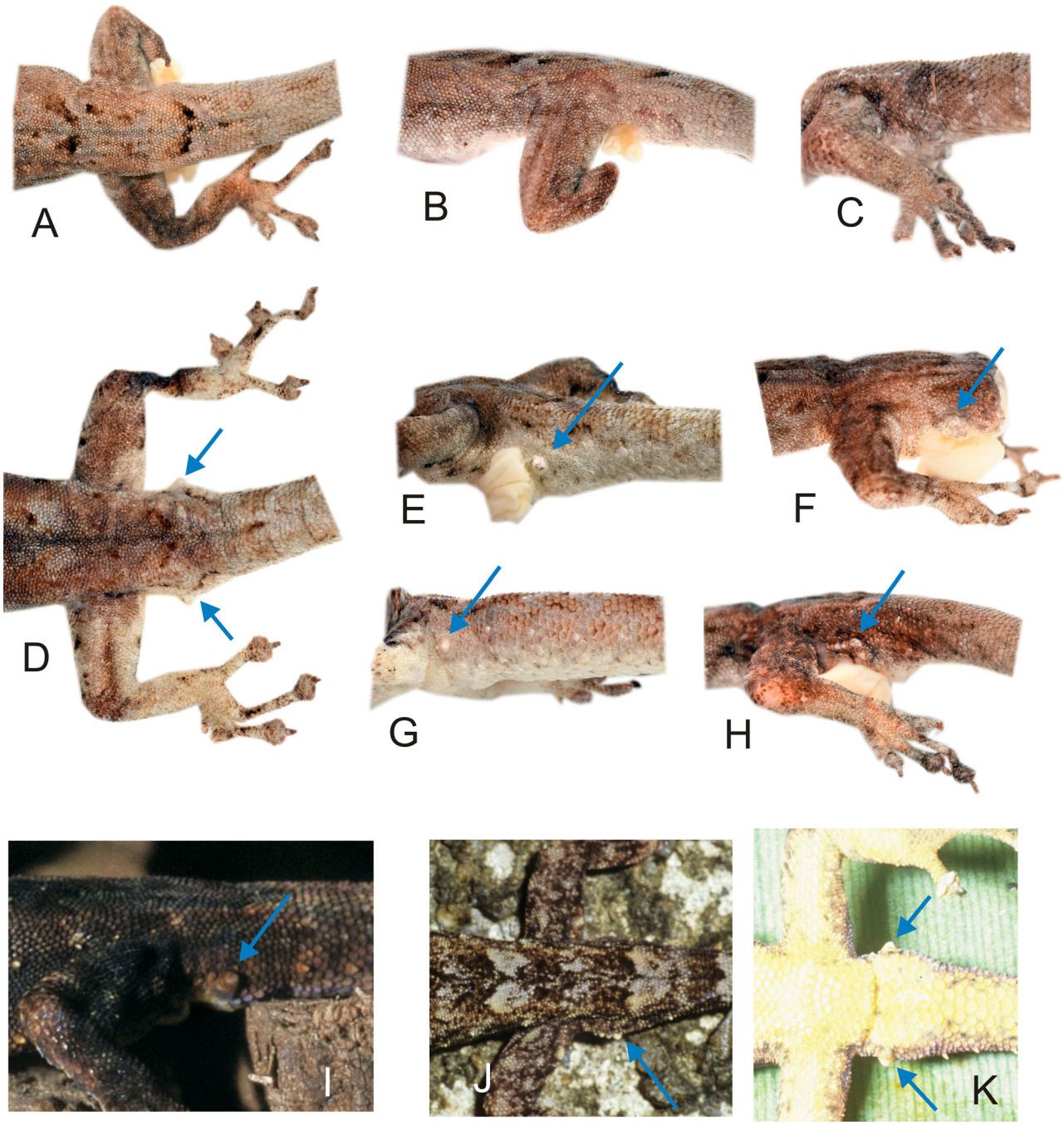

FIGURE 5. Tail base in males of different species of the *Lygodactylus madagascariensis* group, showing presence of distinct tail base tubercles in species primarily belonging to the *Domerguella* subclade A5 (panels D–K) and its absence in two other species (panels A–C). A–B, dorsal and lateral view of tail base in *L. petteri*, ZSM 195/2018. C, lateral view of tail base in *L. expectatus,* ZSM 1540/2008. D–E, dorsal and lateral view of tail base in *L. winki* **sp. nov.**, ZSM 48/2016. F, lateral view of tail base in *L. ulli* **sp. nov.**, ZSM 154/2005. G, lateral view of tail base in *L. guibei*, ZSM 349/2010. H, lateral view of tail base in *L. salvi* **sp. nov.**, ZSM 783/2001 (subclade A3). I, lateral view of tail base in life of a specimen assigned to *L. guibei.* J, dorsal view of tail base in life of a specimen from Nahampoana assigned to *L. miops.* K, ventral view of tail base in life in a specimen assigned to *L. guibei.* Blue arrows point to lateral tail base tubercles. Whitish structures in A, B, E, F, H are everted hemipenes. All specimens facing to the left. Not to scale.

Most scale counts were not particularly informative in diagnosing species-level lineages in the *L. madagascariensis* group, except two: many species and candidate species differed from others (often including close relatives) in the longitudinal counts of ventral and dorsal scales. While the ventral scales can be objectively counted

(from mental shield to cloaca), this is more difficult for dorsal scales, where our counts started after the internasals and ended at the first scale row or whorl of the tail, an ending point that is sometimes not easy to define. However, given that our counts of dorsal scales are much less variable within than between species, we are convinced that they constitute a valid indicator for morphological differentiation if accompanied by very high genetic differentiation as in the case of the geckos studied herein.

Systematic accounts

The following accounts are ordered to facilitate first clarifying the identity of all nominal species of the *Lygodactylus madagascariensis* group (subgenus *Domerguella*), and next diagnosing the new species identified by our molecular screening. Given the high morphological similarity of these geckos, the absence of molecular data for the name-bearing types of all nomina coined to date, and the uncertainty surrounding the morphological variation of most species, this approach is the most efficient option, even if species are not listed in alphabetical or historical order.

We start by defining two microendemic species of the Ankarana limestone massif in northern Madagascar which, according to our molecular phylogenetic tree, form a monophyletic group, that is sister to the clade of all other *Domerguella*: *L. expectatus* and *L. rarus*. These two species are morphologically very different from each other, and each of them is characterized by several unique morphological character states, which allow us to reliably assign the type specimens to the molecular lineages identified from our own samples.

Next, we discuss the identity of two further species from northern Madagascar: *L. madagascariensis* and *L. petteri.* The former was described from the offshore island of Nosy Be, and the type material matches morphologically those specimens belonging to the only genetic *Domerguella* lineage represented in our own Nosy Be collections. The second species, *L. petteri,* was first described as a subspecies of *L. madagascariensis* from Montagne d'Ambre in Madagascar's extreme north; its species status is demonstrated by our results as it occurs syntopically with typical *L. madagascariensis*, has substantial genetic differentiation from *L. madagascariensis* and lacks haplotype sharing with syntopic individuals of that species, and can be distinguished by a few subtle morphological characters. We therefore elevate *petteri* to species level in this paper (see account below).

The last set of nomina we discuss were all described from a rather narrow area in the Northern Central East of Madagascar, around the small town of Moramanga. Assigning these nomina (*guibei, miops, septemtuberculatus, spinulifer*) to the lineages occurring in this area of Madagascar has proven difficult due to a lack of data from several of the genetically identified lineages, but we here tentatively define these taxa based on the available data and applying a taxonomically parsimonious approach—i.e., leaving the definition of these taxa in line with previous accounts, pending future study.

After having assigned all existing nomina to lineages, we proceed with formally proposing scientific names and describing most of the candidate species of the *L. madagascariensis* group, given (i) the extremely deep divergences in mtDNA, (ii) their concordant differentiation in nucDNA, and (iii) the weak but consistent differences in some morphological characters, (iv) partly under conditions of sympatry or parapatry. All this leaves no doubt that they are distinct evolutionary and biological species.

Lygodactylus expectatus Pasteur & Blanc, 1967

Lygodactylus (Domerguella) expectatus Pasteur & Blanc, 1967

Chresonyms:
Lygodactylus expectatus: Kluge (1991); Glaw & Vences (1992, 1994, 2007); Puente *et al*. (2009); Röll *et al.* (2010); Gippner *et al.* (2021)
Lygodactylus (Domerguella) expectatus: Rösler (2000b)

Name-bearing type: male holotype MNHN 1990.1 (original number BP 640).—Type locality: "Karst d'Ambilobe (Ankarana), à une douzaine de kilomètres au NNW de cette localité", according to the original description.—Other types: according to the original description, five specimens were examined but explicitly only two of these were

designated as paratypes, namely MNHN 1990.2–3 (BP 641, female, and BP 642, young female, according to original description).—Etymology: From Latin expectatus = expected. As explained in the original description, G. Pasteur and C.P. Blanc were expecting to find a new species in the karstic regions of the Ambilobe region.

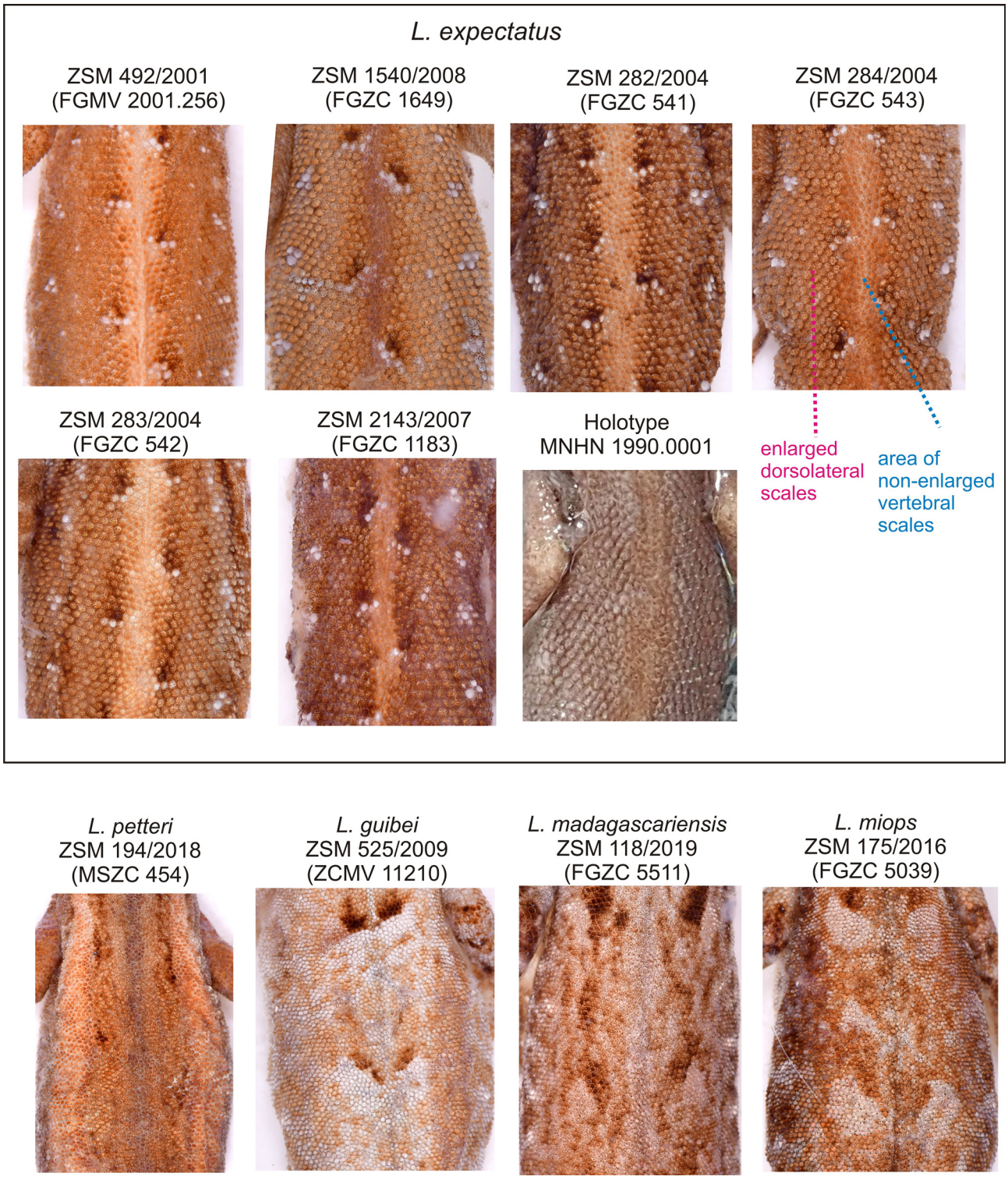

FIGURE 6. View of central dorsum (posterior to forelimb insertion) in seven specimens of *Lygodactylus expectatus*, and four representative individuals of other species. In all *L. expectatus,* including the holotype, the scales in the dorsolateral area are distinctly enlarged, while the vertebral scales are much smaller. In the other species, all scales are roughly of similar size, without obviously enlarged dorsolateral scales. Pictures not to scale.

Identity and Diagnosis. According to the diagnosis given by Puente *et al.* (2009), the species differed from all species in the *L. madagascariensis* group known at the time by its dorsolateral scales, which are enlarged relative to

the dorsal and lateral scales (not distinctly enlarged in the other species), and by the presence of two dark spots in the region of the neck (not distinct in the other species). The enlarged scales in the dorsolateral region, contrasting with the very small scales in the vertebral region, indeed represent a diagnostic character of this species that we could not observe in any other species of *Domerguella* (Fig. 6). This typical character state of *L. expectatus* is visible in all of the genetically characterized specimens collected, as well as the holotype (examined in June 2021, in relatively poor state of preservation). It is also reflected by a low longitudinal count of dorsal scales, of 130 scales or less if counting the enlarged scales (slightly more, with a maximum of 164, if counting the small vertebral scales, but also this value is still smaller than in all other nominal *Domerguella*, overlapping with only one candidate species, *L.* sp. 17). The dark spot in the region of the neck is located anterodorsal to the forelimb region, roughly in the scapular region, and we here name it the scapular semi-ocellus, considering that it is bordered by a whitish row of tubercles dorsally, giving the impression of an ocellus but lacking a ventral light lining. This semi-ocellus is typical for *L. expectatus*, but sometimes weakly expressed, and in such cases easy to confuse with dark lateral markings that can also be seen in other species of *Domerguella*, but often in slightly different positions (Figs. 7–8).

FIGURE 7. Lateral view of head and anterior body in seven specimens of *Lygodactylus expectatus*, and four representative individuals of other species. In all *L. expectatus,* a black spot is visible in the shoulder region, with at least traces of light color along its dorsal edge; this spot, poorly expressed in some specimens, is here called the scapular semi-ocellus. Individuals of other species of *Domerguella* may also have dark markings in the scapular region, but these usually are not at all bordered by light color dorsally, and often are in a more anterior position, as exemplified by four representative pictures of other species. Asterisks mark photos that were mirrored. Pictures not to scale.

Given these two diagnostic character states, which both have been verified in the holotype and in the genotyped specimens, along with the provenance of all these specimens from the Ankarana Massif, there is no doubt about the correct attribution of our specimens to *L. expectatus*.

The species is rather small sized, with adult SVL 24.3–29.7 mm vs. a maximum size larger than 30 mm in several other species. There are no dorsolateral tubercles and no spiny tubercles at the tail base as they are characteristic for several other *Domerguella*, and no distinct, regular broad crossbands on the tail as in *L. rarus* (see below). According to the available counts, the species has 87–98 ventral scales longitudinally.

Distribution. *L. expectatus* is only known from its type locality, the Ankarana Massif. According to the original description (Pasteur & Blanc 1967), additional specimens also came from "Ambilobé" and from "Region de Diégo-Suarez", but we have not verified the identity of the respective vouchers, and the localities are not precise enough for firmly concluding they are not in the Ankarana Massif (which is geographically located inbetween the towns of Ambilobe and Antsiranana (=Diego-Suarez).

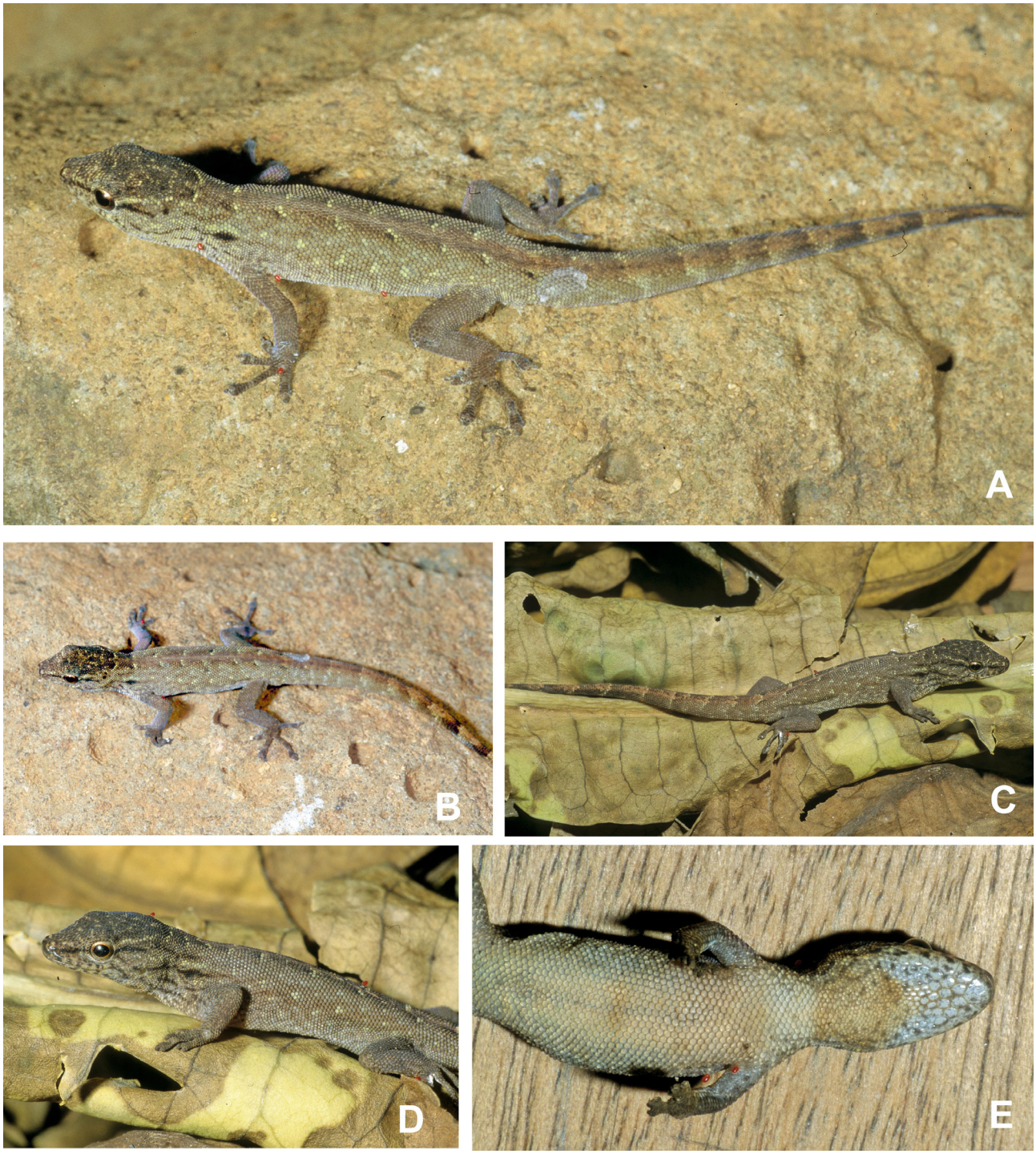

FIGURE 8. Photos of specimens of *Lygodactylus expectatus* from Ankarana in life. A, B, Adult male ZSM 284/2004 (FGZC 543), photographed in 2004. C, D, E, Specimen photographed in 2001 by Gerardo García, not collected.

Lygodactylus rarus Pasteur & Blanc, 1973

Lygodactylus (*Domerguella*) *rarus* Pasteur & Blanc, 1973

Chresonyms:

Lygodactylus rarus: Kluge (1991); Glaw & Vences (1992, 1994, 2007); Puente *et al.* (2005, 2009); Röll *et al.* (2010); Gippner *et al.* (2021)

Lygodactylus (Domerguella) rarus: Rösler (2000b)

Name-bearing type: female holotype, MNHN 1990.6—Type locality: "haute de la falaise orientale du karst d'Ambilobe (extrémité nord-est du Massif de l'Ankarana)", according to the original description.—Other types: none according to original description.—Etymology: derived from Latin *rarus* (rare, unusual).

Identity and Diagnosis. According to the diagnosis of Puente *et al.* (2009) this is a rather large-sized endemic of limestone karst areas of northern Madagascar, characterized by a long-legged, long-tailed and slender appearance. It differs from all species in the *L. madagascariensis* group by the presence of broad crossbands in the tail, of alternate light gray/brown color (Figs. 9–10). Although other *Domerguella* also can have tail crossbands, these are usually irregular, typically with alternating sections which start light brown or beige, gradually become darker to end in a somewhat posteriorly concave narrow dark line that then posteriorly borders sharply on the next light portion. In contrast, the crossbands of *L. rarus* typically consist of alternating brownish vs. gray portions which rather sharply border at each other, the brown portions typically being broader than the gray portions (Fig. 9). This typical pattern is also visible in the holotype which, upon examination in 2021, was in a quite poor state of preservation. The species also differs from all other *Domerguella* by the highest number of longitudinal ventral scales along the body (119–139, with 125 longitudinal ventral scales in the holotype; all other *Domerguella* have at most 110 ventral scales).

FIGURE 9. Tails of preserved specimens of *Lygodactylus rarus* and six other species of the subgenus *Domerguella* for comparison. Note the very regular dark-light crossbands characterizing *L. rarus,* including the holotype. Not to scale.

