

SPIXIANA	49	1	101–114	München, Oktober 2026	ISSN 0341-8391
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Molecular and morphological variation in the *Lycodryas granuliceps* complex, with description of a new snake species from southern Madagascar

(Serpentes: Pseudoxyrhophiidae)

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Glaw, F., Kucharzewski, C., Nagy, Z. T., Hyde Roberts, S., Miralles, A., Raselimanana, A. P. & Vences, M. 2026. Molecular and morphological variation in the *Lycodryas granuliceps* complex, with description of a new snake species from southern Madagascar (Serpentes: Pseudoxyrhophiidae). Spixiana 49 (1): 101-114.

We revise the taxonomy of the snakes in the *Lycodryas granuliceps* complex within the Malagasy–Comoran snake genus *Lycodryas*, using an integrative approach based on morphology, coloration, and molecular data, for which we combine DNA sequences from previous studies and sequences of newly obtained tissue samples. We describe *Lycodryas juergmeieri* sp. nov., ranging from Andohahela National Park in southeastern Madagascar to Kirindy Mitea National Park in the West of the island. The new species is morphologically similar and most closely related to *L. granuliceps* from northern Madagascar and *L. pseudogranuliceps* from the Northwest and central West, but differs from these species by generally fewer, broader and more regular dark crossbands on body and tail, fewer ventral scales, and possibly a smaller maximum body size.

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Introduction

Madagascar harbours a fascinating assemblage of snake species, mainly dominated by a diverse and largely endemic radiation of colubroid snakes (known as the family Pseudoxyrhophiidae with 79 species in Madagascar; Uetz et al. 2026), referred to as Malagasy gemsnakes by Burbrink et al. (2019). The name of this snake family was recently changed to Pseudoxyrhopidae by Wallach (2026). However, this change may not be in accordance with the International Code of Zoological Nomenclature and requires review. Therefore, we continue to use the name Pseudoxyrhophiidae throughout the manuscript. Molecular phylogenies (e.g., Nagy et al. 2003, Crottini et al. 2012, Burbrink et al. 2019, Zaher et al. 2019) and phylogenomic studies (Ruane et al. 2015, Burbrink et al. 2019, DeBaun et al. 2023) have placed these snakes as a distinct, primarily Malagasy clade whose diversification began in the early Miocene and proceeded at relatively steady rates, with little evidence for abrupt slowdowns despite substantial ecological opportunity (e.g., Nagy et al. 2003, Crottini et al. 2012, Burbrink et al. 2019, Zaher et al. 2019). Within this radiation, arboreality evolved repeatedly, and several lineages show striking ecomorphological specializations, underscoring Madagascar's role as a natural laboratory for snake evolution (Cadle et al. 2022). Although many new species have been identified and described from Madagascar since the beginning of this century (Nussbaum & Raxworthy 2000, Mercurio & Andreone 2005, Glaw et al. 2005a, 2005b, 2007, 2009, 2013, 2014, Nagy et al. 2007, Franzen et al. 2009, Vieites et al. 2010, Ruane et al. 2016) the species inventory of the Pseudoxyrhophiidae remains far from complete (Burbrink et al. 2019).

Within the Pseudoxyrhophiidae, the tree-snakes currently placed in the genus *Lycodryas* Günther, 1879 form a distinct group. They are all characterized by a distinctly elongated and slender body, with a proportionally large head clearly distinguished from the body by a thin and elongated neck and prominent eyes with vertically slit pupils. They are widely distributed across Madagascar, exhibit predominantly arboreal and nocturnal activity, and primarily prey upon small vertebrates (lizards, and presumably frogs and avian nestlings). The nomenclatural and taxonomic definitions of *Lycodryas* have shifted over the past century. In the 1990s, Domergue (1995) advocated rehabilitating *Stenophis* Boulenger, 1896 (with *Phisalixella* Domergue, 1995 and *Parastenophis* Domergue, 1995 recognized as new subgenera) to accommodate several Malagasy arboreal forms that until then were often included in *Lycodryas*. Vences et al. (2004) provided new morphological data on these snakes and made previously unpublished

morphological data collected by the late Charles A. Domergue available. A subsequent molecular revision by Nagy et al. (2010) clarified the evolutionary relationships among these taxa: *Stenophis* was considered a junior synonym of *Lycodryas*, and *Phisalixella* and *Parastenophis* were recognized as distinct genera within the Malagasy pseudoxyrhophiid radiation. The genus name *Lycodryas* has since then been applied to a clade of arboreal snakes from Madagascar and the Comoros (e.g., Hawlitschek et al. 2012).