In addition, this species is also characterized by a particularly slender body and long limbs (Fig. 10): relative hindlimb length (HIL/SVL) is 0.56–0.60 in *L. rarus,* vs. a maximum of 0.50 in all but one other *Domerguella*. The only other *Domerguella* species with long hindlimbs >0.5 is *L.* sp. 18, but also this species only reaches a ratio value of 0.54, thus shorter than in *L. rarus*.

The three diagnostic character states (tail crossbands, large number of ventral scales, long hindlimbs) are all recognizable in the holotype, and in the genetically characterized specimens collected by us. All these specimens were collected in the Ankarana Massif. Therefore, there is no doubt about the identity of *L. rarus,* and the molecular data herein can confidently be assigned to this species.

Furthermore, *L. rarus* is distinguished from *L. miops* and especially *L. guibei* by the absence (vs. presence) of dorsolateral tubercles and spiny tubercles at the tail base. It is further distinguished from the sympatric *L. expectatus* by its non-enlarged dorsolateral scales (vs. enlarged), absence of dark spots on the neck (vs. presence), and larger size (adult SVL 31.6–36.5 mm vs. 27.0–29.7 mm).

Distribution. *L. rarus* is reliably only known from its type locality, the Ankarana Massif. Pasteur & Blanc (1973) also report the species from Mangindrano (located at 1300 m a.s.l. on the Tsaratanana Massif), based on two juveniles that hatched from eggs collected in an abandoned bird nest. We here consider this record as in need of confirmation, given the uncertain attribution of these two hatchlings.

FIGURE 10. Specimen of *Lygodactylus rarus* from Ankarana in life, photographed in 2003 (not corresponding to any of the morphologically examined voucher specimens).

Lygodactylus madagascariensis (Boettger, 1881)

Scalabotes madagascariensis Boettger, 1881

Chresonyms:
Lygodactylus madagascariensis: Boulenger (1885), Puente *et al.* (2005)
Lygodactylus madagascariensis (partim; including *petteri* as subspecies): Kluge (1991); Glaw & Vences (1992, 1994, 2007); Puente *et al.* (2009); Röll *et al.* (2010); Gippner *et al.* (2021);
Lygodactylus (Domerguella) madagascariensis: Pasteur (1965a)
Lygodactylus (Domerguella) madagascariensis (partim; including *petteri* as subspecies): Pasteur & Blanc (1967)
Lygodactylus (Domerguella) madagascariensis madagascariensis: Rösler (2000b)

Name-bearing type: male lectotype SMF 8937 (designated by Mertens 1967), collected by A. Stumpff. Krüger (2001) considered SMF 8937 as holotype.—Type locality: Nosy Be; "hab. in insula Nossi-Bé rarus", according to the original description.—Other types: One paralectotype (the description was based on two specimens "(2 spec.)" according to the original description).—Etymology: name derived from its general provenance, Madagascar.

Identity and Diagnosis. The lectotype of *Lygodactylus madagascariensis* was collected on the offshore island of Nosy Be. It is an adult male characterized by the absence of character states diagnostic for other species: it has no enlarged dorsolateral tubercles (as *L. expectatus*), no regular crossbands on the tail and not particularly long hindlimbs (as *L. rarus*), and no enlarged tubercles at the base of the tail.

According to our molecular data, only one genetic lineage of *Domerguella* has been found on Nosy Be (two sequences available). This same lineage also occurs in several forests of relatively low elevation in the Sambirano region (to which Nosy Be also belongs): Tsaratanana (Andampy), Manongarivo, Maromiandra. These localities also host many other species of amphibians and reptiles occurring on Nosy Be (e.g. Penny *et al*. 2017), supporting the biogeographic assignment of the name *L. madagascariensis* to this lineage.

The available material of this lineage also agrees in all studied morphological characters with the holotype, for instance in the number of longitudinal ventral scales (106 in the holotype vs. 106–138 in the other specimens) and dorsal scales (246 vs. 205–258). The species is comparatively small (SVL 28.5–34.0 mm) and in many specimens

shows a rather typical color pattern of irregular beige patches arranged in longitudinal rows on the brown dorsum, along with irregular dark brown pattern (Fig. 11).

A genetically slightly divergent variant of *L. madagascariensis* is also present on Montagne d'Ambre, an isolated mountain in extreme northern Madagascar. This is of relevance because *L. madagascariensis petteri* has been described from this mountain as a subspecies. In the subsequent species account we will show that the name *petteri* does not apply to the *L. madagascariensis* specimens from Montagne d'Ambre but to another, sympatric lineage, thus justifying the elevation of *petteri* to species status.

Distribution. *L. madagascariensis* is reliably known from (1) its type locality Nosy Be, (2) Manarikoba Forest on the western slope of the Tsaratanana Massif (Andampy Campsite), (3) Manongarivo, (4) Maromiandra, (5) Andrafainkona, and (6) Montagne d'Ambre. These localities are in the Sambirano region and the North regions of Madagascar.

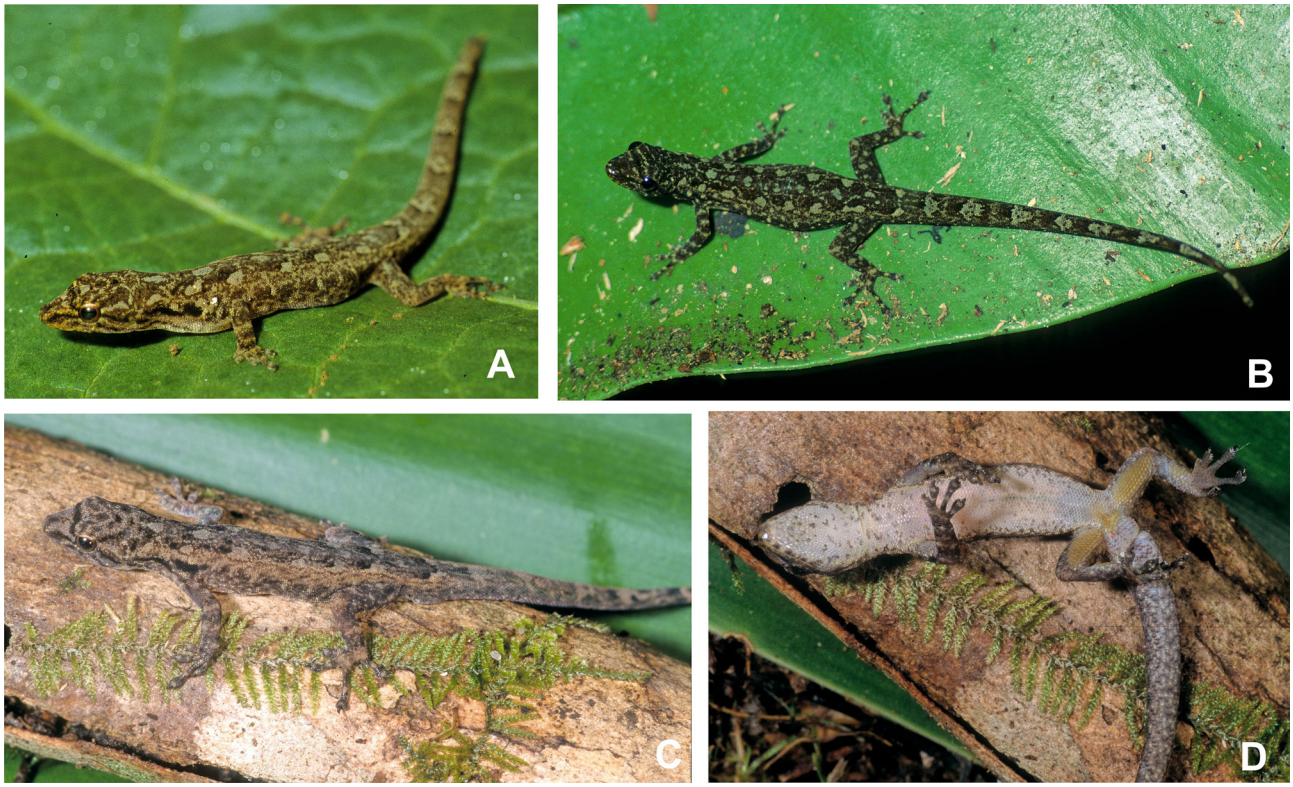

FIGURE 11. Specimens of *Lygodactylus madagascariensis* in life. A, B, Specimens from the type locality Nosy Be photographed in 1992 (not corresponding to any voucher or sample studied herein; identification by typical color pattern and provenance. C, D, Adult male ZSM 832/2003 from Manongarivo, photographed 2003.

Lygodactylus petteri Pasteur & Blanc, 1967

Lygodactylus madagascariensis petteri Pasteur & Blanc, 1967

Chresonyms:
Lygodactylus madagascariensis petteri: Kluge (1991); Glaw & Vences (1992, 1994, 2007); Puente *et al.* (2009); Gippner *et al.* (2021)
Lygodactylus (Domerguella) madagascariensis petteri: Rösler (2000b)

Name-bearing type: holotype MNHN 1990.4, female.—Type locality: "Montagne d'Ambre, forêt ancienne-Roussettes" according to the original description.—Other types: two paratypes; MNHN 1990.5, male; and MNHN 1893.194.—Etymology: eponym for Jean-Jacques Petter.

Identity and Diagnosis. This nomen was coined for specimens from Montagne d'Ambre that were considered to be a subspecies of *L. madagascariensis*. According to the original description, this subspecies was purported to differ from typical *L. madagascariensis* by fewer scales in general (i.e., lower values in various scale counts), sug-

gesting overall larger scales; a larger body size; a different coloration (beige vs. brown); and some other possible differences. Indeed, our measurements and scale counts of the name-bearing type (holotype) and one paratype confirmed these are relatively large-sized (SVL 33.2–35.0, thus at and slightly beyond the upper size limit of *L. madagascariensis*) and have lower longitudinal counts of dorsal scales (189 in the holotype; vs. 205–258 in *L. madagascariensis*) and ventral scales (102 in the holotype and 103 in one paratype; vs. 106–138 in *L. madagascariensis*). This suggests the name *petteri* should be applied to one of the *Domerguella* lineages occurring at Montagne d'Ambre.

One of these (called *L.* sp. 10 by Gippner *et al.* 2021) appears to reach rather large-sizes (36.9 mm SVL in one specimen) but has relatively high longitudinal counts of dorsal scales (239–240 in two available specimens), thus differing from the types of *L. petteri.* This lineage (known only from the west slope of Montagne d'Ambre) represents a new species that will be formally named and described below.

Another lineage from Montagne d'Ambre (*L.* sp. 24) is represented by only one genetic sample, the voucher of which was not available for examination. Unfortunately, no information at all on the coloration or morphology of this lineage is available. We can only hypothesize from its rarity (no further specimens found despite intensive surveys in Montagne d'Ambre) that it is unlikely to correspond to the types of *petteri*.

The third lineage is the one that we have genetically assigned to *L. madagascariensis* above, and the one individual from Montagne d'Ambre examined (Table 1) agrees well with topotypical specimens of this species, but not with the *petteri* types.

However, a fourth lineage from Montagne d'Ambre agrees in all morphological characters very well with the *petteri* types: it consists of relatively large specimens (SVL in our material 30.3–38.5 mm) with few ventral scales (101–113 vs. 102–103 in the types) and dorsal scales (209–222 vs. 189 in the holotype). We therefore are confident that the specimens belonging to this lineage are conspecific with the types of *L. petteri*. Since this lineage co-occurs on Montagne d'Ambre with *L. madagascariensis* with deep genetic differentiation in both mitochondrial and nuclear genes, we conclude that the nomen *petteri* applies to a full species, *Lygodactylus petteri*, and we therefore herewith formally elevate it to species level.

It needs to be emphasized that due to a lack of comparative morphological data of the only specimen of *L.* sp. 24 we cannot fully exclude that this lineage also matches morphologically the holotype of *L. petteri* and may be conspecific with it. Collection of additional material of *L.* sp. 24, or alternatively, molecular "archival DNA" data from the holotype of *L. petteri,* is needed to fully ascertain the identity of these geckos from Montagne d'Ambre. However, independent from these remaining questions, it appears we can conclude with sufficient reliability that *L. petteri* is not conspecific with *L. madagascariensis* from which it differs morphologically, and we confirm it is distinct from *L*. sp. 10, which is described as a new species below.

No clear and consistent differences in color or pattern were found between *L. madagascariensis* and *L. petteri*; both showed a considerable variation in dorsal pattern (near-uniform to heavily patterned in *L. madagascariensis* vs. asymmetrical series of rather small dorsolateral markings or striped phenotype in *L. petteri*). However, the two specimens of *L. petteri* for which life coloration is known (Fig. 12) do not show the longitudinal rows of large beige patches typical for many *L. madagascariensis,* and furthermore, the male specimen ZSM 195/2018 has yellow elements dorsally, which we have not seen in any *L. madagascariensis.* Ventrally the throat is yellowish and ranged from near unspotted to weakly and irregularly spotted in both species.

According to the original description of *L. petteri* by Pasteur & Blanc (1967), it differs from *L. madagascariensis* by several characters, which we review here. First of all, *L. petteri* purportedly has fewer scales (and thus larger ones) in general (characters 9, 12, 13, 17, 31, 32, 33 of Pasteur & Blanc 1967). This agrees with our findings for longitudinal counts of dorsal and ventral scales, while for instance the number of supralabials (character 9 of Pasteur & Blanc 1967) does not clearly differ between the two species according to our data. The authors also reported a larger body size for *L. petteri,* which is in agreement with our data, as well as differences in coloration and in sexual dimorphism, and a possibly larger size of preanal pores in *L. petteri.* Once more extensive series of both species become available, it will be worth examining whether these characters may indeed constitute diagnostic differences.

Natural history. A half-digested specimen of *L. petteri* was regurgitated by a young *Compsophis* sp. aff. *laphystius* (Hutter *et al.* 2018). Two specimens of *L. petteri* (ACZC 1407 and ACZC 1427) were found under the bark of *Eucalyptus* sp. trees at the Gîte d'Étape site on Montagne d'Ambre.

Distribution. *L. petteri* is only known from its type locality, Montagne d'Ambre.

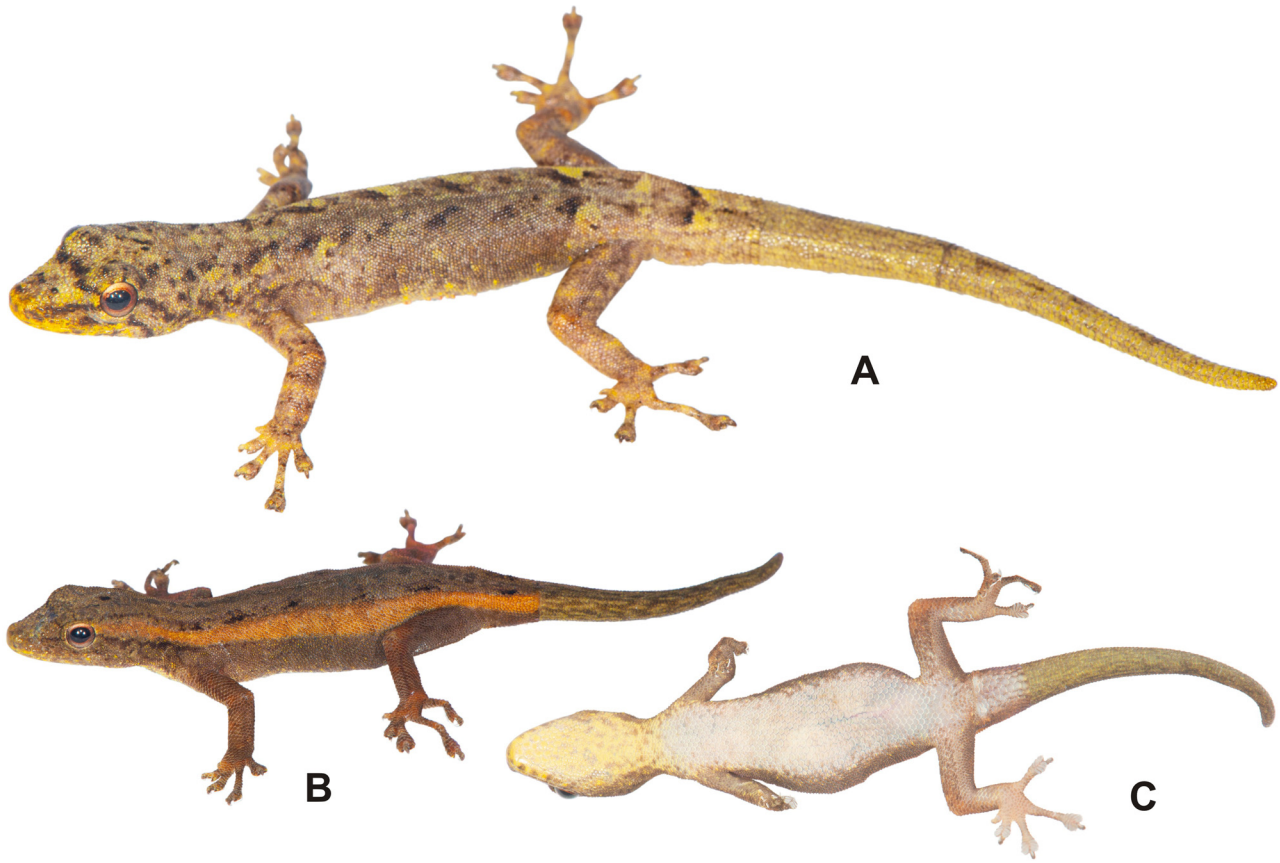

FIGURE 12. Photos of specimens of *Lygodactylus petteri* from Montagne d'Ambre in life. A, Adult male ZSM 195/2018 (MSZC 485); B, C, Female ZSM 194/2018 (MSZC 454) in dorsolateral and ventral views. Not to scale.

Lygodactylus miops Günther, 1891

Lygodactylus miops Günther, 1891

Synonyms
Microscalabotes spinulifer Boettger, 1913
Lygodactylus septemtuberculatus Angel, 1942

Chresonyms:
Lygodactylus septemtuberculatus: Kluge (1991)
Lygodactylus (Domerguella) miops: Pasteur (1965a)
Lygodactylus (Lygodactylus) septemtuberculatus: Rösler (2000b)
Lygodactylus miops: Kluge (1991); Glaw & Vences (1992, 1994, 2007); Puente *et al.* (2005, 2009); Röll *et al.* (2010); Gippner *et al.* (2021)

Name-bearing type: holotype, BMNH 1946.8.22.55, female.—Type locality: "Senbendrana", Madagascar according to the original description (probably referring to Sahembendrana; see Blommers-Schlösser & Blanc 1991).—Other types: none according to original description.—Etymology: From Latin (originally Greek) miops = short sighted and probably referring to the large eyes of the species highlighted in the original description.

Identity and Diagnosis. Our data show the presence of five genetic lineages in the general area of the Northern Central East of Madagascar whence *L. miops* has been described. These include the lineages commonly named *L. guibei* and *L. miops*, as well as the candidate species *L.* sp. 11, *L.* sp. 19, and *L.* sp. 20, all belonging to subclade A5. Of these lineages, no material for morphological examination was available for *L.* sp. 19 and *L.* sp. 20. At the same time, there are four historical nomina described from this general region, all without genetic data for the name-bear-

ing types: *Lygodactylus miops* Günther, 1891; *Microscalabotes spinulifer* Boettger, 1913; *Lygodactylus septemtuberculatus* Angel, 1942; *Lygodactylus guibei* Pasteur, 1965a.

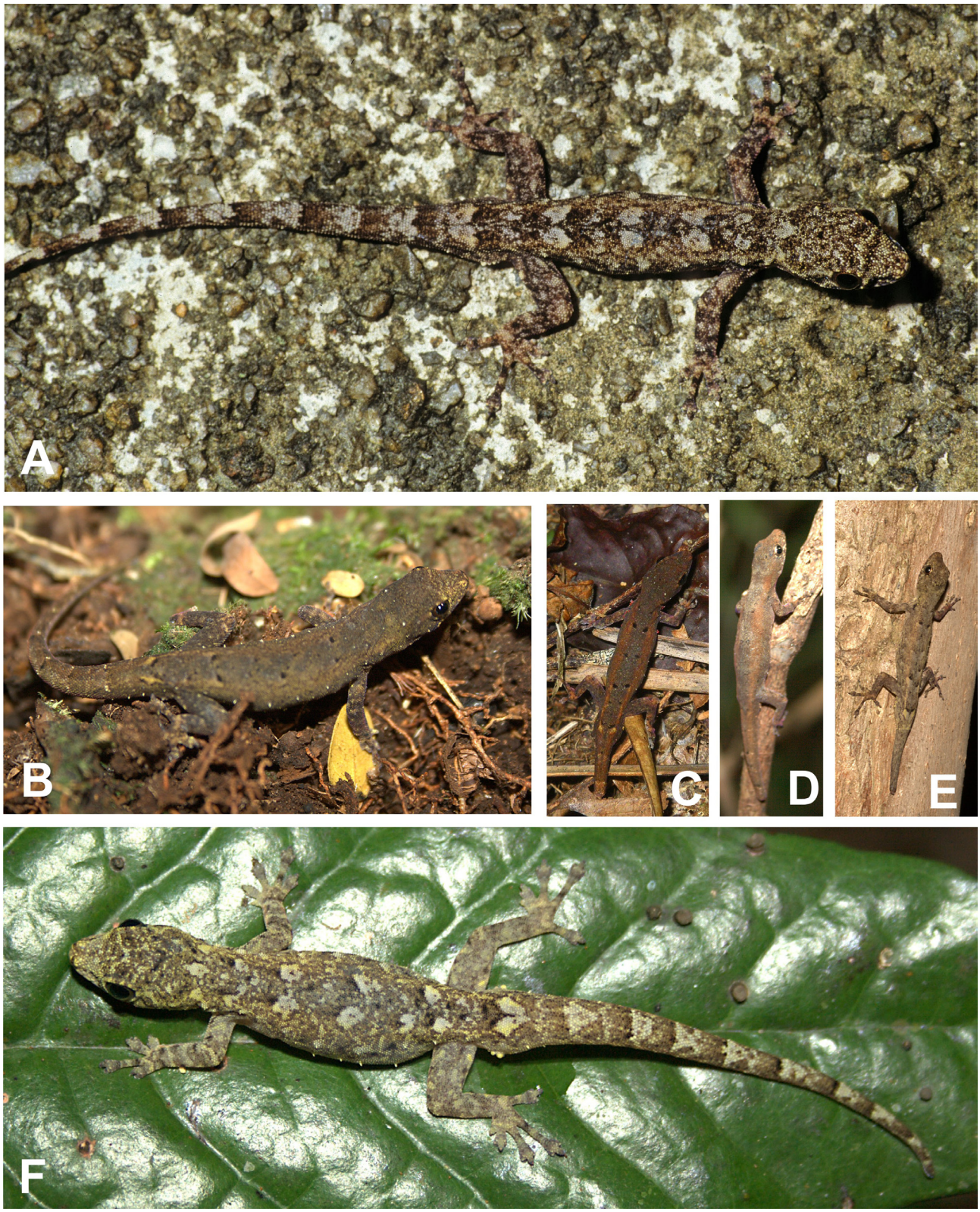

FIGURE 13. *Lygodactylus miops* in life. A, specimen from Nahampoana probably assignable to this species, photographed 1992 (not genotyped and not assignable to a voucher specimen). B–F, specimens from Betampona, all genetically identified by DNA barcoding with sequences of the COI gene (voucher specimens not collected). B, sample number ACZC 5544 (ACP1884); C, sample number ACZC 5666 (ACP1947); D, sample number ACZC 5478 (ACP1843); E, sample number ACZC 5420 (ACP1807); F, sample number ACZC 5467 (ACP1839).