At present, *Lycodryas* comprises nine described species, seven endemic to Madagascar and two to the Comoros (Uetz et al. 2026), although a further taxon from Madagascar, *L. capuroni* (Domergue, 1995) has been informally revalidated by Burbrink et al. (2019). One subclade within the genus, herein referred to as the *L. granuliceps* species complex, contains *L. granuliceps* (Boettger, 1877) from northern Madagascar (type locality: Nosy Be) and *L. pseudogranuliceps* (Domergue, 1995) considered to occur in northwestern, western and southern Madagascar (type locality: Ampijoroa/Ankarafantsika). Basic natural-history data remain sparse for both taxa. Phylogenetic studies by Nagy et al. (2010) and Hawlitschek et al. (2012) and the phylogenomic tree of Burbrink et al. (2019) revealed the existence of an additional genetic lineage within this *Lycodryas* subclade, designated *L. sp. 5* by the latter authors. Additional records of *L. sp. 5* were subsequently made by Cocca et al. (2018) and Hyde Roberts et al. (2025). Here, we present molecular and morphological data on the *L. granuliceps* complex supporting the recognition of the genetic lineage *L. sp. 5* as a distinct species, and provide a formal description of this new taxon.

Materials and methods

Specimens were collected by various teams during field expeditions in Madagascar and the Comoros between 2003 and 2019. Vouchers were anesthetized and subsequently euthanized by injection of approved anesthetics, and tissue samples (usually tongue, tail tip or muscle) were excised before fixation of the vouchers in 95% ethanol or 5% formalin. Vouchers were preserved in 70–80% ethanol and tissue samples in separate vials with 100% ethanol.

Museum acronyms used herein are: MNHN – Muséum National d'Histoire Naturelle, Paris, France; MRSN R – Museo Regionale di Scienze Naturali, Torino, Italy (reptile collection); MTKD – Senckenberg Naturhistorische Sammlungen Dresden, Germany; SMF – Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany; UADBA – Université d'Antananarivo, Mention Zoologie et Biodiversité Animale, Madagascar; ZFMK – Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany; ZSM –

Zoologische Staatssammlung München, Germany. Additional acronyms used are ACP (laboratory sample numbers of A. Crottini), APR (field numbers of A. P. Raselimanana), FGMV, FGZC and ZCMV (field numbers of F. Glaw and M. Vences), MSZC (field numbers of M. D. Scherz), RAX and RAN (field numbers of C. J. Raxworthy and R. A. Nussbaum), and THC (sample numbers of T. R. Fulgence). Geographic regions within Madagascar are named according to Boumans et al. (2007) and Brown et al. (2016).

Measurements and counts were taken as follows: Snout–vent length (from the tip of snout to the posterior margin of the cloacal scute); tail length (from the posterior margin of the cloacal scute to tip of tail); head length (from tip of snout to the angle of the jaws); head width (at the widest point at level of temporals). Scale dimensions were ascertained at their widest point by using a digital calliper under a dissecting microscope. Midbody refers to half of the snout–vent length. Ventrals were counted according to Dowling (1951a) without preventrals. Preventrals include all scales anterior to the ventrals that are broader than long. Subcaudals in *Lycodryas* are usually divided. Hence, counts are given in the left/right order concerning divided subcaudals and as a single number concerning entire scales. The terminal spine is not included within the subcaudal counts. Circumoculars include all scales in contact with the eye including the supraocular. Symmetric characters are given in the left/right order if they differ. Measurements were rounded as follows: Snout–vent length and tail length to the nearest millimeter, all other dimensions to the nearest 0.1 mm. The dorsal scale row reduction formula is given according to Dowling (1951b) but with the modification that the vertebral row is given as “V”. In the cases of even numbers of dorsal scale rows the two vertebral rows are regarded as paravertebrals and abbreviated as “PV”. Places without reduction are marked as “x”. The term “dorsocaudal scale rows” include all scale rows around the tail without counting the subcaudals. The reduction formula for the dorsocaudal scales is used analogously to the dorsal scale row reduction scheme.

Our molecular phylogenetic analysis is based on sequences determined in previous studies, i.e., Nagy et al. (2010), Hawlitschek et al. (2012), Penny et al. (2017), Cocca et al. (2018), Burbrink et al. (2019), and Fulgence et al. (2022), and was complemented by newly generated sequences. The new samples were processed in different laboratories with slight variations of standard methods. Total genomic DNA was extracted either using traditional phenol–chloroform or salt protocols, or with commercial kits (e.g. NucleoSpin Tissue kit, Macherey–Nagel, Düren, Germany). COX1, COB, CMOS and 16S fragments were amplified from these samples using previously published primers and protocols (Nagy et al. 2003) and, after purification, PCR products were resolved on capillary sequencers. All newly determined sequences were submitted to GenBank. Accession numbers are PX519167–PX519174 (COX1), PX549200–PX549204 (COB) and PX549205–PX549212 (CMOS), and PX629895–PX629896 (16S).

We composed a data set of all available sequences of the ingroup (i.e., *L. granuliceps*, *L. pseudogranuliceps*, and the new species), plus one sequence each of all other species of *Lycodryas* and two outgroups (*Phisalixella variabilis* (Boulenger, 1896), and *Ph. tulearensis* (Domergue, 1995)). Sequences were downloaded from GenBank and curated in a spreadsheet along with meta-data (collecting localities, field numbers and catalogue numbers). The data set consisted of four mitochondrial genes (16S rRNA, 16S; Cytochrome b, COB; Cytochrome Oxidase Subunit 1, COX1; and NADH Dehydrogenase Subunit 4, ND4), as well as one nuclear-encoded gene (Oocyte Maturation Factor mos; CMOS). The full table with all sequences, metadata and GenBank accession numbers of all sequences used is available on Zenodo (<https://doi.org/10.5281/zenodo.21009202>).

DNA sequences were aligned using the G-INS-i option in MAFFT (Katoh & Standley 2013) as implemented in the program Concatenator (Vences et al. 2022) for each gene fragment separately. The mitochondrial gene fragments (16S, COB, COX1, ND4) were then concatenated with the same program. The final mitochondrial data set consisted of 2980 bp, with 528 bp for 16S (22 sequences), 1113 bp for COB (17 sequences), 671 bp for COX1 (35 sequences), and 668 bp for ND4 (9 sequences).

We reconstructed a Maximum Likelihood tree of the concatenated alignment using IQ-Tree v.2.4.0 (Nguyen et al. 2015), determining substitution models and data partitions using ModelFinder (Kalyaanamoorthy et al. 2017) and assessing bootstrap support with 500 full non-parametric bootstrap replicates. We used a partitioning scheme by gene (not by codon) to avoid overparametrization given the relatively short length of the fragments. Uncorrected pairwise genetic distances were calculated for the 16S and COX1 sequences using MEGA7 (Kumar et al. 2016). For this, we used alignments of both genes trimmed to roughly equal length of all sequences for better comparability, by trimming sequences to similar lengths and removing excessively short sequences (16S: 519 bp for 7 sequences; COX1: 593 bp for 23 sequences). All alignments, distance tables, and treefiles are available on Zenodo (<https://doi.org/10.5281/zenodo.21009202>).

The alignment of the nuclear-encoded CMOS fragment was analysed independently to understand presence or absence of concordance with the signal from the mitochondrial markers. We used a genealogy visualization approach to graphically represent the relationship among alleles (haplotypes). Alignments were trimmed by removing regions of poor quality and sequences with missing data. Alleles were inferred using the PHASE algorithm (Stephens et al. 2001) implemented in the software Hapsolutely (part of iTaxoTools) (Vences et al. 2021, 2024b), and haplotype genealogies following the Fitch tree algorithm (Salzburger et al. 2011, Matschiner 2016) were inferred using the same program.