We here continue to define the relatively small-sized lineage that is widespread mostly in low elevations along much of Madagascar's east coast as *L. miops* (as in Puente *et al.* 2009), based on the following rationale: (i) several of the specimens genetically assigned to this lineage share with the *L. miops* holotype a high count of infralabial scales (INFL = 8), which is not observed in specimens assigned to *L. guibei* (INFL = 6 or 7)*;* (ii) the count of internasal scales (IN = 3) of the *L. miops* holotype is higher than in any specimen assigned to *L. guibei* (IN = 1 or 2) but is found in two other individuals of this genetic lineage; (iii) with an SVL of 29.9 mm (according to our own, new measurements) the holotype fits well the size range of other individuals usually assigned to *L. miops* (27.2–31.2 mm), while several specimens of *L. guibei* reach SVLs between 34.0–39.5 mm; (iv) most importantly, the longitudinal counts of dorsal and ventral scales are larger than in all individuals assigned to *L. guibei* (LCDS 233 vs. 170–220; LCVS 113 vs. 87–109)*,* and agree with those of other specimens usually assigned to *L. miops* (LCDS 205–242, LCVS 98–113); (v) the tail base tubercles are distinct and medium-sized as in other males usually assigned to *L. miops*; (vi) finally, the *L. miops* holotype has a distinct pattern with light dorsolateral bands (already mentioned in the original description), which is rarely found in subclade A5 but observed in genotyped individuals from Betampona (e.g. Fig. 13C). The *L. miops* holotype also differs from the sole voucher specimen of *L.* sp. 11 available for morphological examination by a higher number of dorsal tubercles, lower dorsal scale count, higher ventral scale count, and more distinct tubercles at tail base. We here consider *L.* sp. 11 as a distinct species, *L. fritzi* **sp. nov.**, and provide additional comparisons and justifications (including a detailed discussion of the *L. miops* type locality) in the diagnosis of that species below. However, based on the available data we cannot fully exclude that the *L. miops* holotype is conspecific with *L.* sp. 19 or *L.* sp. 20 for which no morphological data are available.

Synonyms. We consider two nomina to be synonyms of *L. miops*, in agreement with current taxonomy: *Microscalabotes spinulifer* Boettger, 1913 with the lectotype (designated by Mertens 1967) SMF 8931, collected by F. Sikora at Moramanga; and *Lygodactylus septemtuberculatus* Angel, 1942 with the holotype MNHN 1893.63 as well from Moramanga. Both these nomina agree with the lineage here considered to represent *L. miops* by their relatively high longitudinal counts of dorsal and ventral scales (LCDS 240 (*spinulifer)* and 225 (*septemtuberculatus*); LCVS 107 and 102, vs. LCDS 205–242 and LCVS 98–113 for specimens assigned to *L. miops*; Table 1), and relatively small body size (28.5 and 29.0 mm, vs. 27.2–31.2 mm for specimens assigned to *L. miops*; Table 1). The same morphological characters are also found in *L.* sp. 11, but this lineage is known from coastal localities and has not been found in or nearby Moramanga so far.

Natural history. In Betampona this species is very common and can be found both in disturbed areas and in densely forested habitat. Here the species is often found in the leaflitter, on twigs or along the partially aerial roots of larger trees. This species generally roosts on the leaves of small bushes (including the invasive strawberry guava).

Distribution. *L. miops* as understood here is one of the most widespread species of the *L. madagascariensis* group, occurring in multiple localities along the eastern coast of Madagascar, which encompass the regions South East, Southern Central East, Northern Central East, and North East. It is known from (1) the type locality Senbendrana (=Sahembendrana or Sahambendrana? For a detailed discussion of this locality, see the account of *L. fritzi* **sp. nov.** below), and the type locality of its two synonyms, (2) Moramanga. Furthermore, genetically verified records (in a south–north direction) originate from (3) Manantantely, (4) Andohahela, (5) a site north of Andohahela, (6) Sainte Luce, (7) Sampanandrano, (8) Tsitongambarika, (9) Ranomafana, (10) Ambohitsara, (11) Mahakajy, (12) Anosibe Anala, (13) Vohimana, (14) Sahafina, (15) Betampona, (16) Makira (Ambodivoahangy)..

Lygodactylus guibei Pasteur, 1965

Lygodactylus (Domerguella) guibei Pasteur, 1965

Partial chresonymy
Lygodactylus guibei: Kluge (1991); Glaw & Vences (1992, 1994, 2007); Puente *et al.* (2005, 2009); Röll *et al.* (2010); Gippner *et al.* (2021)
Lygodactylus (Domerguella) guibei: Rösler (2000b).

Name-bearing type: holotype MNHN 1993.60 from "Périnet (Est)" (=Andasibe), according to the original description.—Other types: According to the original description, there were two paratypes; we only were able to locate MNHN 1933.156.—Etymology: Eponym for Jean Guibé.

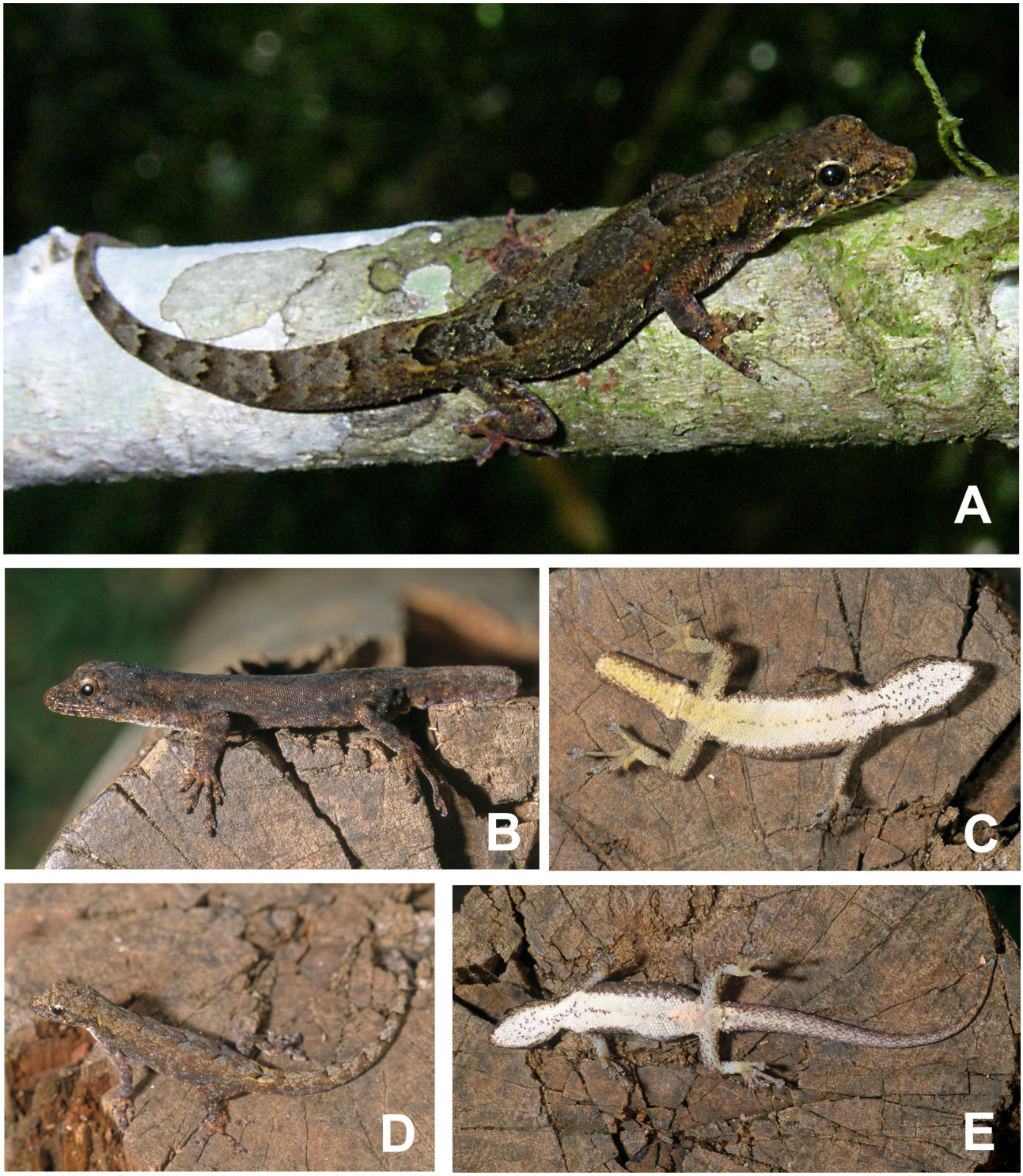

FIGURE 14. Photos of specimens of *L. guibei* in life. A, female specimen ZSM 525/2009 (ZCMV 11210) from the western slope of the Makira Massif, photographed on 23 June 2009. B–C, male and D–E, female, from Andasibe, in dorsolateral and ventral views, photographed 2003, not attributable to a voucher specimen and not genotyped, and thus only tentatively attributable to the species.

Identity and Diagnosis. The holotype agrees well morphologically with most other individuals assigned to this species by relatively low longitudinal counts of dorsal scales (<200) and ventral scales (<100) while most individuals assigned to *L. miops* have higher counts (>200 / >100). Despite some overlap in these variables, the differences between the two lineages seem to allow a distinction of most individuals. Furthermore, *L. guibei* does not reach the high INFL and NNS counts of some *L. miops* individuals, reaches larger body sizes, and males are characterized by

more distinct lateral tubercles at the base of the tail, judging from the specimens morphologically examined herein. Specimens appear to have a rather indistinct dorsal pattern (Fig. 14). Two photographed individuals have a conspicuous stripe-like row of dark spots on the chest (Fig. 14C, E) but this pattern is absent in most other individuals examined.

Distribution. *L. guibei* is known from several localities in the Northern Central East of Madagascar: (1) the type locality Andasibe, (2) Vohidrazana, (3) Moramanga, (4) Anjozorobe, (5) Mahasoa Forest (based on ND4 sequences of Gippner *et al.* 2021), and (6) Angozongahy on the west slope of the Makira Reserve.

New species

Lygodactylus tantsaha sp. nov.

Lygodactylus sp. 10: Gippner *et al.* (2021)

Holotype. ZSM 196/2018 (field number MSZC 0772), adult male, collected by M.D. Scherz, J.H. Razafindraibe, A. Razafimanantsoa, and S.M. Rasolonjavato at Montagne d'Ambre, west slope, northern Madagascar, at geographical coordinates S12.58503, E49.11596, 817 m. a.s.l., on 8 December 2017 at 22h20 (Fig. 15).

Paratype. ZSM 197/2018 (MSZC 0771), collected by M.D. Scherz, J.H. Razafindraibe, A. Razafimanantsoa, and S.M. Rasolonjavato at Montagne d'Ambre, west slope, Madagascar, at geographical coordinates S12.58548, E49.11697, 820 m a.s.l., on 8 December 2017 at 21h36.

Diagnosis. *Lygodactylus tantsaha* **sp. nov.** corresponds to a genetically highly distinct lineage from northern Madagascar that is not closely related to any nominal species of *Lygodactylus* as defined in the previous sections. It belongs to subclade A2 within *Domerguella* as defined herein. It can also be assigned to the subgenus *Domerguella* by an undivided mental scale with two postmentals, absence of a claw on the first finger, and 7 preanal pores in males. Within *Domerguella*, the new species is only known from Montagne d'Ambre in northern Madagascar and differs from the other *Domerguella* occurring in this region as follows: from *L. expectatus* by non-enlarged dorsolateral scales (longitudinal count of dorsal scales >230 vs. <170), from *L. rarus* by lack of regular crossbands on tail (vs. presence) and different body shape without elongated limbs (relative hindlimb length 0.45–0.50 vs. >0.55); from *L. madagascariensis* by asymmetrical postmental scales (vs. symmetrical); from *L. petteri* by a larger longitudinal count of dorsal scales (239–240 vs. 189–222). Genetically, the new species is highly distinct from all species in subclade A5, and differs from almost all of them (potentially not *L. fritzi* **sp. nov.** described below) by an absent or only weakly expressed lateral spine at the tail base of males (vs. presence of a distinct spine).

Tentatively, *L. tantsaha* **sp. nov.** differs in coloration from other *Domerguella* by the distinctly white upper lip (vs. brown in all other species) and white spots along the flank (vs. absent or at most light gray in *L. madagascariensis* and *L. miops*).

The new species, on Montagne d'Ambre, occurs sympatrically with *L. madagascariensis* and *L. petteri* and is morphologically quite similar to these species, differing only in faint meristic characters as specified above. However, the fully concordant differentiation in mitochondrial genes (deep divergence in 16S: >13% to both *L. madagascariensis* and *L. petteri*) and in the unlinked loci CMOS and RAG-1, despite close syntopy, confirms this lineage represents a distinct species with restricted or absent gene flow to other co-occurring *Domerguella*.

For a distinction from other species newly named and described herein, see the respective diagnoses below.

Etymology. We are pleased to dedicate this species to Aaron M. Bauer in recognition of his extraordinary work fostering our knowledge about gecko diversity, biology, and evolution. The species name is derived from the Malagasy word tantsaha = farmer, in allusion to the original root of Aaron's surname Bauer (German) = farmer. Coincidentally, individuals assignable to this species were found at the edge of an area of illegal farming within the park on the west slope, giving the name a second local meaning.

Description of the holotype. Adult male, hemipenes everted, in moderately good state of preservation (Fig. 15), although the tail is detached, and the right forelimb is largely removed as a tissue sample for molecular analysis. SVL 31.9 mm, original tail (TAL 36.9 mm); for other measurements see Table 1. Head slightly broader than body. The distance from the tip of the snout to the anterior border of the eye (4.0 mm) is greater than the interorbital distance anteriorly (3.7 mm), and slightly greater than the distance between the eye and ear opening. Snout covered

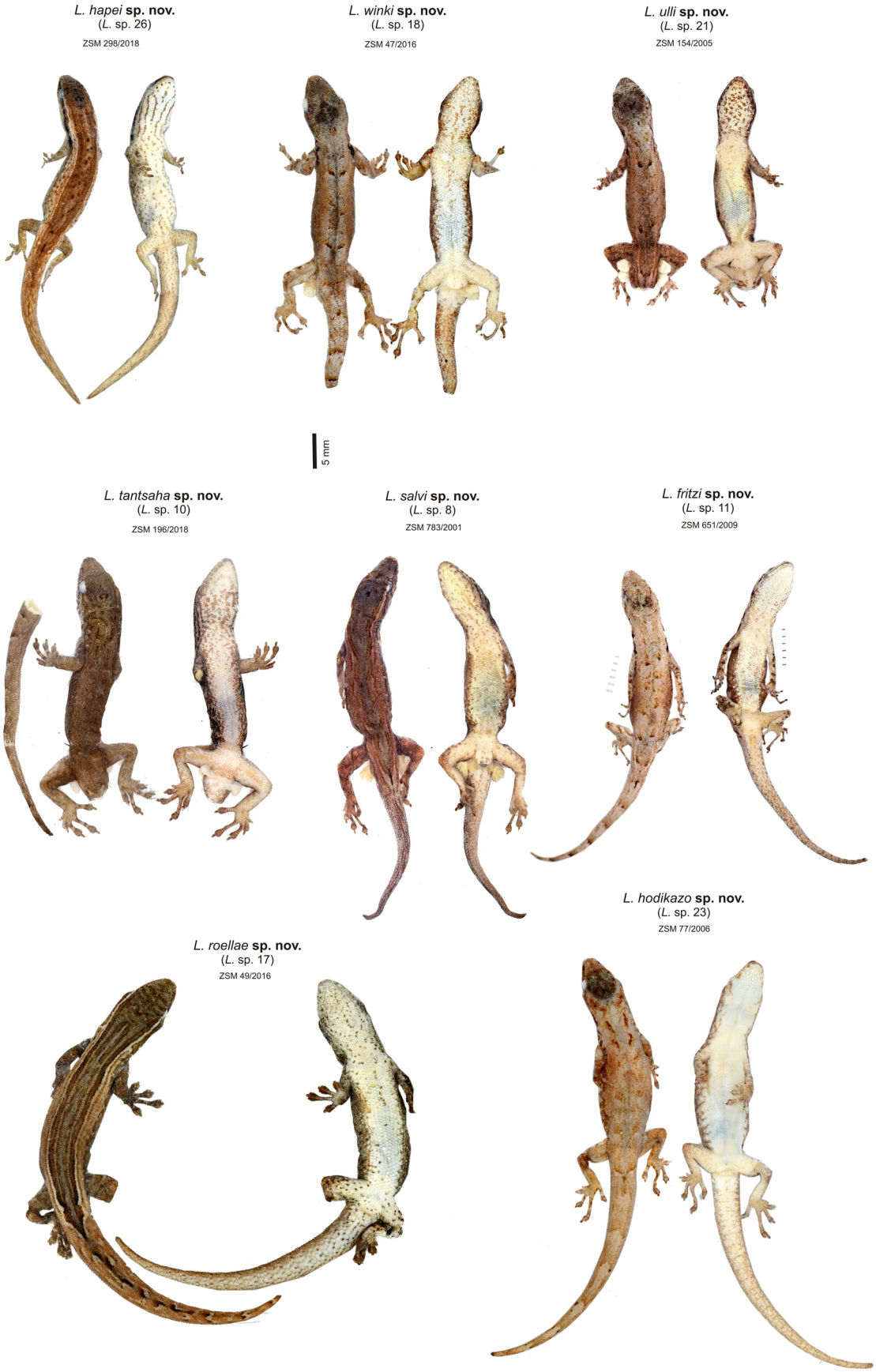

FIGURE 15. Dorsal and ventral views of preserved holotypes of new species of the *Lygodactylus madagascariensis* group named in the current study.

with enlarged granular scales, larger anteriorly on snout, becoming smaller laterally and anteriorly above the eye. Nostril surrounded by three scales: rostral, first supralabial and one supranasal. Mental scale undivided; only slight contact between posterior projection of mental scale and first infralabial; two asymmetrical postmental scales; four postpostmental scales; seven infralabial scales; seven supralabial scales; three internasal scales; granular dorsal scales; dorsum with small, homogeneous, granular and unkeeled scales of similar size to those on trunk, the scales on limbs are distinctly larger; 239 dorsal scales longitudinally along the body; 111 ventral scales between mental and cloaca; venter with large homogeneous smooth scales; no obvious lateral spines at the base of the tail; first finger present but very small, without bearing a claw; three pairs of subdigital lamellae on the fourth toe; one weakly expressed dorsolateral tubercle on either side, each composed of 1–2 scales; 7 preanal pores; tail without whorls.

The holotype's coloration in life based on available photographs was dorsally brown with a diffuse pattern consisting of dark and light spots, venter whitish. Flanks brighten towards venter with a diffuse ocelli-like pattern. Brown color on head with distinct border on supralabials to whitish venter. Six black stripes radially arranged around the eye. Tail slightly brighter than dorsum with pairs of black and white spots running posteriorly along the caudal spine (Fig. 16A). After four years of preservation in ethanol, the specimen darkened and patterns faded. Preserved specimen displays dark irregular spots on whitish gular region expanding to the anterior ventral torso.

Variation. The coloration of this species appears tentatively to be characteristic, with a series of white spots always present along the flank in life (Fig. 16). The upper lip is also white.