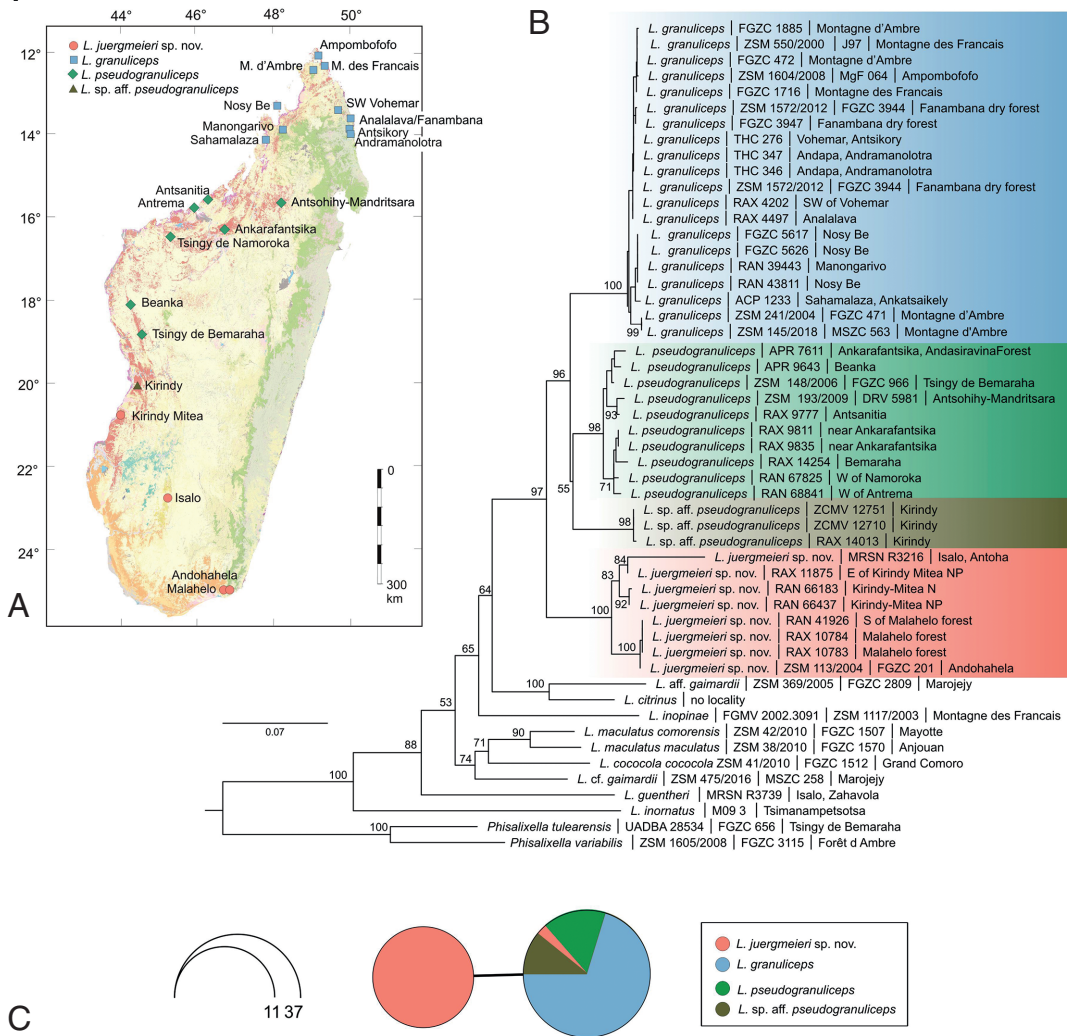


Fig. 1. **A.** Distribution records of the *Lycodryas granuliceps* complex, showing only localities confirmed by genetic data. **B.** Maximum likelihood tree based on a concatenated dataset of DNA sequences of fragments of the mitochondrial genes 16S, COB, COX1 and ND4 (2980 bp). Numbers at nodes are support values in percent from a bootstrap analysis (500 replicates; not shown if <50 % and on shallow nodes). **C.** Haplotype network from a 405 bp alignment of the nuclear-encoded CMOS gene (25 samples, each represented twice after phasing) of the *L. granuliceps* complex.

Results

Molecular phylogeny

The concatenated maximum likelihood tree inferred from 2980 bp mitochondrial DNA sequences from four concatenated gene fragments (Fig. 1) confirms previous analyses (Nagy et al. 2010, Burbrink et al. 2019) in strongly supporting a monophyletic

group (bootstrap support BS=97 %) containing four main lineages, each in turn strongly supported as monophyletic: *Lycodryas granuliceps* (BS=100 %), *L. pseudogranuliceps* (BS=98 %), the focal lineage described herein as new species (BS=100 %), plus three additional samples here considered as *L. sp. aff. pseudogranuliceps* (BS=98 %). Within this clade, the focal lineage was sister to the other three lineages which formed a subclade supported by BS=96 %.

Lycodryas sp. aff. *pseudogranuliceps* (represented only by COX1 sequences) was sister to *L. pseudogranuliceps*, but only with negligible support (BS=55%).