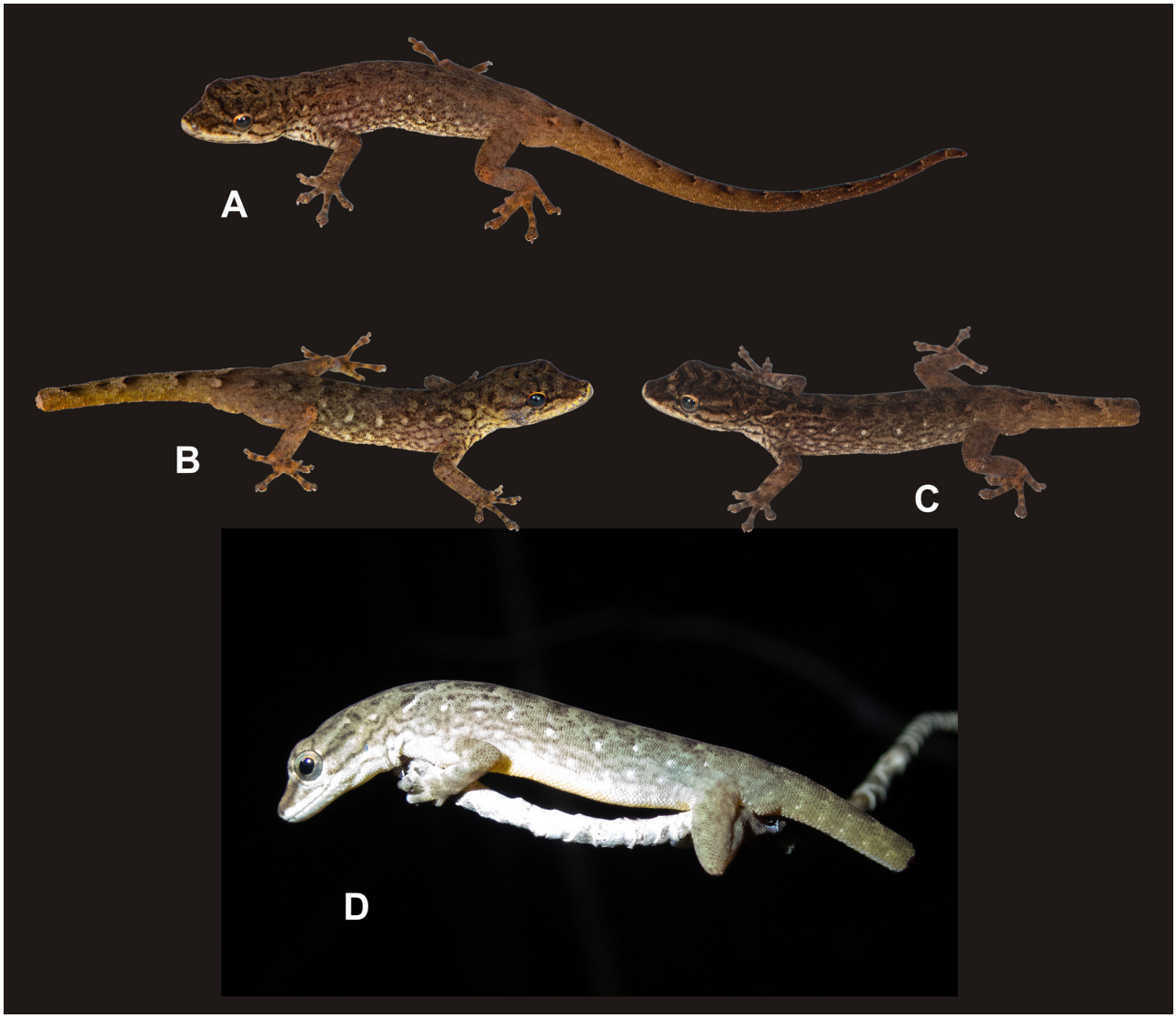

FIGURE 16. Photos of specimens of *Lygodactylus tantsaha* **sp. nov.** from Montagne d'Ambre in life. A, Adult male holotype, ZSM 196/2018 (MSZC 0772); B, specimen MSTIS 928 (voucher not collected); C, D, Adult male paratype, ZSM 197/2018 (MSZC 0771). Not to scale.

Natural history. All individuals were encountered and collected at night sleeping at the ends of very thin twigs, narrower than their bodies (Fig. 16D).

Distribution. *L. tantsaha* is only known from the type locality, western Montagne d'Ambre.

Lygodactylus salvi sp. nov.

Lygodactylus sp. 8: Gippner *et al.* (2021).

Holotype. ZSM 783/2001 (FGMV 2001.74), an adult male collected by F. Andreone, F. Mattioli, J. Randrianirina, and M. Vences on the western slope of the Tsaratanana massif (Manarikoba forest, Antsahamanara campsite), northern Madagascar, at geographical coordinates S14.0450, E48.7844 , ca. 1000 m a.s.l., between 4–9 February 2001 (Fig. 15).

Paratype. ZSM 557/2014 (DRV 6327), a female collected by F.M. Ratsoavina, D. R. Vieites, M. Vences, R.D. Randrianiaina, S. Rasamison, A. Rakotoarison, E. Rajeriarison, and T. Rajoafiarison, from Ambodikakazo, a site south of the Tsaratanana Massif, northern Madagascar, at geographical coordinates S14.2098, E48.8981, 1411 m a.s.l., on 16 June 2010.

Diagnosis. *Lygodactylus salvi* **sp. nov.** corresponds to a genetically highly distinct lineage from northern Madagascar that is not closely related to any nominal species of *Lygodactylus* as defined in the previous sections. It belongs to subclade A3 within *Domerguella* as defined herein. It can also be assigned to the subgenus *Domerguella* by an undivided mental scale with two postmentals, absence of a claw on the first finger, and 6 preanal pores in males. Within *Domerguella*, the new species is only known from two localities in northern Madagascar and differs from the other nominal species of *Domerguella* occurring in this part of the island as follows: from *L. expectatus* by non-enlarged dorsolateral scales (longitudinal count of dorsal scales >210 vs. <170), from *L. rarus* by lack of regular crossbands on tail (vs. presence) and different body shape without elongated limbs (relative hindlimb length 0.48–0.50 vs. >0.55); from *L. madagascariensis* by smaller longitudinal dorsal scale count (211–217 vs. 219–258); and from *L. petteri* by a larger longitudinal count of ventral scales (107–112 vs. 101–105 in all but one individual of *L. petteri*); and from *L. tantsaha* by a smaller longitudinal count of dorsal scales (211–217 vs. 239–240).

Given the somewhat uncertain allocation of the *nomina* to the eastern species in subclade A5, a morphological diagnosis from these species is convoluted. However, genetically, the new species is highly distinct from all species in this subclade, and differs from *L. guibei* as well as from many specimens of *L. miops* by a less distinctly expressed lateral spine at the tail base of males (vs. presence of a distinct, large spine in *L. guibei,* and an at least slightly more distinct spine in *L. miops*). Furthermore, the new species can be distinguished from *L. guibei* and *L. miops* by smaller relative eye diameter (ED is 4.8–5.0% of SVL, vs. 5.3–7.7% in *L. guibei* and *L. miops*). Finally, this species shows concordant differentiation in mitochondrial genes (deep divergence in 16S to all other species: >11%) and the unlinked loci CMOS and RAG-1 (haplotype sharing with lineage *L.* sp. 17 only in some CMOS haplotypes).

For a distinction from the sister lineage, described below as. *L. roellae*, see Diagnosis of that species. For a distinction from additional species newly named and described herein, see the respective diagnoses below.

Etymology. The name is dedicated to Salvador "Salvi" Carranza, Institut de Biologia Evolutiva (CSIC-UPF), Barcelona, in recognition for his substantial contributions to gecko taxonomy, and conservation of herpetofauna. The species epithet name is defined as a noun in apposition (not a noun in the genitive case) to avoid ending with a non-euphonious double-i.

Description of the holotype. Adult male, hemipenes everted, in moderate state of preservation, tail regenerated, right forelimb is removed as source of tissue for molecular analysis (Fig. 15). SVL 29.9 mm, TAL 24.9 mm; for other measurements see Table 1. Long head with distinct neck, body broader than head. The distance from the tip of the snout to the anterior border of the eye (4.2 mm) is greater than the interorbital distance anteriorly (3.6 mm), and greater than the distance between the eye and ear opening. Snout covered with enlarged granular scales compared to the rest of the dorsum. Nostril surrounded by four scales: rostral, first supralabial, and two supranasals. Mental scale undivided; no contact between posterior projection of mental scale and first infralabial; two symmetrical postmental scales with four postpostmental scales; seven infralabial scales; seven supralabial scales; three internasal scales; granular dorsal scales; dorsum with small, homogeneous, granular and unkeeled scales of similar size to those on trunk, the scales on limbs are slightly larger; 217 dorsal scales longitudinally along the body; 107 ventral scales between mental and cloaca; venter with large homogeneous smooth scales that are a bit smaller in the gular

region; first finger present but very small, not bearing a claw; three pairs of subdigital lamellae on the fourth toe; six dorsolateral tubercles, each consisting of one scale; six preanal pores; tail without whorls; small lateral spines at the base of the tail.

Life coloration of the holotype based on available photographs (Fig. 17) was grayish with a slightly distinct red-brownish lateral stripe running from the eye to the base of the tail. Both colors are also distinctly present on the limbs. Overall, the appearance is cryptic with no distinct black markings (Fig. 17). Color after 20 years in preservative ethanol is almost uniformly gray brownish, with a weak dorsal pattern. In the preserved specimen, the ventral side is uniformly whitish with a slight yellowness. Small brown spots are present on the throat and the rest of the venter.

FIGURE 17. Photo of *Lygodactylus salvi* **sp. nov.,** adult male holotype ZSM 783/2001 (FGMV 2001.74) from Tsaratanana (Antsahamanara) in life.

Variation. The female paratype (ZSM 557/2014) is bigger than the holotype, with an SVL of 36.2 mm, but has relatively shorter hindlimbs (HIL/SVL 0.48). The relative size of tubercles at the tail base is a bit smaller, while the lateral tubercles between the legs contain a few more scales (1–3). The animal has bigger eyes in relation to its size. While the dorsal scale count is a bit lower (211), the ventral scale count is a bit higher (112). Coloration in preservative is uniformly grayish-brown, without lateral stripe, and with very small symmetrical dark dorsal markings anterior to hindlimb insertion; ventrally with dense dark mottling on throat, chest and belly. The differences between holotype and paratype could be due to different sex or just random variation.

Distribution. *L. salvi* is known from (1) the type locality, Manarikoba forest on the west slope of the Tsaratanana Massif, and (2) Ambodikakazo south of Tsaratanana.

Natural history. Practically nothing is known of the natural history of this enigmatic species.

Lygodactylus roellae sp. nov.

Lygodactylus sp. 17: Gippner *et al.* (2021).

Holotype. ZSM 49/2016 (MSZC 0072), adult female, collected by M.D. Scherz, J. Borrell, L. Ball, T. Starnes, E. Razafimandimby, D.H. Nomenjanahary, and J. Rabearivony at Ampotsidy mountains, 15.7 km NNW of Bealanana

(8.7 km NNW of Beandrarezona), northern Madagascar, at geographical coordinates S14.41974, E48.71935, 1344 m a.s.l., on 22 December 2015 (Fig. 15).

Paratypes. ZSM 556/2014 (DRV 6289), adult male, collected by F.M. Ratsoavina, D. Vieites, M. Vences, R.D. Randrianiaina, S. Rasamison, A. Rakotoarison, E. Rajeriarison, and T. Rajoafiarison at Andrevorevo, a site south of the Tsaratanana Massif, northern Madagascar, at geographical coordinates S14.3464, E49.1028, 1717 m a.s.l., on 21 June 2010; UADBA-R 70855 (MSZC 0010), adult female, with the same collection data as the holotype but collected at S14.41878 E48.71896, 1354 m a.s.l. on 18 December 2015 at 20h20.

Diagnosis. *Lygodactylus roellae* **sp. nov.** corresponds to a genetically highly distinct lineage from northern Madagascar that is the sister species of *L. salvi* described above, but differs by high genetic divergence and several scale counts. It belongs to subclade A3 within *Domerguella* as defined herein. It can also be assigned to the subgenus *Domerguella* by an undivided mental scale with two postmentals, absence of a claw on the first finger, and 5 preanal pores in males. Within *Domerguella*, the new species is only known from two localities in northern Madagascar and differs from the other nominal species of *Domerguella* occurring in this part of the island as follows: from *L. expectatus* by a different color pattern, without scapular semi-ocellus and with a striped pattern apparently in most individuals (vs. scapular semi-ocellus usually present, and striped pattern unknown); from *L. rarus* by lack of regular crossbands on tail (vs. presence) and different body shape without elongated limbs (relative hindlimb length 0.41–0.45 vs. >0.55); from *L. madagascariensis, L. petteri, L. salvi,* and *L. tantsaha* by smaller longitudinal dorsal scale count (159–169 vs. >188) and smaller longitudinal ventral scale count (83–92 vs. >96).

Genetically, the new species is highly distinct from all species in subclade A5, and differs at least from *L. guibei* by a less distinctly expressed lateral spine at the tail base of males (vs. presence of a distinct, large spine). Furthermore, the longitudinal dorsal scale count is smaller than in all known individuals of subclade A5.

The new species differs from its sister lineage, *L. salvi* (described above), by a lower longitudinal dorsal scale count (159–169 vs. 211–217) and a lower ventral scale count (83–92 vs. 107–112). The two sister species also differ by a high genetic divergence of 11.2–12.6% in the 16S gene, and do not share haplotypes in RAG1 despite occurring in geographical proximity.

For a distinction from additional species newly named and described herein, see the respective diagnoses below.

Etymology. We are pleased to dedicate this beautiful gecko species to Beate Röll, in recognition for her substantial contributions to *Lygodactylus* biology and phylogeny. The name is a matronym (i.e., a noun in the genitive case).

Description of the holotype. Adult female, in a good state of preservation, the right hind limb is partly removed as a source of tissue for molecular analysis (Fig. 15). SVL 35.9 mm, TAL 39.6 mm; for other measurements see Table 1. Head and neck thick, body broader than head. The distance from the tip of the snout to the anterior border of the eye (3.8 mm) is less than the interorbital distance anteriorly (4.2 mm), and greater than the distance between the eye and ear opening. Snout covered with granular scales larger than those on the rest of the dorsum. Nostril surrounded by five scales: rostral, first supralabial, and three supranasals. Mental scale undivided; no contact between posterior projection of mental scale and first infralabial; two asymmetrical postmental scale with five postpostmental scales; seven infralabial scales; seven supralabial scales; two internasal scales; granular dorsal scales; dorsum with small, homogeneous, granular, and unkeeled scales of similar size to those on trunk, smaller than on head and tail, the scales on limbs can be slightly larger; 169 dorsal scales longitudinal along the body; 92 ventral scales between mental and cloaca; venter with large homogeneous smooth scales; first finger present but very small, not bearing a claw; three pairs of subdigital lamellae on the fourth toe; no dorsolateral tubercles; tail without whorls; small lateral spines at the base of the tail.

Based on available photographs (Fig. 18A–B), the life coloration of the holotype exhibited a distinct pattern of dark brownish to yellowish stripes on the dorsum reaching from the eye to base of the tail. The stripes continue in an irregular pattern of more elongated dark and brighter spots on the caudal spine. The dark wide area on the back is slightly emarginated at the level of the hindlimbs before ending at the base of the tail. The flanks and limbs are gray to brownish (Fig. 18A). The ventral side is whitish with few small brown spots predominately on the throat and the tail (Fig. 18B). The specimen has darkened after 6 years of preservation in ethanol; however, the striped pattern is still distinctly visible.

Variation. The coloration of the dorsum is characteristic with a distinct pattern of dark brownish to yellowish stripes on the dorsum with a variable strength of expression on the tail (Fig. 18A and 18E), which appears to weaken greatly or be lost upon regeneration (Fig. 18C).

FIGURE 18. Photos of *Lygodactylus roellae* **sp. nov.** in life**.** A and B, adult female holotype ZSM 49/2016 (MSZC 0072) from Ampotsidy. C,D, adult female paratype UADBA-R 70855 from Ampotsidy. E, male paratype ZSM 556/2014 (DRV 6289) from Andrevorevo.

TABLE 1. Selected morphometric and meristic data for voucher specimens of the *Lygodactylus madagascariensis* group examined for this study. All morphometric measurements (SVL, TAL, HIL, HW, ED, SED) in mm. All specimens in the table were genotyped by 16S sequences, except for historical types from BMNH, MNHN, and SMF, and two further individuals of *L. expectatus*. Abbreviations are those described in Materials and Methods section; additional abbreviations and symbols as follows: NA, not assessed or not applicable; * counts and measurements partly or fully taken by M. Puente (Puente *et al.* 2009); § specimen not genotyped; # tail broken or incomplete; ## tail regenerated. HT (sep) and HT (spi) mark the holotypes of *Lygodactylus septemtuberculatus* Angel, 1942 and *Microscalabotes spinulifer* Boettger, 1913, here considered to be junior synonyms of *L. miops*. First LCDS value for *L. expectatus* refers to the enlarged dorsolateral scales, the second value to the non-enlarged vertebral scales. See species account of *L. fritzi* **sp. nov** for the identity of the historical locality "Senbendrana".

Specimen voucher	Field number	Locality	Type	Sex	SVL	TAL	HIL	HW	ED	SED	size STT
L. expectatus—subclade A1											
MNHN 1990.1 *§	NA	Ankarana	HT	M	29.7	32.6	13.1	NA	NA	NA	0
MNHN 1990.2 * §	NA	Ankarana	PT	F	27.8	25.3	NA	NA	NA	NA	0
MNHN 1990.3 * §	NA	Ankarana	PT	NA	19.7	20.8	NA	NA	NA	NA	NA
MNHN 1933.168 * §	NA	Ankarana		F	27.5	0.0	NA	NA	NA	NA	NA
ZSM 282/2004	FGZC 541	Ankarana		M	27.7	16.8#	12.8	5.3	1.7	6.7	0
ZSM 492/2001 §	MV 2001.256	Ankarana		M	26.3	30.7	11.8	5.2	1.6	7.2	0
ZSM 284/2004	FGZC 543	Ankarana		M	29.4	38.1#	12.8	5.5	1.6	7.3	0
ZSM 1540/2008	FGZC 1649	Ankarana		M	29.2	31.5	13.9	5.8	1.5	8.0	0
ZSM 2143/2007	FGZC 1183	Ankarana		F	24.7	28.6	11.6	4.6	1.4	6.6	0
ZSM 283/2004	FGZC 542	Ankarana		F	24.3	31.8	11.0	5.1	1.4	6.7	0
UADBA 06059 * §	NA	Ankarana		NA	21.9	0.0	NA	NA	NA	NA	NA
L. rarus—subclade A1											
MNHN 1990.6 * §	NA	Ankarana	HT	F	22.6	NA	12.9	NA	NA	NA	0
MNHN 1990.1887 * §	NA	Ankarana		NA	13.2	13.0	NA	NA	NA	NA	NA
MNHN 1990.1888 * §	NA	Ankarana		NA	22.5	13.4	NA	NA	NA	NA	NA
ZSM 860/2003	FGMV 2002.833	Ankarana		M	33.5	37.0	20.0	5.9	1.3	8.3	0
ZSM 913/2003	FGMV 2002.941	Ankarana		M	36.5	44.0	20.6	6.3	1.6	8.6	0
ZSM 1085/2003	FGMV 2002.837	Ankarana		F	35.5	23.0#	20.7	6.1	1.4	9.5	0
L. tantsaha **sp. nov.** (sp. 10)—subclade A2											
ZSM 196/2018	MSZC 772	Montagne d'Ambre	HT	M	31.9	36.9#	15.8	6.3	1.6	8.5	0
ZSM 197/2018	MSZC 771	Montagne d'Ambre	PT	M	36.9	12.2#	16.8	6.4	1.8	9.1	1
L. hapei **sp. nov.** (sp. 26)—subclade A2											
ZSM 298/2018	NA	Djohahely (Djangoa)	HT	F	26.3	27.4§	11.4	4.3	1.6	6.3	0

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TABLE 1. (Continued)

Specimen voucher	Field number	Locality	Type	Sex	SVL	TAL	HIL	HW	ED	SED	size STT
L. salvi **sp. nov.** (sp. 8)—subclade A3											
ZSM 557/2014	DRV 6327	Ambodikakazo	PT	F	36.2	29.0#	17.2	6.8	1.8	8.7	1
ZSM 783/2001	FGMV 2001.74	Tsaratanana (Antsahamanara)	HT	M	29.9	24.9##	15.0	5.2	1.2	8.0	1–2
L. roellae **sp. nov.** (sp. 17)—subclade A3											
ZSM 49/2016	MSZC 72	Ampotsidy	HT	F	35.9	39.6	14.7	6.4	1.8	8.7	1
ZSM 556/2014	DRV 6289	Andrevorevo	PT	M	36.0	45.3	16.1	7.0	1.7	9.0	1
L. madagascariensis—subclade A4											
SMF 8937 §	NA	Nosy Be	HT	M	31.6	37.1	14.4	5.4	2.0	7.7	1
ZSM 782/2001	MV 2001.55	Tsaratanana (Andampy)		F	31.5	10.2#	13.1	5.6	1.5	8.1	1
ZSM 118/2019	FGZC 5511	Maromandria		M	34.0	38.7	14.3	5.9	1.9	8.3	1
ZSM 119/2019	FGZC 5515	Maromiandra		M	29.5	35.0	13.3	5.7	1.7	8.0	1
ZSM 120/2019	FGZC 5596	Nosy Be (Lokobe)		F	28.5	35.0	13.6	4.9	1.7	7.1	1
ZSM 813/2003	FGMV 2002.721	Manongarivo		M	31.7	36.2	12.6	5.2	1.7	7.6	1
ZSM 832/2003	FGMV 2002.778	Manongarivo		M	30.4	40.9#	14.5	5.8	1.7	7.4	1
ZSM 270/2004	FGZC 518	Montagne d'Ambre		F	30.2	29.0	14.1	5.3	1.7	7.4	0–1
L. hodikazo **sp. nov.** (sp. 23)—subclade A4											
ZSM 77/2006	FGZC 828	Tsingy de Bemaraha	HT	F	29.4	37.2	12.9	5.6	1.6	7.2	1–2
L. petteri—subclade A4											
MNHN 1990.4 * §	1346-L	Montagne d'Ambre	HT	F	35.0	12.0#	16.9	NA	NA	NA	1
MNHN 1990.5 §	1347-L	Montagne d'Ambre	PT	M	33.2	0.0	NA	NA	NA	NA	1
ZSM 914/2003	FGMV 2002.942	Montagne d'Ambre		F	36.7	42.1	16.0	6.2	1.9	8.8	1
ZSM 2087/2007	FGZC 1065	Montagne d'Ambre		M	37.8	48.0	19.0	7.1	2.0	9.4	1
ZSM 194/2018	MSZC 454	Montagne d'Ambre		F	30.3	15.5#	15.3	6.0	1.5	8.0	0
ZSM 195/2018	MSZC 485	Montagne d'Ambre		M	38.5	34.6##	18.4	6.7	2.0	9.4	0
L. guibei—subclade A5											
MNHN 1933.156 * §	NA	Moramanga	PT	M	30.2	36.3	NA	NA	NA	7.7	2–3
MNHN 1993.60 * §	NA	Andasibe	HT	M	30.8	37.0	13.8	NA	NA	7.8	3
ZSM 5117/2005	FGZC 2689	Andasibe		F	34.0	41.7	15.3	6.5	1.9	8.0	2
ZSM 525/2009	ZCMV 11210	Makira (Angozongahy)		F	31.3	17.9#	15.3	6.0	1.7	7.7	1–2
ZSM 319/2004	FGZC 613	Moramanga region		F	35.8	31.3	15.6	6.7	2.3	10.0	1–2