The geographic distributions of the four lineages are allopatric (Fig. 1A): *Lycodryas granuliceps* was found in several localities in northern Madagascar, the southernmost locality being Sahamalaza. *Lycodryas pseudogranuliceps* occupied an area in the Northwest and West of Madagascar, from Ankarafantsika to the Tsingy de Bemaraha. The focal lineage described herein as a new species occurred in the South and Southeast, at various sites from Kirindy-Mitea to Andohahela. *Lycodryas* sp. aff. *pseudogranuliceps* was only found at one site, Kirindy (CNFEREF), located in between the ranges of *L. pseudogranuliceps* and the new species.

Genetic distances between the four lineages in the *L. granuliceps* complex were relatively low. Genetic distances in 16S (COX1 in parentheses) were as follows: 1.6–1.9% (5.7–7.1%) between *L. granuliceps* and *L. pseudogranuliceps*, 1.6–1.7% (7.9–9.4%) between the focal lineage and *L. granuliceps*, and 1.6–1.7% (6.9–7.8%) between the focal lineage and *L. pseudogranuliceps*. The samples of *L. sp. aff. pseudogranuliceps* differed in COX1 by 6.8–7.3% from *L. granuliceps*, by 5.1–6.1% from *L. pseudogranuliceps*, and by 7.3–7.8% from the focal lineage.

The haplotype network of the CMOS gene fragment (Fig. 1C) revealed only two alleles (haplotypes) separated by a single mutational step. One allele was shared by *L. granuliceps*, *L. pseudogranuliceps*, *L. sp. aff. pseudogranuliceps*, and one sequence of the focal lineage; the second allele was exclusive to all other samples of the focal lineage.

Taxonomy

The molecular data confirm the existence of multiple genetic lineages within the *Lycodryas granuliceps* complex. The focal lineage from southern Madagascar (*Lycodryas* sp. 5 sensu Burbrink et al. 2019) is supported as an evolutionarily independent entity by several lines of evidence. Firstly, it is inferred to be sister to a clade containing *L. granuliceps* and *L. pseudogranuliceps*, both by the mitochondrial tree herein (Fig. 1), and by the phylogenomic tree of Burbrink et al. (2019); thus, if the gene trees correctly

Fig. 2. Representative individuals of *Lycodryas granuliceps* and *L. pseudogranuliceps*. **A.** *L. granuliceps* from Fanambana forest (ZSM 1572/2012); **B.** *L. granuliceps* from Montagne des Français (ZSM 550/2000); **C.** *L. granuliceps* from Nosy Be (specimen not assignable to a voucher specimen); **D.** *L. pseudogranuliceps* from Tsingy de Bemaraha (ZSM 148/2006).



represent the species tree, the focal lineage cannot be readily assigned to either of these nominal species without assuming complex evolutionary patterns of ancestral admixture. Secondly, the focal lineage is

concordantly differentiated from *L. granuliceps* and *L. pseudogranuliceps* (Fig. 2) by a substantial mitochondrial divergence, comparable to that between several other closely related Malagasy snake species,

Table 1. Measurements (in mm) and meristic data of *Lycodryas* specimens examined. Abbreviations used: HT, holotype; PT, paratype; SVL, snout-vent length; TaL, tail length; V, number of ventral scales; SC, number of subcaudal scales; CB, number of crossbands on body and tail. Values in parentheses refer to incomplete data, mostly due to mutilated tails. Asterisks mark individuals included in the molecular analysis; other specimens were assigned to lineages based on their distribution and morphology.