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TABLE 1. (Continued)

Specimen voucher	Field number	Locality	Type	Sex	SVL	TAL	HIL	HW	ED	SED	size STT
ZSM 320/2004	FGZC 616	Moramanga region		M	34.9	36.8	15.4	6.7	2.2	8.7	3
ZSM 321/2004	FGZC 617	Moramanga region		M	33.2	39.0	14.5	6.0	2.0	8.0	2
ZSM 330/2004	FGZC 627	Moramanga region		F	39.5	29§	16.5	6.7	2.2	9.0	2–3
ZSM 349/2006	ZCMV 2484	-		F	30.1	10.2#	13.4	5.6	2.0	7.7	2–3
ZSM 349/2010	FGZC 4362	Anjozorobe		M	37.6	46.5#	15.3	7.0	2.0	9.1	2
L. miops—subclade A5											
BMNH 1946.8.22.55 §	NA	"Senbendrana"	HT	F	29.9	21.4#	12.8	5.3	2.1	7.4	2
MNHN 1893.63 * §	NA	Moramanga	HT (sep)	F	29.0	19.0##	13.1	NA	NA	NA	2
SMF 8931 * §	NA	Moramanga	HT (spi)	F	28.5	27.6#	14.2	5.1	2.2	7.0	1–2
ZSM 351/2010	FGZC 4295	Ambodivoahangy		F	29.2	28.8	13.7	5.6	1.8	7.4	1–2
ZSM 731/2003	FGMV 2002.456	Ranomafana		M	27.2	3.6#	12.8	5.0	1.6	7.0	1–2
ZSM 732/2003	FGMV 2002.458	Ranomafana		F	30.4	30.8	13.2	5.2	1.7	6.7	1–2
ZSM 733/2003	FGMV 2002.459	Ranomafana		F	29.8	31.7	13.8	5.2	1.7	7.5	2
ZSM 352/2006	ZCMV 3350	Mahakajy Reserve		F	30.8	10.4#	15.1	6.0	1.9	7.6	2
ZSM 116/2004	FGZC 205	Andohahela		M	26.2	5.5#	11.7	5.7	1.5	7.0	2
ZSM 117/2004	FGZC 206	Andohahela		F	31.2	16.5#	15.1	6.0	1.8	7.6	2
ZSM 165/2004	FGZC 307	Manantantely		M	30.0	29.8	13.0	5.6	2.3	7.6	2
ZSM 352/2010	FGZC 4503	Anosibe An'Ala		F	29.4	30.5	13.4	5.6	1.6	7.0	2
ZSM 175/2016	FGZC 5039	Vohimana		F	30.1	33.2#	13.1	5.4	1.8	7.4	1–2
ZSM 376/2016	ZCMV 14832	Sampanandrano		F	28.9	16.3#	12.1	5.3	1.6	7.0	1
L. fritzi **sp. nov.** (sp.. 11)—subclade A5											
ZSM 651/2009	ZCMV 8902	Ankanin'ny Nofy		F	26.4	26.5	10.7	4.9	1.8	6.8	0–1
L. winki **sp. nov.** (sp. 18)—subclade A5											
ZSM 555/2014	DRV 6288	Andrevorevo	PT	M	33.0	45.0	17.4	7.1	2.0	8.6	3
ZSM 48/2016	MSZC 110	Ampotsidy	PT	M	29.8	37.8	14.9	6.0	1.9	7.7	3
ZSM 1763/2010	ZCMV 12502	Bemanevika	PT	F	33.4	18.7#	16.2	6.5	1.8	8.2	2
ZSM 47/2016	MSZC 0075	Ampotsidy	HT	M	29.5	15.6#	15.8	5.5	1.8	7.3	3
L. ulli **sp. nov.** (sp. 21)—subclade A5											
ZSM 154/2005	FGZC 2811	Marojejy	HT	M	28.8	2.6#	13.6	5.3	1.7	6.7	2

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TABLE 1. (Continued)

Specimen voucher	Field number	Locality	Type	Sex	PPM	INFL	SUPL	IN	PCL	NDT	LCDS	LCVS
L. expectatus—subclade A1												
MNHN 1990.1 *§	NA	Ankarana	HT	M	4	5	5	1	7	4	122/162	95
MNHN 1990.2 * §	NA	Ankarana	PT	F	4	6	6	1	0	0	NA	96
MNHN 1990.3 * §	NA	Ankarana	PT	NA	4	5	6	1	0	0	NA	94
MNHN 1933.168 * §	NA	Ankarana		F	4	5	6	2	0	0	NA	NA
ZSM 282/2004	FGZC 541	Ankarana		M	4	7	8	1	5	4	127/164	91
ZSM 492/2001 §	MV 2001.256	Ankarana		M	4	6	7	1	7	5	124/139	98
ZSM 284/2004	FGZC 543	Ankarana		M	4	6	7	1	5	3	128/157	92
ZSM 1540/2008	FGZC 1649	Ankarana		M	4	6	7	1	7	4	127/155	96
ZSM 2143/2007	FGZC 1183	Ankarana		F	4	5	6	1	0	4	130/154	86
ZSM 283/2004	FGZC 542	Ankarana		F	4	6	7	2	0	3	125/162	87
UADBA 06059 * §	NA	Ankarana		NA	4	6	6	1	0	0	NA	NA
L. rarus—subclade A1												
MNHN 1990.6 * §	NA	Ankarana	HT	F	4	NA	NA	3	0		215	125
MNHN 1990.1887 * §	NA	Ankarana		NA	4	6	7	3	0	0	NA	NA
MNHN 1990.1888 * §	NA	Ankarana		NA	4	5	6	1	0	0	NA	NA
ZSM 860/2003	FGMV 2002.833	Ankarana		M	5	5	6	1	7	0	260	120
ZSM 913/2003	FGMV 2002.941	Ankarana		M	4	5	7	2	7	0	224	119
ZSM 1085/2003	FGMV 2002.837	Ankarana		F	5	7	8	2	0	0	223	139
L. tantsaha **sp. nov.** (sp. 10)—subclade A2												
ZSM 196/2018	MSZC 772	Montagne d'Ambre	HT	M	4	7	7	3	7	1	239	111
ZSM 197/2018	MSZC 771	Montagne d'Ambre	PT	M	5	7	7	1	7	6	240	97
L. hapei **sp. nov.** (sp. 26)—subclade A2												
ZSM 298/2018	NA	Djohahely (Djangoa)	HT	F	5	7	8	3	0	0	179	87
L. salvi **sp. nov.** (sp. 8)—subclade A3												
ZSM 557/2014	DRV 6327	Ambodikakazo	PT	F	4	6	7	2	0	5	211	112
ZSM 783/2001	FGMV 2001.74	Tsaratanana (Antsahamanara)	HT	M	4	7	7	3	6	6	217	107

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TABLE 1. (Continued)

Specimen voucher	Field number	Locality	Type	Sex	PPM	INFL	SUPL	IN	PCL	NDT	LCDS	LCVS
L. roellae **sp. nov.** (sp. 17)—subclade A3												
ZSM 49/2016	MSZC 72	Ampotsidy	HT	F	5	7	7	2	0	0	169	92
ZSM 556/2014	DRV 6289	Andrevorevo	PT	M	6	6	8	1	5	6	159	83
L. madagascariensis—subclade A4												
SMF 8937 §	NA	Nosy Be	HT	M	4	6	8	2	7	0	246	106
ZSM 782/2001	MV 2001.55	Tsaratanana (Andampy)		F	5	7	8	3	0	4	205	106
ZSM 118/2019	FGZC 5511	Maromandria		M	4	8	9	1	7	5	236	121
ZSM 119/2019	FGZC 5515	Maromiandra		M	4	8	9	2	7	5	251	138
ZSM 120/2019	FGZC 5596	Nosy Be (Lokobe)		F	4	7	8	2	0	3	219	128
ZSM 813/2003	FGMV 2002.721	Manongarivo		M	5	7	9	2	7	4	258	126
ZSM 832/2003	FGMV 2002.778	Manongarivo		M	4	6	7	1	7	0	244	124
ZSM 270/2004	FGZC 518	Montagne d'Ambre		F	4	7	8	2	0	4	258	109
L. hodikazo **sp. nov.** (sp. 23)—subclade A4												
ZSM 77/2006	FGZC 828	Tsingy de Bemaraha	HT	F	4	8	10	1	0	3	231	109
L. petteri—subclade A4												
MNHN 1990.4 * §	1346-L	Montagne d'Ambre	HT	F	4	6	6	1	0	0	189	102
MNHN 1990.5 §	1347-L	Montagne d'Ambre	PT	M	4	7	6	1	7	5	NA	105
ZSM 914/2003	FGMV 2002.942	Montagne d'Ambre		F	4	7	7	2	0	0	222	113
ZSM 2087/2007	FGZC 1065	Montagne d'Ambre		M	4	7	7	1	7	3	209	101
ZSM 194/2018	MSZC 454	Montagne d'Ambre		F	4	7	8	1	0	0	214	101
ZSM 195/2018	MSZC 485	Montagne d'Ambre		M	4	7	8	1	7	0	214	103
L. guibei—subclade A5												
MNHN 1933.156 * §	NA	Moramanga	PT	M	4	6	6	1	7	1	198+	99+
MNHN 1993.60 * §	NA	Andasibe	HT	M	4	NA	NA	2	6	9+	170	88
ZSM 5117/2005	FGZC 2689	Andasibe		F	5	6	7	2	0	5	206	94
ZSM 525/2009	ZCMV 11210	Makira (Angozongahy)		F	4	7	7	1	0	3	220	95
ZSM 319/2004	FGZC 613	Moramanga region		F	4	7	8	1	0	3	195	87
ZSM 320/2004	FGZC 616	Moramanga region		M	6	7	9	1	6	4	180	91

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TABLE 1. (Continued)

Specimen voucher	Field number	Locality	Type	Sex	PPM	INFL	SUPL	IN	PCL	NDT	LCDS	LCVS
ZSM 321/2004	FGZC 617	Moramanga region		M	4	6	6	2	7	4	201	87
ZSM 330/2004	FGZC 627	Moramanga region		F	4	7	7	1	0	0	181	89
ZSM 349/2006	ZCMV 2484	-		F	4	6	7	1	0	0	191	109
ZSM 349/2010	FGZC 4362	Anjozorobe		M	5	6	6	2	5	6	191	89
L. miops—subclade A5												
BMNH 1946.8.22.55 §	NA	"Senbendrana"	HT	F	6	7	7	3	0	3	233	113
MNHN 1893.63 * §	NA	Moramanga	HT (sep)	F	5	5	7	1	0	3	225	102
SMF 8931 * §	NA	Moramanga	HT (spi)	F	5	7	8	3	0	5	240	107
ZSM 351/2010	FGZC 4295	Ambodivoahangy		F	5	6	8	2	0	4	205	102
ZSM 731/2003	FGMV 2002.456	Ranomafana		M	4	7	7	3	7	4	236	106
ZSM 732/2003	FGMV 2002.458	Ranomafana		F	4	8	8	2	0	3	237	108
ZSM 733/2003	FGMV 2002.459	Ranomafana		F	6	7	8	2	0	3	237	113
ZSM 352/2006	ZCMV 3350	Mahakajy Reserve		F	3	6	8	2	0	4–5	220	98
ZSM 116/2004	FGZC 205	Andohahela		M	4	7	8	2	7	4	207	109
ZSM 117/2004	FGZC 206	Andohahela		F	5	8	8	2	0	4	229	108
ZSM 165/2004	FGZC 307	Manantantely		M	5	6	7	2	8	6	233	106
ZSM 352/2010	FGZC 4503	Anosibe An'Ala		F	6	6	7	2	0	4	216	105
ZSM 175/2016	FGZC 5039	Vohimana		F	5	6	7	2	0	5	242	106
ZSM 376/2016	ZCMV 14832	Sampanandrano		F	5	6	6	2	0	4	210	102
L. fritzi **sp. nov.** (sp.. 11)—subclade A5												
ZSM 651/2009	ZCMV 8902	Ankanin'ny Nofy		F	4	7	8	2	0	2	247	98
L. winki **sp. nov.** (sp. 18)—subclade A5												
ZSM 555/2014	DRV 6288	Andrevorevo	PT	M	4	7	7	1	7	6–8	187	93
ZSM 48/2016	MSZC 110	Ampotsidy	PT	M	4	7	8	2	7	5	208	83
ZSM 1763/2010	ZCMV 12502	Bemanevika	PT	F	4	7	8	1	0	6	204	98
ZSM 47/2016	MSZC 0075	Ampotsidy	HT	M	4	6	7	2	7	8	222	93
L. ulli **sp. nov.** (sp. 21)—subclade A5												
ZSM 154/2005	FGZC 2811	Marojejy	HT	M	5	6	7	2	7	2	253	110

The examined male paratype specimen (ZSM 556/2014) is almost the same size as the holotype with a SVL of 36.0 mm and has a longer tail (45.3 mm) and hindlimbs (HIL/SVL 0.45). On the fourth toe it has four instead of three subdigital lamellae, which differs from all other examined specimens. Unlike the holotype it has tubercles between the limbs (6) that consist of one scale each. It has fewer dorsal (159) and ventral scales (83). These differences could be due to different sex or just random variation.

Natural history. Specimens of this species were collected sleeping at night on roosts up to 1 m above the ground in Ampotsidy. UADBA-R 70855 was found sleeping on the tip of a *Pandanus* frond. It occurs in close sympatry with *Lygodactylus winki* **sp. nov.**, described below.

Distribution. *L. roellae* is known from (1) the type locality Ampotsidy and (2) Andrevorevo.

Lygodactylus hapei sp. nov.

Lygodactylus sp. 26: Gippner *et al.* (2021).

Holotype. ZSM 298/2018, female, collected at Djangoa (Djohahely) in the Sambirano Region in north-western Madagascar, approximately at geographical coordinates S13.7993, E48.3361, 20 m a.s.l. (Fig. 15), by unspecified local collectors.

Diagnosis. *Lygodactylus hapei* **sp. nov.** corresponds to a genetically highly distinct lineage from a poorly known site in north-western Madagascar, and forms a clade with *L. tantsaha* (described above) and *L.* sp. 24, both from Montagne d'Ambre in the North. Considering this lineage as a new species is justified by its very deep genetic divergence of over 14% to all other *Domerguella* (16.3–16.4% to *L. tantsaha*), differences in scale counts, and a distinct longitudinally striped pattern on the throat not known from any other *Domerguella*. The new species belongs to subclade A2 within *Domerguella* as defined herein. It can also be assigned to the subgenus *Domerguella* by an undivided mental scale with two postmentals, and absence of a claw on the first finger. Within *Domerguella*, the new species is only known from one locality in the Sambirano region in northern Madagascar, and differs from the other nominal species of *Domerguella* by the presence of a longitudinally striped pattern on the throat, and additionally from the species occurring in northern Madagascar as follows: from *L. expectatus* by non-enlarged dorsolateral scales (longitudinal count of dorsal scales >185 vs. <170), and by a pattern of dorsolateral stripes (vs. unstriped in the only known specimen (vs. scapular semi-ocellus usually present, and striped pattern unknown); from *L. rarus* by lack of regular crossbands on tail (vs. presence) and different body shape without elongated limbs (relative hindlimb length 0.43 vs. >0.55); from *L. madagascariensis, L. petteri, L. salvi,* and *L. tantsaha* by smaller longitudinal dorsal scale count (179 vs. >188) and smaller longitudinal ventral scale count (87 vs. >96). The new species appears to be very similar to *L. roellae*, a species from subclade A3, in scale counts and color pattern, but it may differ by smaller body size (SVL 26.3 vs. 35.9–36.0). The new species is genetically highly distinct from all species in subclade A5, based on concordant differentiation in mitochondrial genes (with deep divergence in 16S to all other species: >14%) and the unlinked loci CMOS and RAG-1. In addition it appears to differ by the absence of a spine at the tail base, which is weakly recognizable also in the females of all subclade A5 species except *L. fritzi*. Furthermore, the longitudinal dorsal scale count is smaller than in all known individuals of this subclade.

For a distinction from additional species newly named and described herein, see the respective diagnoses below.

Etymology. We dedicate this species to Hans-Peter "HaPe" Berghof, in recognition of his contributions to the knowledge of Madagascar geckos, especially *Phelsuma*. The name is a patronym (i.e., a noun in the genitive case).

Description of the holotype. Adult female, in good state of preservation, tail regenerated, fourth toe on the left hind limb is removed as source of tissue for molecular analysis (Fig. 15). SVL 26.3 mm, TAL 27.4 mm; for other measurements see Table 1. Head slender with long neck, body broader than head. The distance from the tip of the snout to the anterior border of the eye (3.5 mm) is greater than the interorbital distance anteriorly (3.2 mm), and greater than the distance between the eye and ear opening. Snout covered with granular scales equally sized compared to the rest of the dorsum. Nostril surrounded by three scales: rostral, first supralabial, and two supranasal. Mental scale undivided; no contact between posterior projection of mental scale and first infralabial; two symmetrical postmental scales with five postpostmental scales; seven infralabial scales; eight supralabial scales; three internasal scales; granular dorsal scales; dorsum with small, homogeneous, granular, and unkeeled scales of similar

size to those on trunk, the scales on limbs are not distinctly larger; 179 dorsal scales longitudinally along the body; 87 ventral scales between mental and cloaca; venter with large homogeneous smooth scales; first finger present but very small, not bearing a claw; three pairs of subdigital lamellae on the fourth toe; no dorsolateral tubercle; tail without whorls; no obvious lateral spines at the base of the tail.

TABLE 2. List of localities of *Lygodactylus* samples included in this study, with geographical coordinates and elevation. Numbers of decimals in coordinates reflect precision of collecting site information; values with 4–5 digits refer to coordinates taken with GPS devices, other coordinates were usually estimated or inferred from maps. Note that GPS coordinates often refer to campsites and specimens were collected at walking distance from these. * Exact location of Senbendrana unknown but close to Toamasina (type locality of *L. miops*); ** record of *L. miops* from Moramanga relies on types of two junior synonyms (*septemtuberculatus, spinulifer*).

Locality	Species	Latitude	Longitude	Elevation (m)
Ankarana	*L. rarus, L. expectatus*	S12.95	E49.12	120
Nosy Be	*L. madagascariensis*	S13.41	E48.33	100
Tsaratanana (Manarikoba: Antsahamanara)	*L. salvi*	S14.0450	E48.7853	1000
Tsaratanana (Manarikoba: Andampy)	*L. madagascariensis*	S14.0422	E48.7617	730
Manongarivo	*L. madagascariensis*	S13.9755	E48.4266	690
Maromiandra	*L. madagascariensis*	S13.9965	E48.2177	283
Andrafainkona	*L. madagascariensis*	S13.7133	E49.4911	780
Montagne d'Ambre	*L. madagascariensis, L. petteri, L.* sp. 24	S12.52	E49.18	1000–1100
Montagne d'Ambre (low elevation)	*L. madagascariensis*	S12.4903	E49.1716	687
Montagne d'Ambre (west slope)	*L. tantsaha*	S12.585	E49.116	815–820
Senbendrana (=Sahembendrana) *	*L. miops*	NA	NA	NA
Moramanga **	*L. miops, L. guibei*	S18.92	E48.22	900
Manantantely	*L. miops*	S24.983	E46.917	ca. 20
Andohahela	*L. miops*	S24.76	46.85	ca. 250
N Andohahela	*L. miops*	NA	NA	NA
Sainte Luce	*L. miops*	S24.7667	E47.1833	30
Sainte Luce	*L. miops*	S24.7701	E47.1707	14
Sampanandrano	*L. miops*	S24.1399	E47.0742	530
Tsitongambarika:	*L. miops*	S24.6950	E46.9776	ca. 720
Tsitongambarika: Andranomaizina	*L. miops*	S24.5838	E47.1474	42
Tsitongambarika: Ivohibe	*L. miops*	S24.5612	E47.1924	424
Ranomafana	*L. miops*	S21.26	E47.46	ca. 900
Ambohitsara	*L. miops*	S21.3571	E47.8153	850
Mahakajy	*L. miops*	S21.2792	E47.5304	580
Anosibe Anala	*L. miops*	S19.43	E48.22	ca. 800
Vohimana	*L. miops*	S18.9208	E48.5158	770
Sahafina	*L. miops*	S18.8106	E48.9803	60
Betampona: Betakonana	*L. miops*	S17.9141	E49.2167	356

.....continued on the next page

TABLE 2. (Continued)

Locality	Species	Latitude	Longitude	Elevation (m)
Betampona: Maintimbato	*L. miops*	S17.8938	E49.2251	274
Betampona: Piste Fotsimavo	*L. miops*	S17.9231	E49.2087	205
Betampona: Sahabefoza	*L. miops*	S17.9127	E49.2107	481
Betampona: Sahaindrana	*L. miops*	S17.8968	E49.1996	344
Betampona: Sahambendrana	*L. miops*	S17.9014	E49.2110	458–558
Betampona: Vohitsivalana	*L. miops*	S17.8850	E49.2034	481
Ambodivoahangy (Makira)	*L. miops*	S15.2899	E49.6203	100–300
Andasibe	*L. guibei, L.* sp. 19	S18.9333	E48.4166	900
Vohidrazana	*L. guibei*	S18.95	E48.50	700–800
Anjozorobe	*L. guibei*	S18.40	E47.87	1250
Mahasoa	*L. guibei*	S17.2977	E48.7020	1030
Angozongahy (Makira west slope)	*L. guibei*	S15.4370	E49.1167	1010
Ambodikakazo	*L. salvi*	S14.2131	E48.9052	1310
Ampotsidy	*L. roellae, L. winki*	S14.42–14.43	E48.71–48.72	1315–1405
Andrevorevo	*L. roellae, L. winki*	S14.3464	E49.1028	1720
Djangoa	*L. hapei*	S13.7993	E48.3361	20
Bemanevika	*L. winki*	S14.4306	E48.6018	1470
Marojejy	*L. ulli*	S14.4376	E49.7755	480
Ankanin'ny Nofy	*L. fritzi*	S18.6058	E49.2138	0
Vohibola	*L. fritzi*	S18.5897	E49.2307	10
Tsingy de Bemaraha	*L. hodikazo*	S18.7844	E44.8603	430
Antanambe	*L.* sp. 20	S16.4299	E49.7846	ca. 320

FIGURE 19. Photo of *Lygodactylus hapei* **sp. nov.**, holotype ZSM 298/2018 from Djangoa (Djohahely), in life. Photo by H.-P. Berghof.

Based on available photograph (Fig. 19), the holotype in life displayed a broad brown stripe on the back with a brighter center running along the spine reaching from the snout to the base of the tail. Along the brighter center, irregularly scattered black spots are present. Flanks are yellowish brown with irregular small dark spots. A distinct black stripe is running from the snout through the eye to the shoulder ending in a black marking somewhat reminiscent of a scapular semi-ocellus, but positioned more posteriorly. Above this, a second whitish and broader stripe is present, reaching from the eye to the shoulder. Dorsally brown with a diffuse pattern consisting of dark and light spots, venter whitish. Flanks brighten towards venter with a diffuse ocelli-like pattern. Brown color on head with distinct border on supralabials to whitish venter. Six black stripes radially arranged around the eye. Tail slightly brighter than dorsum with pairs of black and white spots running posteriorly along the caudal spine (Fig. 19). During preservation in ethanol, the specimen darkened and patterns faded. Preserved specimen displays dark irregular spots on whitish gular region expanding to the anterior ventral torso.

Variation. Only a single individual of this species (the holotype) is known.

Natural history. The only known specimen was photographed millimeters from the posterior end of a planthopper larva (Fig. 19), and was presumably consuming honeydew excreted by the insect, as is known from other gecko species (Fölling *et al.* 2001).

Distribution. *L. hapei* is only known from its type locality, Djohahely.

Lygodactylus winki sp. nov.

Lygodactylus sp. 18—Gippner *et al.* (2021).

Holotype. ZSM 47/2016 (MSZC 0075), adult male, collected by M.D. Scherz, J. Borrell, L. Ball, T. Starnes, E. Razafimandimby, D.H. Nomenjanahary, and J. Rabearivony, at Ampotsidy, 15.7 km NNW of Bealanana (8.7 km NNW of Beandrarezona), northern Madagascar, at geographical coordinates S14.41900, E48.71883, 1364 m a.s.l., on 22 December 2015 (Fig. 15).

Paratypes. ZSM 48/2016 (MSZC 0110), adult male, collected by same collectors and at same locality as holotype, at geographical coordinates S14.42843, E48.72285, 1315 m a.s.l., on 29 December 2015; UADBA-R 70856–70859 (MSZC 0011, 0019, 0023, 0077), two males and two females, respectively, collected by same collectors and at same locality as holotype, between coordinates S14.41455–14.42317, E48.71149–48.71916, 1320–1404 m a.s.l., on 18–22 December 2015; ZSM 1763/2010 (ZCMV 12502), by M. Vences, D.R. Vieites, R.D. Randrianiaina, F.M. Ratsoavina, S. Rasamison, A. Rakotoarison, E. Rajeriarison, and T. Rajoafiarison, at Bemanevika, Antsirakala campsite, geographical coordinates S14.43061, E48.60179, 1466 m a.s.l., on 27 June 2010; ZSM 555/2014 (DRV 6288), collected by F.M. Ratsoavina, D.R. Vieites, M. Vences, R.D. Randrianiaina, S. Rasamison, A. Rakotoarison, E. Rajeriarison, and T. Rajoafiarison at Andrevorevo, geographical coordinates S14.3464, E49.1028, 1717 m a.s.l., on 21 June 2010.

Diagnosis. *Lygodactylus winki* **sp. nov.** corresponds to a lineage forming part of the subclade A5 of *Domerguella*, and is one of only two representatives of this subclade known to reach northern Madagascar. The lowest genetic divergences of the lineages are 8.7% uncorrected 16S distance to *L. guibei* and 10.3% to *L. miops.* It is characterized by the presence of very distinct lateral spine-like scales at the base of the tail in males, as are found in several representatives of subclade A5 but not in other *Domerguella*. It can also be assigned to the subgenus *Domerguella* by an undivided mental scale with two postmentals, absence of a claw on the first finger, and 7 preanal pores in males. Within *Domerguella*, the new species is one of only two species of subclade A5 known from northern Madagascar. It differs from the other nominal species of *Domerguella* occurring in the same general area as follows: from *L. expectatus* by non-enlarged dorsolateral scales (longitudinal count of dorsal scales >185 vs. <170); from *L. rarus* by lack of regular crossbands on tail (vs. presence) and different body shape with less elongated limbs (relative hindlimb length 0.49–0.54 vs. >0.55); from *L. madagascariensis, L. petteri,* and *L. salvi* by a lower longitudinal count of ventral scales (83–98 vs. >100); from *L. roellae* and *L. hapei,* by a higher longitudinal count of dorsal scales (187–222 vs. 159–179); and from *L. tantsaha* by a lower longitudinal count of dorsal scales (187–222 vs. 239–240). Furthermore, the new species differs from all of these species of the subclades A1–A4 by the presence of a distinct lateral spine at the base of the tail, especially large in males but also clearly recognizable in females (vs. more weakly expressed or absent in the other species).

From the other two nominal species in subclade A5 (*L. guibei* and *L. miops*, according to current taxonomy;

see above) the new species differs as follows: from *L. miops* by a lower longitudinal count of ventral scales despite minimal overlap (83–98 vs. 98–113); and from *L. guibei* by apparently relatively longer hindlimbs (HIL/SVL 0.49–0.54 vs. 0.42–0.49). Further comparative examination of specimens also revealed a different head shape in *L. winki* compared to *L. guibei*, with apparently more expressed supraocular bulges (also visible in specimens in life; Fig. 14 vs. Fig. 20). Additional measurements taken on selected specimens in good, fully comparable state of preservation (Table 3) revealed that *L. winki* individuals have proportionally longer and higher heads than *L. guibei,* with non-overlapping values (relative snout tip to tympanum distance in percent, 24.7–28.8 vs. 23.0–24.6; relative head height in percent, 12.5–14.2 vs. 11.1–12.4; see Table 3). *L. winki* **sp. nov.** does not share haplotypes in CMOS or RAG1 with *L. miops*, and only one instance of haplotype sharing in RAG1 is detected with *L. guibei.*

TABLE 3. Measurements of head proportions (in mm) in selected specimens of *Lygodactylus guibei* and *L. winki* **sp. nov.** to illustrate relatively shallower and shorter heads in *L. guibei*. Only specimens in good state of preservation were included. STD, snout-tympanum distance; HH, head height; relSTD, relHH are relative values (in percent) given as ratio to SVL. For additional measurements and metadata of specimens, see Table 1.

Specimen voucher	Field number	Sex	SVL	STD	HH	**relSTD (%)**	**relHH (%)**
L. winki **sp. nov.** (sp. 18)							
ZSM 47/2016 (HT)	MSZC 0075	male	29.5	7.3	3.7	24.7	12.5
ZSM 48/2016 (PT)	MSZC 0110	male	29.8	7.6	4.0	25.5	13.4
ZSM 555/2014 (PT)	DRV 6288	male	33.0	9.5	4.7	28.8	14.2
ZSM 1763/2010 (PT)	ZCMV 12502	female	33.4	9.3	4.5	27.8	13.5
L. guibei							
ZSM 320/2004	FGZC 616	male	34.9	8.6	4	24.6	11.5
ZSM 321/2004	FGZC 617	male	33.2	8.1	3.7	24.4	11.1
ZSM 349/2010	FGZC 4362	male	37.6	9.0	4.5	23.9	12.0
ZSM 319/2004	FGZC 613	female	35.8	8.9	4.3	24.9	12.0
ZSM 330/2004	FGZC 627	female	39.5	9.1	4.6	23.0	11.6
ZSM 5117/2005	FGZC 2689	female	34.0	8.0	4.2	23.5	12.4
ZSM 525/2009	ZCMV 11210	female	31.3	7.6	3.8	24.3	12.1

For a distinction from additional species newly named and described herein, see the respective diagnoses below.

Etymology. This species is dedicated to Michael Wink, pharmacologist, herpetologist, ornithologist and professor emeritus of the University of Heidelberg, in recognition for his support of research in squamate systematics. The name is a patronym (i.e., a noun in the genitive case).

Description of the holotype. Adult male, hemipenes everted, in good state of preservation, tail is broken and missing, second toe on the left forelimb is removed as source of tissue for molecular analysis (Fig. 15). SVL 29.5 mm, TAL 15.6 mm; for other measurements see Table 1. Head and neck short, head broader than body. The distance from the tip of the snout to the anterior border of the eye (3.9 mm) is less than the interorbital distance anteriorly (4.0 mm), and greater than the distance between the eye and ear opening. Snout covered with granular scales larger than those on the rest of the dorsum. Nostril surrounded by five scales: rostral, first supralabial, and three supranasals. Mental scale undivided; no contact between posterior projection of mental scale and first infralabial; two symmetrical postmental scales with four postpostmental scales; six infralabial scales; seven supralabial scales; two internasal scales; granular dorsal scales; dorsum with small, homogeneous, granular, and unkeeled scales of similar size to those on trunk, smaller than on head and tail, the scales on limbs can be slightly larger; 222 dorsal scales longitudinally along the body; 93 ventral scales between mental and cloaca; venter with large homogeneous smooth scales; first finger present but very small, not bearing a claw; three pairs of subdigital lamellae on the fourth toe; eight not very distinct dorsolateral tubercles, consisting of one scale; seven preanal pores; tail without whorls; large lateral spines at the base of the tail.

Based on available photographs (Fig. 20), the holotype displayed a light marbled yellow grayish dorsal coloration with more brownish flanks before preservation. Distinct yellow spots are present on the head, the flank, the limbs, and the tail. Two black markings are present on the shoulder on either side of the body, reminiscent of double scapular semi-ocelli. Along the spine a narrow brown line reaches from the neck to the base of the tail.

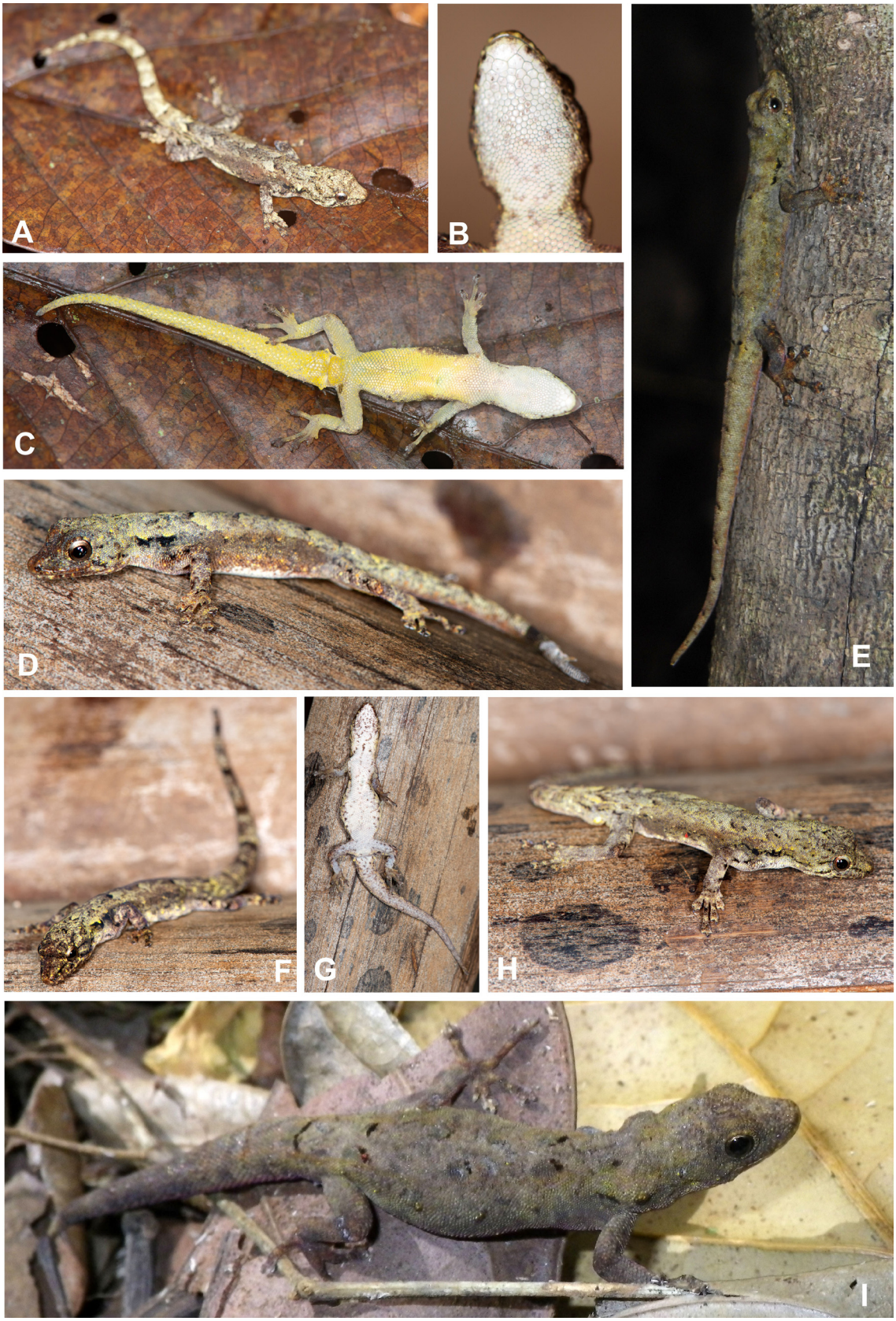

FIGURE 20. Photos of *Lygodactylus winki* **sp. nov.** in life. A–C, adult male paratype UADBA-R 70857 (MSZC 0019) from Ampotsidy in dorsolateral and ventral view, and ventral view of throat. D, male holotype ZSM 47/2016 (MSZC 0075) from Ampotsidy. E, female paratype ZSM 555/2014 (DRV 6288) from Andrevorevo. F–G, female paratype UADBA-R 70859 (MSZC 0077) from Ampotsidy. H, male paratype ZSM 48/2016 (MSZC 0110) from Ampotsidy. I, female paratype ZSM 1763/2010 (ZCMV 12502) from Bemanevika.

Adjacent to this line two pairs of symmetrical dark spots are present (forming two disrupted chevrons), one pair on forelimb level and one pair 10 mm posterior (Fig. 20D). After six years of preservation in ethanol, the preserved specimen is more uniformly brownish and most of the marbled pattern is faded. The ventral side is fawn with few small brown spots, most of them in the gular region.

Variation. Males display a light marbled yellow grayish dorsal coloration with more brownish flanks and yellow spots. The dorsal and ventral coloration on females is darker without a pattern except for a few dark dorsal spots (Fig. 20E and 20I in comparison to Fig. 20A–G).

Three additional specimens (two males [ZSM 555/2014, ZSM 48/2016], one female [ZSM 1763/2010]) were examined. The SVL ranges between 29.8 and 33.4 mm with the female being the largest. The two males have a TAL of 37.8 and 45.0 mm. The relative hindlimb length is 0.49 to 0.53 with the female having the smallest. The female also has the smallest eyes relative to the size of the body and with a medium size smaller tubercles at the tail base than the males, which have large tubercles. The number of dorsal scales ranges between 187 and 208. The ventral scales range between 83 and 98.

Natural history. The holotype was collected in primary rainforest, on the trunk of a big tree, 0.2 m above the ground. The paratypes from Ampotsidy were mostly collected at night sleeping on leaves, twigs, or vines. UADBA-R 70856 was collected in the afternoon, on the ground during heavy rain.

Distribution. *L. winki* is known from three localities in the North and Sambirano regions in northern Madagascar: (1) the type locality, Ampotsidy, (2) Andrevorevo, and (3) Bemanevika.

Lygodactylus ulli sp. nov.

Lygodactylus sp. 21: Gippner *et al.* (2021)

Holotype. ZSM 154/2005 (FGZC 2811), adult male, collected by F. Glaw, M. Vences, and R.D. Randrianiaina at Marojejy National Park, at Camp 1 "Mantella", North-East of Madagascar, geographical coordinates S14.4377, E49.7756, 481 m a.s.l., on 14 February 2005 (Fig. 15).

Referred material. UADBA-R uncatalogued (MSZC 0272), female, collected by M.D. Scherz, J. Razafindraibe, and A. Razafimanantsoa at the same locality as the holotype, at night on 23 November 2016.

Diagnosis. *Lygodactylus ulli* **sp. nov.** corresponds to a lineage forming part of subclade A5 of *Domerguella*, and is the second representative of this subclade reaching northern Madagascar. It is characterized by the presence of distinct lateral spine-like scales at the base of the tail in males, as is found in several representatives of A5 from eastern Madagascar but not in other *Domerguella*. The smallest genetic distances are 10.7% uncorrected 16S distance to specimens of *L. guibei*. It can also be assigned to the subgenus *Domerguella* by an undivided mental scale with two postmentals, absence of a claw on the first finger, and 7 preanal pores in males. Within *Domerguella*, the new species (together with *L. winki*) is one of only two species of subclade A5 known from northern Madagascar, and the only species of *Domerguella* so far known from the rainforests of the Marojejy Massif.

It differs from the nominal species of *Domerguella* occurring in northern Madagascar and belonging to subclades A1–A4 as follows: from *L. expectatus* by non-enlarged dorsolateral scales (longitudinal count of dorsal scales >250 vs. <170); from *L. rarus* by lack of regular crossbands on tail (vs. presence) and different body shape with less elongated limbs (relative hindlimb length 0.47 vs. >0.55); from *L. petteri, L. tantsaha, L. salvi, L. roellae,* and *L. hapei* by a higher longitudinal count of dorsal scales (253 vs. <241); and from *L. madagascariensis* as well as most of the previously mentioned species by a small but distinct spine-like tubercle at the base of the tail in males. From the other nominal species in subclade A5 (*L. miops,* and *L. guibei* and *L. winki*) the new species differs by higher longitudinal counts of dorsal scales (253 vs. 170–242) and ventral scales (110 vs. 87–109). We did not detect haplotype sharing in RAG1 or CMOS between *L. ulli* and the other nominal species in subclade A5 (*L. miops,* and *L. guibei* and *L. winki*). Haplotpe sharing was detected only at the CMOS marker with *L.* sp. 20.

For a distinction from additional species newly named and described herein, see the respective diagnoses below.

Etymology. We are pleased to dedicate this species to Ulrich "Ulli" Joger, director emeritus of the Braunschweig Natural History Museum, in recognition of his contribution to the taxonomy of reptiles, especially geckos. The species epithet name is defined as a noun in apposition (not a noun in the genitive case) to avoid ending with a non-euphonious double-i.

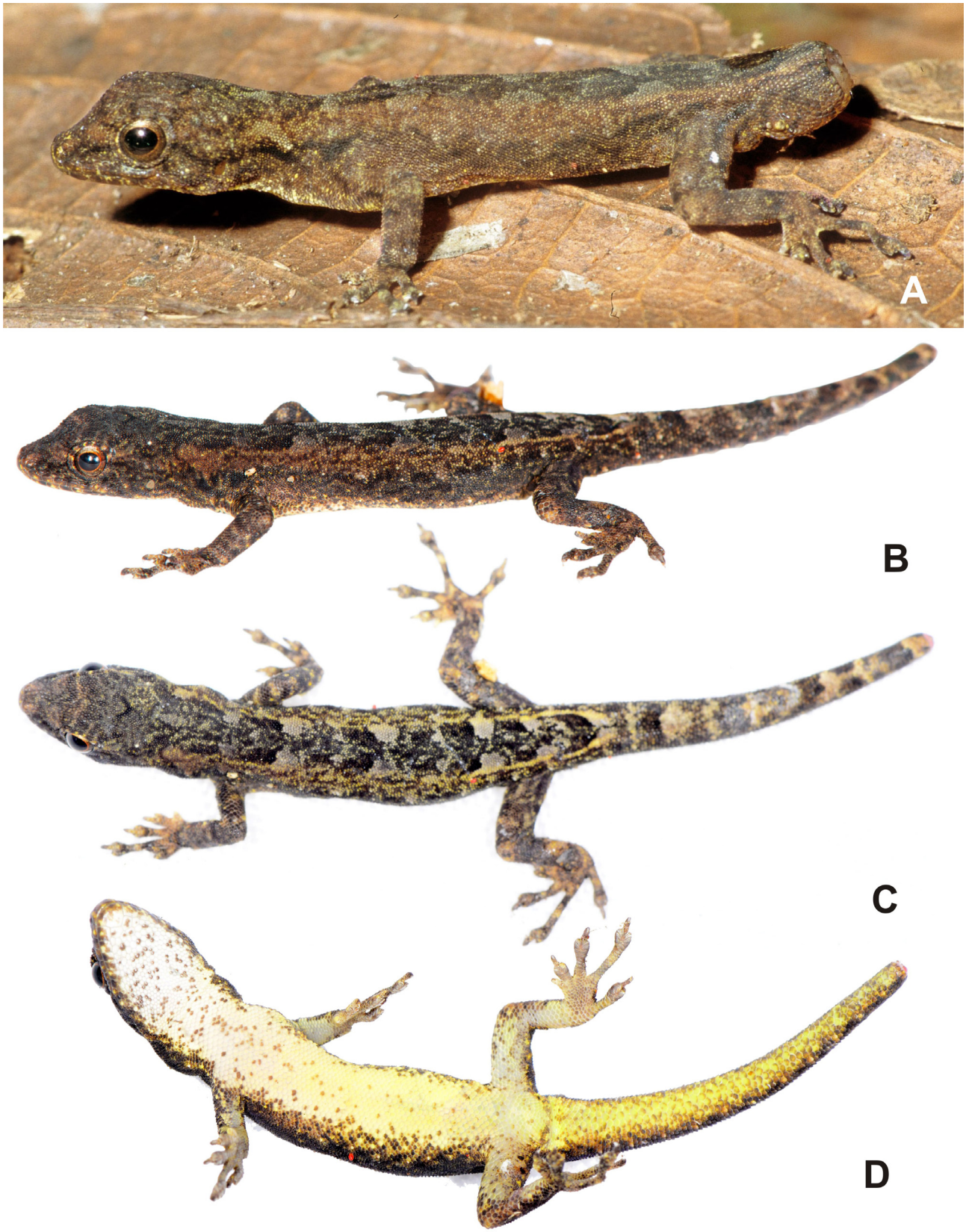

FIGURE 21. Photos of *Lygodactylus ulli* **sp. nov.**, specimen from Marojejy in life. A, male holotype ZSM 154/2005 (FGZC 2811). B, C, D, female specimen UADBA-R-MSZC 272 in dorsolateral, dorsal, and ventral views. Not to scale.

Description of the holotype. Adult male, hemipenes everted, in moderate state of preservation, tail is broken and missing, right forelimb is removed as source of tissue for molecular analysis (Fig. 15). SVL 28.8 mm, TAL 2.6 mm; for other measurements see Table 1. Head broader than body. The distance from the tip of the snout to the anterior border of the eye (3.5 mm) is lesser than the interorbital distance anteriorly (3.9 mm), and greater than the distance between the eye and ear opening. Snout covered with granular scales larger than those on the rest of the dorsum. Nostril surrounded by five scales: rostral, first supralabial, and three supranasals. Mental scale undivided; no contact between posterior projection of mental scale and first infralabial; three asymmetrical postmental scales with five postpostmental scales; six infralabial scales; seven supralabial scales; two internasal scales; granular dorsal scales; dorsum with small, homogeneous, granular, and unkeeled scales of similar size to those on trunk, no distinct size difference to scales on limbs; 253 dorsal scales longitudinally along the body; 110 ventral scales between mental and cloaca; venter with large homogeneous smooth scales; first finger present but very small, not bearing a claw; three pairs of subdigital lamellae on the fourth toe; two not very distinct dorsolateral tubercles, each consisting of one scale; seven preanal pores; tail without whorls; small lateral spines at the base of the tail.

Based on available photographs (Fig. 21), the live holotype displays a brownish to grayish pattern on the dorsum and the limbs. From the snout, a narrow black stripe runs irregularly to two elongated spots on the shoulder. At the forelimb level two symmetrical black spots are present on the spine (Fig. 21A). After 16 years in ethanol, the preserved specimen is more grayish. The ventral side is whitish. While there are only a few small brown spots on the venter, multiple larger brown spots are irregularly scattered on the throat.

Variation. Comparing the two photographed specimens, dorsal coloration and patterns are less pronounced on the male (Fig. 21A), maybe because it appears to be close to skin shedding. The female has a blackish and grayish alternating dorsal pattern, surrounded by a yellowish base layer (Fig. 21B+C). The female is laterally darker than the male (Fig. 21A+B), has a white throat and yellow venter and ventral tail.

Natural history. Specimens were collected in primary rainforest.

Distribution. *L. ulli* is only known from its type locality, the Marojejy Massif in the North East region of Madagascar.

Lygodactylus fritzi sp. nov.

Lygodactylus sp. 11: Gippner *et al.* (2021).

Justification. This new species from coastal areas in Madagascar's Northern Central East has previously been called *L*. sp. 11 in Gippner *et al.* (2021). It corresponds to a lineage forming part of subclade A5 of *Domerguella*, and occurs in a general area where *L. miops* is also present. It is characterized by the presence of distinct lateral spine-like scales at the base of the tail in males, as are found in several representatives of subclade A5 but not in other *Domerguella*. The smallest genetic distance is 9.0% to specimens assigned to *L. miops*. However, it differs from this species by phylogenetic position and lack of haplotype sharing in nuclear-encoded genes. While species status of these two lineages is validated by the molecular evidence, the assignment of the holotype of *L. miops*, and of the types of the other earlier names *septemtuberculatus* and *spinulifer*, to either of them requires further justification (see also the account of *L. miops*).

The following arguments support our decision to assign the holotype of *miops, septemtuberculatus* and *spinulifer* to what we will in this section call the "widespread lowland lineage" rather than to *L.* sp. 11:

(1) The specimens of the widespread lowland lineage (including the three historical types) differ from *L.* sp. 11 by a 3–6 vs. 2 dorsolateral tubercles between limbs; dorsal scale count 207–242 vs. 247; ventral scale count 102–113 vs. 98; lateral tubercles at tail base recognizable (also in females) vs. barely recognizable. While each of these meristic differences by itself is rather weak, taken together they characterize *L.* sp. 11 as morphologically distinct, and the three type specimens of the earlier names as better fitting the widespread eastern lineage.
(2) *L.* sp. 11 is only known from two low-elevation localities near sea level (0–20 m a.s.l.), and seems to be relatively localized; for instance, it has not been found at other nearby localities at slightly higher elevation such as Sahafina or Betampona, despite a substantial number of specimens sequenced from Betampona, which all belonged to the widespread lowland lineage. It is therefore less likely that historical specimens of *L.* sp. 11 were

collected historically, and that its range extends into the type localities of the three historical nomina, especially up to Moramanga (the type locality of *septemtuberculatus* and *spinulifer*).

(3) The type locality of *L. miops*, "Senbendrana" according to the original description (Günther 1891), cannot be located reliably at present. Senbendrana has been reported with the addition "near Tamatave" (= Toamasina) as a collecting locality of spiders (Pocock 1895); or as corresponding to Sahembendrana or Sahambendrana. This latter synonymy is supported by the fact that the type of *L. miops* was provided by "Majastre" (see Puente *et al.* 2009), probably corresponding to A. Majastre, a collector who provided specimens of many animals and plants from this area. Some of Majastre's collections are labelled "Sahambendrana", e.g., the type of the orchid *Eulophia grandibracteata* (see Schultz 2013). The locality apparently was often misspelled; for example, we assume that "Sen Bendrana" (Michaelsen 1891), "Senbendra" (Sharp & Ogilvie-Grant 1898), or "Schambendrama" (Bott 1963) refer to the same site as well. Blommers-Schlösser & Blanc (1991) located Sahembendrana close to Akkoraka (at higher elevations in eastern Madagascar), but it is likely that Majastre's collecting site was situated closer to Toamasina. We could not locate current or historical maps mentioning a site with this or a similar name, but Ramananjara (2009) documents the sale of a property in 1931, in the "Canton d'Antetezambaro; sur la rivière Sahambendrana", and more specifically "au sud d'Ambodisatrana", which likely refers to a coastal village about 30 km north of Toamasina that can be located in historical maps from 1934 (Service Géographique de Madagascar, map "Fénérive", 1/500,000). On the other hand, Rosa *et al.* (2012) report a campsite from Betampona Reserve (about 35 km north-east of Toamasina) locally known as Sahambendrana, at coordinates S17.8984, E49.2154, 458 m a.s.l. Other sources refer to a Sahambendrana river on the northern versant of Betampona (Randriatavy 2003; Randrianarimanana 2009). Whether any of these sites corresponds to Majastre's collecting locality cannot be decided without further evidence, but these references demonstrate that the toponym has been and is in use for sites to the north and northeast in the vicinity of Toamasina.

The available evidence, however, points to the original collecting site being not directly at sea level. According to Günther (1891), the same collection that included the *L. miops* holotype also contained "*Rhacophorus luteus*", which almost certainly corresponds to a treefrog species of the *Boophis luteus* group, which is not known from coastal sites in Madagascar (but known to be present in Betampona), and for instance has not been collected at Vohibola or Ankanin'ny Nofy (Gehring *et al.* 2010) where *L.* sp. 11 occurs. Furthermore, Pellegrin (1933) reported fish specimens of the genus *Sicyopterus* from a "rivière Sahembendrana (région de Tamatave)". These specimens were identified by Sparks & Nelson (2004) as *S. franouxi*, a species that according to these authors inhabits clear, swift-flowing waters and is frequently captured quite far inland, again in agreement that this site is within the range of the widespread eastern lineage but not a coastal locality within the range of *L.* sp. 11. The fact that Sahambendrana / Sahembendrana has on various occasions been used to refer to a river (e.g., Pellegrin 1993; Randriatavy 2003; Randrianarimanana 2009; Ramananjara 2009) allows for the possibility of an upstream collecting site of the *L. miops* holotype, at some distance from the coast, and thus at a moderate elevation as indicated by the accompanying fish and amphibian fauna; and probably in the area close to Betampona where our collections have only yielded individuals of the widespread lowland *Domerguella* lineage.

In summary, the available evidence thus suggests that none of the earlier available names *miops, septemtuberculatus,* or *spinulifer* is likely to apply to *L.* sp. 11, which we therefore formally name as species new to science, *L. fritzi* **sp. nov.**

Holotype. ZSM 651/2009 (ZCMV 8902), female, collected by P.-S. Gehring, F. Ratsoavina, and E. Rajeriarison at Ankanin'ny Nofy, east coast of Madagascar, geographical coordinates -S18.6058, E49.2138, roughly at sea level, on 8 April 2009.

Diagnosis. *Lygodactylus fritzi* **sp. nov.** is a species of the *Lygodactylus* subgenus *Domerguella* based on molecular phylogenetic relationships, and it can also be assigned to the subgenus *Domerguella* by an undivided mental scale with two postmentals, absence of a claw on the first finger, and 7 preanal pores in males. Within *Domerguella*, the new species is one of several species of subclade A5 known from the Northern Central East of Madagascar.

It differs from the nominal species of *Domerguella* occurring in northern Madagascar and belonging to subclades A1–A4 as follows: from *L. expectatus* by non-enlarged dorsolateral scales (longitudinal count of dorsal scales >250 vs. <170); from *L. rarus* by lack of regular crossbands on tail (vs. presence) and different body shape with less elongated limbs (relative hindlimb length 0.47 vs. >0.55); from *L. petteri, L. tantsaha, L. salvi, L. roellae,* and *L. hapei* by a higher longitudinal count of dorsal scales (253 vs. <241); and from *L. madagascariensis* as well as most

of the previously mentioned species of clades A1–A4 by a rudimentary spine-like tubercle at the base of the tail in the only known female (vs. absence).

From other species of subclade A5, the new species differs as follows: from *L. miops* by fewer dorsolateral tubercles between limbs (2 vs. 3–6), higher longitudinal dorsal scale count (247 vs. 207–242), lower longitudinal ventral scale count (98 vs. 102–113), and weakly expressed lateral tubercles at tail base vs. clearly recognizable in males and females; from *L. guibei* by higher longitudinal dorsal scale count (247 vs. 170–220), and weakly expressed lateral tubercles at tail base vs. clearly recognizable, usually large in males and females; from *L. winki* by fewer dorsolateral tubercles between limbs (2 vs. 5–8), higher longitudinal dorsal scale count (247 vs. 187–222), and weakly expressed lateral tubercles at tail base vs. clearly recognizable usually large in males and females; from *L. ulli* possibly by more weakly expressed lateral tubercles at tail base and a lower longitudinal count of ventral scales (98 vs. 110). From all these species, it differs by phylogenetic position, at least 9% 16S distance, and absence of haplotype sharing in both nuclear-encoded genes studied.

For a distinction from one other species newly named and described in the following, see the respective diagnosis below.

Etymology. We are pleased to dedicate this species to Uwe Fritz, director of the Museum of Zoology, Dresden (part of the Senckenberg Natural History Collections), in recognition of his substantial contributions to the taxonomy of chelonians and squamates, and his tireless efforts to spearhead the fight for continued funding of basic taxonomic research. The name is a patronym (i.e., a noun in the genitive case).

Description of the holotype. Female in a good state of preservation, tail partly detached. SVL 26.4 mm, TAL 26.5 mm; for other measurements see Table 1. Body broader than head. The distance from the tip of the snout to the anterior border of the eye (3.1 mm), is less than the interorbital distance anteriorly (3.5 mm), and greater than the distance between the eye and ear opening. Snout covered with granular scales larger than those on the rest of the dorsum. Nostril surrounded by four scales: rostral, first supralabial, and two supranasals. Mental scale undivided; no contact between posterior projection of mental scale and first infralabial; two asymmetrical postmental scales with four postpostmental scales; 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, no distinct size difference to scales on limbs; 247 dorsal scales longitudinally along the body; 98 ventral scales between mental and cloaca; venter with large homogeneous smooth scales; first finger present but very small, not bearing a claw; three pairs of subdigital lamellae on the fourth toe; two not very distinct dorsolateral tubercles, each consisting of one scale; tail without whorls; small lateral spines at the base of the tail.

Coloration of the holotype is only described from the specimen that was preserved in ethanol for 12 years. The dorsum is fawn to brownish with scattered darker brown spots, the flanks are darker than the dorsum. A distinctive dark stripe is displayed on the shoulder. The parietal exhibits two darker areas. The tail is fawn with equispaced darker brown stripes on it. Venter and the snout are uniformly whitish with small irregular brown spots.

Variation. Morphometric and meristic data are only known from a single voucher specimen. However, color patterns could be assessed from photographs of three additional individuals (Fig. 22), some of which were dorsally gray-beige with an irregular contrasted pattern of larger light and smaller dark spots (Fig. 22A), others more uniform with a more or less symmetrical pattern of dark spots (Fig. 22E), or dark brown with weakly contrasted light brown dorsolateral bands with a somewhat reddish tone (Fig. 22B–C). Ventrally irregularly dark spotted (Fig. 22D).

Distribution. *L. fritzi* is only known from (1) the type locality Ankanin'ny Nofy and (2) Vohibola, two coastal lowland localities (0–20 m a.s.l.) in the Northern Central East of Madagascar. Littoral forest harbours a high species richness especially of plants, with several genera endemic to this habitat (de Gouvenain & Silander 2003; Bollen & Donati 2005). Fisher & Girman (2000) identified littoral forests as one of four major areas for ant endemism in Madagascar. Previous studies in south-eastern littoral forests found no vertebrate species strictly endemic to that forest type (Ganzhorn *et al.* 2000; Goodman & Ramanamanjato 2007) but recent taxonomic revisions have revealed numerous amphibians and reptiles restricted to small areas of forest directly adjacent to the Madagascar's coast, such as for example species of the miniaturized frog genus *Mini* (Scherz *et al*. 2019) or Pandanus-dwelling frogs of *Guibemantis* (Lehtinen *et al*. 2011), or the chameleon *Calumma vohibola* (Gehring *et al.* 2011), *Lygodactylus fritzi* adds to this growing list of species specialized to these highly threatened coastal forests.

Natural history. One adult specimen was photographed millimeters from the posterior end of a bug (Fig. 22), and was presumably consuming honeydew excreted by the insect, as is known from gecko species (Fölling *et al.* 2001).

FIGURE 22. Photos of *Lygodactylus fritzi* **sp. nov.** specimens from Vohibola in life. All specimens correspond to genotyped individuals included in Fig. 1 that were not collected.

Lygodactylus hodikazo sp. nov.

Lygodactylus sp. 23: Gippner *et al*. (2021)

Holotype. ZSM 77/2006 (FGZC 828), collected by F. Glaw, J. Köhler, P. Bora, and H. Enting at Tsingy de Bemaraha National Park, Bendrao Forest, western Madagascar, geographical coordinates S18.7844, E44.8603, 427 m a.s.l., on 25 March 2006 (Fig. 15).

Diagnosis. *Lygodactylus hodikazo* **sp. nov.** is the only *Domerguella* lineage known from the West of Madagascar, and only one specimen is so far known. In our multigene analysis, it forms with high support the sister taxon of the clade of *L. madagascariensis* and *L. petteri*, thus belonging to subclade A4 of *Domerguella* as defined herein. Since these two species are to be considered as distinct species given their sympatric occurrence without allele sharing in the analysed nuclear markers, it is justified to allocate species status also to this western lineage, despite its similarity in morphological characters (scale counts) to *L. madagascariensis*. The justification for this species thus mainly relies on its phylogenetic position, on the high mitochondrial divergence (>8% 16S distance), and large geographical and ecological distance (only *Domerguella* in western Madagascar) to *L. madagascariensis,* which morphologically is the most similar species.

Lygodactylus hodikazo **sp. nov.** can be assigned to the subgenus *Domerguella* morphologically by an undivided mental scale with two postmentals, and absence of a claw on the first finger. Within *Domerguella*, the new species is the only lineage known from western Madagascar, and belongs to subclade A4. From the species of subclades A1–A4 occurring in northern Madagascar except *L. madagascariensis* it differs as follows: from *L. expectatus* by non-enlarged dorsolateral scales (longitudinal count of dorsal scales 231 vs. <170); from *L. rarus* by lack of regular crossbands on tail (vs. presence) and different body shape without elongated limbs (relative hindlimb length 0.44 vs. >0.55); from *L. petteri, L. salvi, L. roellae,* and *L. hapei* by a higher longitudinal count of dorsal scales (231 vs. 159–222), and from *L. roellae* and *L. hapei* also by a higher longitudinal count of ventral scales (109 vs. 83–92); from *L. tantsaha* by a higher number of supralabials (10 vs. 6–7) and infralabials (8 vs. 5–6). Genetically, the new species is highly distinct from all species in subclade A5, and we hypothesize that it will differ from many of these by

less expressed tubercles at the tail base in males (these tubercles are weakly expressed in the female holotype). The new species is morphologically most similar to *L. madagascariensis* from which it differs by 8.4–10.5% pairwise distance in the 16S gene, and has different haplotypes in RAG1 and CMOS (although intermixed with haplotypes of *L. madagascariensis* in the network). The new species also differs as far as known from *L. madagascariensis*, and indeed from all other *Domerguella*, by a high number of supralabials (10 vs. 7–9 in *L. madagascariensis* and 5–9 in all other species; Table 1); this character however requires confirmation by examination of additional specimens.

Etymology. The species epithet is derived from the Malagasy words hodi-kazo (= tree bark), in reference to the habitat of most *Domerguella* (and supposedly also this species) who are typically found on trees in forest and with a color pattern mimicking the bark. The name is used as noun in apposition.

Description of the holotype. Adult female, in a good state of preservation (Fig. 15). SVL 29.4 mm, TAL 37.2 mm; for other measurements see Table 1. Head and neck long, body broader than head. The distance from the tip of the snout to the anterior border of the eye (3.9 mm) is greater than the interorbital distance anteriorly (3.8 mm), and greater than the distance between the eye and ear opening. Snout covered with granular scales larger than those on the rest of the dorsum. Nostril surrounded by five scales: rostral, first supralabial, and three supranasals. Mental scale undivided; small contact between posterior projection of mental scale and first infralabial; two asymmetrical postmental scales with four postpostmental scales; eight infralabial scales; ten supralabial scales; one internasal scale; granular dorsal scales; dorsum with small, homogeneous, granular and unkeeled scales of similar size to those on trunk, smaller than on head and tail, the scales on limbs can be slightly larger; 231 dorsal scales longitudinally along the body; 109 ventral scales between mental and cloaca; venter with large homogeneous smooth scales; first finger present but very small, not bearing a claw; three pairs of subdigital lamellae on the fourth toe; no dorsolateral tubercles; tail without whorls; small lateral spines at the base of the tail.

Coloration of the holotype is only described from the preserved specimen after 15 years in ethanol. The dorsum is fawn to brownish with two symmetrical pairs of brown stripes on the neck. A brownish stripe runs from the snout to the eye and splits into three thinner stripes behind the eye followed by an irregular pattern of brownish stripes on the flanks. The tail is beige with weak patterning. Venter and the snout are uniformly whitish without a distinct pattern.

Variation. Only a single individual (the holotype) is known.

Distribution. *L. hodikazo* is only known from its type locality, Tsingy de Bemaraha National Park in the West region of Madagascar.

Natural history. Practically nothing is known of the natural history of this enigmatic species. Its presence in the dry forests of the Tsingy de Bemaraha National Park indicates a tolerance for more arid environments that may set it apart from other *Domerguella* species (Bora et al. 2010).

Additional candidate species

Three additional deep mitochondrial lineages of *Domerguella* were identified in our analysis, but are not further treated here due to the absence or scarcity of voucher specimens. Their status will be considered below in the Discussion.

- *Lygodactylus* sp. 19 from Andasibe (FGZC 4636), only one sample known, voucher specimen not available for examination.
- *Lygodactylus* sp. 20 from Antanambe (PSG 69), only one sample known, voucher specimen not collected.
- *Lygodactylus* sp. 24 from Montagne d'Ambre (FGZC 1475), only one sample known, voucher specimen not available for examination. This specimen (already briefly mentioned in the account of *L. petteri* above) was genetically placed in subclade A2 with sympatric specimens of *L. tantsaha*, but differed by 15.5–15.7% 16S divergence and by different haplotypes in CMOS and RAG1. We assume it represents a further new species from Montagne d'Ambre but its status will require scrutiny once additional material and voucher specimens become available.

Discussion

This study revealed an unexpectedly high degree of cryptic genetic variation in a clade of dwarf geckos, the *Lygodactylus madagascariensis* group or subgenus *Domerguella* of the genus *Lygodactylus*. We interpreted this puzzling amount of variation as reflecting the existence of at least eight species new to science. In organisms that are, as these geckos, morphologically highly similar to each other, it is important to carefully weigh all evidence to avoid premature taxonomic decisions and taxonomic inflation. In times where differentiation in DNA barcodes is often seen as initial evidence for species delimitation, a deeper analysis is especially needed in groups with fast mitochondrial evolution such as geckos. Ratsoavina *et al.* (2012) documented how even populations of leaf-tailed geckos in eastern Madagascar that occur in close geographical proximity can be characterized by substantial phylogeographic structure, and Nagy *et al.* (2012) reported that intraspecific distances in the mitochondrial COI gene are higher in geckos than in any other group of Malagasy reptiles.

Genetic divergences as probabilistic indicators of species status

In species delimitation studies, genetic divergences (pairwise distances in a reference gene) are often used to establish discrete thresholds above which lineages are regarded as distinct species. We have regularly used genetic distances in species delimitation, both for an initial identification of candidate species and to support species distinctness in integrative taxonomy, but it is important to stress that we consider genetic distances as quantitative, not qualitative indicators: the greater the distance, the greater the probability of speciation. Since genetic distances are also important for species delimitation in *Domerguella*, it is important to elaborate on this often misunderstood aspect. At first sight, genetic distances represent purely phenetic evidence of the kind that has been criticized both for phylogeography and species delimitation (e.g., de Queiroz & Good 1997) and species identification (e.g., DeSalle *et al.* 2005). In fact, it is particularly problematic to define fixed thresholds above which a lineage is categorically defined as a species and below which as an infraspecific unit. Such a rationale is often used in comparison with other, scientifically named species pairs in the taxon of interest—if species A and B are well established as species and differ by a certain genetic distance, then species C and D, differing by the same distance, must be species as well. A more cautious approach has been proposed for Malagasy frogs (e.g., by Vieites *et al.* 2009): they defined candidate species by a divergence threshold, but emphasized that additional evidence is needed to subsequently verify their status as species (or to instead classify them as deep conspecific lineages). More recently, alternatives to fixed and arbitrary threshold have been made possible thanks to new automated methods such as ASAP or ABGD (Puillandre *et al.* 2012, 2021). These tools based on the detection of barcoding-gap present the advantage of not relying on thresholds as they infer species-level lineages based on the structuring of the distances obtained within a dataset, and therefore—indirectly—reflect the sudden acceleration of branching rates occurring in the most recent (intraspecific) clades of a phylogenetic tree which is detected by tree-based delimitation approaches such as GMYC or PTP (Zhang *et al.* 2013; Fujisawa *et al.* 2016). In all these cases, the outcome necessarily depends on dense and comparable sampling across lineages (Ahrens *et al.* 2016); as exemplified by our *Lygodactylus* data set, this is often difficult to achieve due to both logistic challenges and legal restrictions. Furthermore, the risk of oversplitting is a common theme with all these approaches (for examples from Malagasy reptiles, see Miralles & Vences 2013; Hawlitschek *et al.* 2018). In general, due to strikingly different processes of species formation, where new species may arise instantenously through allopolyploidization, very rapidly through ecological adaptation, or gradually over long periods of time, it is clear that one-size-fits-all delimitation approaches relying only on fixed genetic distance thresholds or barcode gaps must remain plagued with uncertainty.

However, an important aspect to keep in mind is that, compared to many other phenetic comparisons, genetic distances are characterized by being more objectively measurable and roughly proportional to time—and thus to overall genomic divergence, and most importantly, to the amount of hybrid incompatibility and cessation of gene flow (Malone & Fontenot 2008; Dufresnes *et al.* 2021). We suggest this correlation is best interpreted in a probabilistic approach to species (Kollár *et al.* 2022): the higher the genomic divergence in a reference or marker gene, the more genomic incompatibilities across a mass of genes two lineages have likely accumulated (Dufresnes *et al.* 2021), and consequently, the more probable it is that these incompatibilities have led to a disruption of gene flow and hence, to a completion of speciation. It is obvious that this relation will be influenced by genetic saturation of the marker used, and in general the underlying process of progressive accumulation of incompatibilities across the genome and their specific consequences is still poorly understood. However, the available data suggest that time

since lineage divergence is a better predictor for cessation of gene flow than mtDNA divergence (Dufresnes *et al.* 2021), and this should be kept in mind when using genetic (mitochondrial) distances as a probabilistic estimator in species delimitation.

One major challenge is that genetic distances are often calculated from mitochondrial genes only. As shown neatly in many amphibian examples (e.g., Zieliński *et al.* 2013; Chan *et al.* 2020), mitochondrial genomes can be replaced in entire populations and species by introgressed genomes of other species, thereby blurring the original signal of divergence and relationships among lineages. To exclude such phenomena, a careful integrative approach is needed—ideally including population genomic analyses if divergence values are within those typical for the "gray zone" of speciation. However, in probabilistic terms, it is obvious that the likelihood of mitochondrial introgression also decreases with divergence time—as hybrids become increasingly infertile or even inviable, introgression becomes less likely. Introgression of highly divergent mitogenomes from one species to the other is not impossible, but not probable. A similar rationale applies to ancestral polymorphism. With more time, the probability of coalescent processes eradicating such polymorphism increases, which means the risk of errors in species delimitation due to ancestral polymorphism is higher with low genetic divergences in a marker. Low divergence values (indicative of the "gray zone of speciation") therefore raise the bar for the quality and quantity of other evidence to demonstrate species status, while conversely, extremely high divergence values lower this bar.

In this continuum, *Lygodactylus*—with 16S distances in all cases above 7% between the sister lineages recognized herein, and often >10%—are certainly on the side of unusually high mitochondrial divergences, even considering that these values tend to be higher in geckos than in other squamates (e.g., Nagy *et al.* 2012). Following this rationale, the high mitochondrial divergences translate into high probabilities of differentiation exceeding that in the "gray zone of speciation", and we therefore see the subtle but full concordance with independent data sets—nuclear-encoded gene haplotypes and scale counts, partly in syntopy—as sufficient to assign full species status to these lineages—even without population genomic evidence or formal hybrid zone analyses, which would not be feasible with the limited material available.

Sympatric occurrence as taxonomic evidence

In *Domerguella*, the most immediate evidence for a status of mitochondrial lineages as species comes from their sympatric or even syntopic occurrence. In the small mountain massif of Montagne d'Ambre, we detected four deep mitochondrial lineages of *Domerguella* within a geographic distance of less than 15 km, and upon closer examination, these also differed by subtle but constant morphological differences (though *L.* sp. 24 could not be examined morphologically), and did not share haplotypes in nuclear-encoded genes. Considering that one *Domerguella* lineage (*L. miops*) occurs over a range spanning roughly 1100 km linear distance, there is no doubt that these animals are sufficiently vagile so that the Montagne d'Ambre lineages would have ample opportunity for getting into direct contact and thus interbreeding. Yet the available evidence does not give any indication for admixture among these lineages, suggesting gene flow among them is probably limited or absent, and these forms thus represent species both under evolutionary and biological criteria. Perhaps most relevant in this respect is the sympatric occurrence on Montagne d'Ambre of two sister species (*L. madagascariensis* and *L. petteri*) that differ by a distance of 9–10% in 16S, a comparatively low value compared to distances among other *Domerguella*. This provides clear evidence that *Lygodactylus* lineages at this level of divergence can represent clearly distinct species.

Because very few individuals are known from several of the Montagne d'Ambre *Domerguella*, we cannot reliably assess possible niche partitioning e.g., through specialization to certain elevational bands. However, the new species *L. tantsaha* described herein was only found on the west slope of the massif while all other species were found on the east/north slope. This forest is substantially drier than the other areas of the forest, and there may therefore be an ecological driver for the differentiation of this species from the other congeners on the mountain. Further surveys at lower elevation in the north of Montagne d'Ambre National Park, in the parcels formally called Forêt d'Ambre Special Reserve, should search for this species as well, as the climate and forest is more similar.

Our study detected a similar situation of sympatric occurrence of various *Domerguella* in the Northern Central East of Madagascar. Here, the area of Andasibe and Moramanga represents a major center of species richness in Madagascar (Brown *et al.* 2016), and served for the formalization of the mid-domain effect (Colwell & Lees 2000) where due to stochastic patterns of range overlap, highest diversity of species occurs in the center of a geographical area. The *Domerguella* species in this region do not all appear to directly co-occur at the same site, although some do; in most cases however there seems to be a certain parapatry in their distribution, and some lineages seem to

be specialized to elevational bands: e.g., *L. miops* and *L. fritzi,* which are only known from rather low elevations. Yet, the linear distance between these populations is quite small to minimal (e.g., about 35 km between Sahafina and Ankanin'ny Nofy, linking *L. fritzi* to *L. miops*; or syntopic occurrence of *L.* sp. 19 and *L. guibei* at Andasibe), with ample opportunity for introgression and admixture across contact zones—which however is not observed. Importantly, all *Domerguella* species from this part of Madagascar—*L. guibei, L. miops, L. fritzi*, *L.* sp. 19—belong to subclade A5 of *Domerguella* and therefore are close relatives to each other. The lack of admixture among them thus provides still greater support for species status among these rather closely related lineages of *Domerguella*, and thereby provides credibility to our hypothesis of an overall severely underestimated species inventory in this group of geckos.

Additional undescribed diversity in *Domerguella*

Besides the previously known species and the new species named herein, several additional mitochondrial lineages are known in *Domerguella*. Two of these belong to subclade A5 and are distributed in the Northern Central East of Madagascar (*L.* sp. 19, *L.* sp. 20), where three other species of the subclade also occur (*L. guibei, L. miops, L. fritzi*). In the general Andasibe/Moramanga area, it is possible that three species of *Domerguella* occur in sympatry (*L. guibei, L. miops,* and *L.* sp. 19). This also highlights that our assignment of lineages to the historical nomina from this area is preliminary; the identity of *L. guibei* and *L. miops* require further in-depth study, for instance by attempting to sequence DNA from their holotypes or by identifying additional, possibly osteological diagnostic features. The same is true for the two junior synonyms of *L. miops* (*septemtuberculatus, spinulifer*), which might well apply to one of the two enigmatic lineages in A5. The high degree of genetic variation in geckos of this subclade is also put in evidence by the somewhat shallower mitochondrial lineages, where in Andasibe, two separate lineages of *L. guibei* co-occur (uncorrected pairwise divergence 7–8%).

The third enigmatic lineage, *L.* sp. 24 from Montagne d'Ambre, is also of high interest to verify we have herein correctly redefined the species *L. petteri,* and to understand the diversity of geckos on this isolated northern massif. If *L.* sp. 24 indeed represents a lineage differentiated at species level, then Montagne d'Ambre would harbor four distinct species of *Domerguella* (*L. madagascariensis, L. petteri, L. tantsaha* and *L.* sp. 24) in sympatry, providing an interesting system to study niche partitioning in these geckos. Almost in all cases, we have been able to provide morphological characters (scale counts, morphometric variables and ratios, or coloration) to diagnose the new species named herein from all other species of *Domerguella*. However, it needs to be emphasized that our comparisons are based on a small amount of material, and with more individuals included it is almost certain that some of the values will overlap among species. One of the meristic characters (longitudinal count of dorsal scales) is furthermore difficult to replicate due to the lack of an objective and fully unambiguous posterior end point of the count. Still, we are convinced that the vast majority of differences identified will hold also with more material examined, at least as a statistically significant difference with overlap of extreme values in outlier specimens.

Natural history and conservation

Domerguella species have cryptic ecology, and as a result, we know little about their natural history, other than the obvious facts that they are all diurnal and arboreal geckos, seemingly restricted to humid rainforest, with a few species occurring in dry deciduous forest as well. This is a distinct difference from the species of the subgenus *Lygodactylus* in Madagascar, most of which occur in drier habitats, including the arid and subarid South and South West of Madagascar. Among *Domerguella* species, *L. hodikazo* stands out, as it is a member of an otherwise rainforest-restricted clade found in the dry Tsingy de Bemaraha. This biogeographic pattern is reminiscent of the cophyline microhylid frog *Plethodontohyla fonetana*, which is also a Bemaraha-endemic most closely related to species from the eastern rainforests and highlands (Glaw *et al.* 2007). These links between Bemaraha and more humid areas of Madagascar hint at a past in which forest corridors or other biogeographic links existed to facilitate the exchange of species over hundreds of kilometres of habitat that is, today, no longer amenable to that dispersal. It is also worth mentioning that the area connecting the West of Madagascar with the central highlands remains one of the the less surveyed areas of the country, and its exploration will improve our understanding of species distribution, and on island biogeography.

Lygodactylus hodikazo is one of the three *Domerguella* species most likely endemic to a limestone karst, joining *L. expectatus* and *L. rarus* from Ankarana in northern Madagascar. The role of karst in generating microendemic species, especially gecko species, is well established (Grismer *et al*. 2020). Karst-endemic species can be found in

Malagasy geckos of the genera *Blaesodactylus*, *Geckolepis*, *Lygodactylus*, *Paroedura*, *Phelsuma*, and *Uroplatus* (Glaw *et al.* 2010, 2014, 2018; Ineich *et al.* 2016; Jono *et al.* 2015; Ratsoavina *et al.* 2019; Scherz *et al.* 2017). In a few cases, colonisation of karst environments has generated distinct morphological adaptation, as for instance in *Lygodactylus rarus* and *Paroedura spelaea*. But even in those cases where strong morphological differences are lacking, genetic differentiation from non-karst species is generally very pronounced. It will be interesting in future to understand how gene flow is affected by entrance into karstic environments, and how it affects the ecologies of colonising species.

The natural diet of *Domerguella* is almost wholly unknown, but there are a few scattered records of different species (probably including the here described *Lygodactylus hapei* and *L. fritzi*) feeding on honeydew produced by planthoppers (Fölling *et al.* 2001). Predators are also largely unknown; a single verified predation record by a pseudoxyrhophiid snake exists (Hutter *et al.* 2018). Collection of such basic information is a research priority. However, given the taxonomic complexity that we have revealed in this species complex, it will also be key to tie any observations to the correct species, best achieved by taking small tissue samples (e.g. tail tips) when possible.

This revision has significant implications for the conservation status of *Domerguella* species. The five currently assessed species will not require substantial modification (only *L. guibei* is likely to be moved from Near Threatened to Least Concern due to new records from Angozongahy) (Table 4). However, almost all of the newly described species, as well as the elevated species *L. petteri*, are threatened with extinction due to their rather small extents of occurrence, few known sites of occurrence, and ongoing declines in habitat extent due to deforestation and especially fire. In particular we are concerned about *L. tantsaha* and *L. fritzi*, both of which occur at relatively low elevation in areas that are prone to fire. *Lygodactylus fritzi* is most likely tied to primary littoral forests as it was not found outside the forest in secondary vegetation during fieldwork. Coastal forests on Madagascar's east coast are particularly threatened and only a few small fragments remain, subject to high anthropogenic pressure. Additionally, the two Near Threatened species, *L. rarus* and *L. expectatus*, along with other endemics of Ankarana National Park, should be carefully observed in the coming decades, in case fire, deforestation, and mining activity increase, which would put them quickly at risk.

Continued sample and voucher collection to discover morphologically cryptic lineages

With the notable exception of Betampona Strict Nature Reserve, where *L. miops* are among the most frequently encountered geckos of the forest, finding and capturing individuals of *Domerguella* species is not easy, and obtaining larger series of specimens from one site can be time consuming. This is reflected in the small numbers of individuals available from many sites in the present study. On the contrary, according to our observations, several species of the nominal subgenus *Lygodactylus* from western Madagascar can occur in high densities, and have in the past often been collected in large quantities—e.g., *L. verticillatus,* of which over 1,400 specimens were collected by C.A. Domergue between 1965–1982 from a single site (Pasteur & Lumaret 1976; Vences *et al.* 2004). Also, according to our own observations, many *Lygodactylus* occurring in montane steppe habitat in Madagascar can easily be collected, typically under rocks. We speculate that this difference may not mainly be caused by a greater rarity of *Domerguella* compared to other *Lygodactylus*, but by a more secretive behavior in their more complex rainforest habitat, which results in a lower detectability.

Our finding of unexpected diversity of *Domerguella* suggests that also in other groups of organisms in Madagascar, species diversity might be underestimated even in well-surveyed areas. The *Domerguella* example shows that these additional lineages may often be cryptic in external morphology and co-occur at lower densities with more common relatives. In such cases, regular survey strategies will often miss these additional lineages, especially because the collection of large series of voucher specimens is often not allowed for ethical reasons. In Madagascar, for instance, the current policy is to allow, if scientifically warranted, the collection of two voucher specimens per candidate species and site. We therefore recommend a double strategy for a more efficient inventory work: (1) For surveys in remote and inaccessible areas which often entail substantial logistic efforts and financial costs and cannot be easily repeated, authorities should consider to allow an increased number of voucher specimens per putative species—obviously only in taxa of high reproductive potential and short lifespan such as most amphibians and reptiles, where population densities are high and thus not impacted by a single-event collection activity. (2) Surveys in more easily accessible areas should instead follow a two-step strategy. At a first visit, we recommend taking samples for molecular analysis from as many individuals of all target taxa as possible, accompanied by photographic documentation of each individual. If DNA barcoding would then lead to suspect the presence of scientifically unknown line-

ages at the site, a second, more targeted fieldwork could be carried out to seek out this lineage specifically, informed by external characteristics visible from the photos of the initially sequenced individuals.

TABLE 4. Former and proposed conservation statuses for the IUCN Red List for all Lygodactylus species of the subgenus Domerguella. EOO = Extent of Occurrence

Species	Current IUCN Status	Current Criteria	Proposed new IUCN Status	Proposed Criteria	Reason for proposed change
L. madagascariensis	VU	B1ab(iii)	VU	B1ab(iii)	New definition increases range size from 16,500 km^2 to ~18,000 km^2, six locations
L. miops	LC	NA	LC	NA	No change
L. guibei	NT	NA	LC	NA	New records increase EOO from 6097 km^2 to ~27,000 km^2
L. rarus	NT	NA	NT	NA	No change
L. expectatus	NT	NA	NT	NA	No change
L. petteri	-	-	EN	B1ab(iii)	EOO ~300 km^2, one threat-defined location, ongoing decline in extent and quality of habitat
L. tantsaha	-	-	CR	B1ab(iii)	EOO <100 km^2, one threat-defined location, intense ongoing decline in extent and quality of habitat
L. salvi	-	-	EN	B1ab(iii)	EOO likely <1000 km^2, two threat-defined locations, ongoing decline in extent and quality of habitat
L. roellae	-	-	EN	B1ab(iii)	EOO likely <1000 km^2, two threat-defined locations, ongoing decline in extent and quality of habitat
L. hapei	-	-	CR	B1ab(iii)	Known from a single site (EOO <100 km^2) with ongoing deforestation
L. winki	-	-	EN	B1ab(iii)	EOO likely <1000 km^2, two threat-defined locations, ongoing decline in extent and quality of habitat
L. ulli	-	-	EN	B1ab(iii)	EOO likely <1000 km^2, two threat-defined locations, ongoing decline in extent and quality of habitat
L. fritzi	-	-	CR	B1ab(iii)	EOO <100 km^2, two threat-defined locations, intense ongoing decline in extent and quality of habitat
L. hodikazo	-	-	EN	B1ab(iii)	EOO likely <1000 km^2, two threat-defined locations, ongoing decline in extent and quality of habitat

Acknowledgments

This work would not have been possible without the help and assistance of numerous colleagues, guides, field assistants and students during field expeditions over the past two decades. We are particularly grateful to F. Andreone, L. Ball, J. Borrell, P. Bora, R. Dolch, H. Enting, Georges, D. J. Harris, J. Köhler, F. Mattioli, J. Nöel, D. H. Nomenjanahary, M. Pabijan, J. Patton, M. Puente, J. Rabearivony, E. Rajeriarison, T. Rajoafiarison, M. Randriamiandrisoa, F. Randrianasolo, R.D. Randrianiaina, S. Rasamison, A. Razafimanantsoa, E. Razafimandimby, J. H. Razafindraibe, G. M. Rosa, D. Salvi, E. Scanarini, J. Solo, T. Starnes, and D.R. Vieites for their help in the field; to M. Kondermann

and G. Keunecke who contributed assistance in the laboratory; and to A. V. Mohan and J. W. Streicher who contributed information that was crucial in examining the type of *L. miops.* G. Garcia provided photos of *L. expectatus.* Special thanks go to A.M. Bauer for his continued support and enthusiasm for our studies on dwarf geckos. Fieldwork was carried out in the framework of collaboration accords of the authors' institutions with the Parc Botanique et Zoologique de Tsimbazaza, the Université d'Antananarivo, and the Ministry of the Environment, Water and Forests of the Republic of Madagascar. Thanks are due to the Malagasy authorities, in particular to the Ministry of the Environment, Water and Forests (now Ministère de l'Environnement et du Développement Durable) and Madagascar National Parks, for research, collection and export permits. Fieldwork at Montagne d'Ambre was funded by a Deutsche Forschungsgemeinschaft grant (VE 247/13-1) to MV and MDS. Other field work was supported, among others, by the Volkswagen Foundation, Saint Louis Zoo's Field Research for Conservation program (FRC# 16-09; FRC# 12-12) of the Wildcare Institute, European Association of Zoos and Aquaria (EAZA), Museo Regionale di Scienze Naturali, Gondwana Conservation and Research, BIOPAT, and the Mohamed Bin Zayed Foundation. Portuguese National Funds through FCT (Fundação para a Ciência e a Tecnologia) support the 2020.00823.CEECIND/CP1601/CT0003 contract for AC. We than M.P. Heinicke, M. P. Marques, and one anonymous reviewer for their helpful comments on a draft of this manuscript.

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