Catalogue number	Locality	SVL	TaL	V	SC	CB
<i>Lycodryas pseudogranuliceps</i>						
MNHN-RA-1978.42 (HT)	Ampijoroa	564	146	234	117	99
MNHN-RA-1961.647	Ampijoroa	543	150	237	103	96
MNHN-RA-1977.1061	Ampijoroa	345	118	231	114	91
MNHN-RA-1929.178	Maroamalona	475	153	225	108	82
ZSM 148/2006*	Tsingy de Bemaraha	628	170	237	102	101
ZSM 193/2009*	near Befandriana	566	170	235	108	87
ZSM 77/2023	Namoroka	388	120	223	110	104
ZSM 78/2023	Namoroka	529	131	243	93	117
<i>Lycodryas</i> aff. <i>pseudogranuliceps</i>						
MNHN-RA-1988.324	Beroboka (near Kirindy?)	523	153	227	101	86
MNHN-RA-1978.2917	Marofandilia	500	136	227	96	84
MNHN-RA-1992.5331	Marofandilia	181	52	232	103	69
MNHN-RA-1992.5330	Marofandilia	170	42	234	75	70
MNHN-RA-1992.5329	Marofandilia	174	49	220	101	67
<i>Lycodryas granuliceps</i>						
SMF 19612 (HT)	Nosy Be	760	223	238	108	99
MNHN-RA-1887.260	Nosy Be	545	174	237	115	103
MNHN-RA-1966.960	Nosy Be	785	(128)	242	?	?
ZFMK 17738	Antsiranana	774	207	231	99	104
ZSM 550/2000*	Montagne des Français	605	180	224	103	113
ZSM 553/2000	Montagne des Français	400	131	224	122	105
MRSN R1974	Nosy Be	400	130	245	120	102
MRSN R1832	Sahamalaza	374	125	245	116	103
MTKD D 37533	Antsiranana	453	150	232	119	98
ZSM 241/2004*	Montagne d'Ambre	545	168	234	119	97
ZSM 1604/2008*	Ampombofofo	520	172	225	115	104
ZSM 1572/2012*	Fanambana forest	538	176	234	107	98
ZSM 103/2015	Nosy Be	560	(24)	249	--	(78)
ZSM 145/2018*	Montagne d'Ambre	552	176	233	118	101
ZSM 97/2019*	Nosy Be	781	220	241	105	102
<i>Lycodryas capuroni</i>						
MNHN-RA-1988.325 (HT)	Ankarana	892	(128)	257	(96)	100
<i>Lycodryas juergmeieri</i> sp. nov.						
ZSM 113/2004 (HT)*	Andohahela	560	(142)	240	(91)	(73)
SMF 57021 (PT)	Tolagnaro	544	(111)	227	(65)	(65)
MNHN-RA-1901.225	Tolagnaro	325	93	221	95	73
MNHN-RA-1901.392	Befaisitra	468	136	229	103	79
MNHN-RA-1906.119	Toliara	438	149	225	115	88
MNHN-RA-1929.177	Fiherenana valley	450	164	226	118	84
MNHN-RA-1899.401	Toliara (vicinity)	365	116	220	97	76



Fig. 3. *Lycodryas juergmeieri* sp. nov. in life (holotype, ZSM 113/2004).

by different haplotypes in CMOS (despite limited haplotype sharing), by phylogenomic divergence (see tree of Burbrink et al. 2019), and subtle morphological differences summarized in the Diagnosis below. We see this evidence as sufficient for considering this lineage as a distinct species and proceed with its formal naming and description below. The status of the lineage from western Madagascar here designated *L. sp. aff. pseudogranuliceps* remains to be clarified in future studies given the currently insufficient morphological and nuclear-encoded genetic data.

Lycodryas juergmeieri sp. nov.

Remark. A photo of the holotype of this species (Fig. 3) was erroneously attributed to *Stenophis carleti* by Glaw & Vences (2007: 415). The species was tentatively named “*Stenophis* sp. F201, Andohahela” and “*Stenophis* sp. from Andohahela” by Nagy et al. (2010), “*L. sp.*” by Hawlitschek et al. (2012), *Lycodryas* sp. aff. *pseudogranuliceps* Ca01 “Andohahela” (MRSN R3216) by Cocca et al. (2018), *Lycodryas* sp. 5 by Burbrink et al. (2019), *Lycodryas* sp. G by DeBaun et al. (2023) and *Lycodryas* sp. aff. *pseudogranuliceps* “Andohahela” by Hyde Roberts et al. (2025).

Holotype: ZSM 113/2004 (field number FGZC 201, Figs 3–4), adult male, collected at “Camp 1” (24.7586°S, 46.8542°E; 247 m a.s.l.) between Isaka-Ivondro and Eminiminy, Andohahela National Park, southeastern Madagascar, by F. Glaw, M. Puente, M. Thomas & R. D. Randrianiaina on 29–31 January 2004.

Paratype: SMF 57021, adult female, collected on 5 March 1953 at Fort Dauphin, Madagascar by K. L. Koch.

Additional material examined: Further specimens and samples here assigned to the new species are listed in Table 1 and included in the tree in Fig. 1 but are not included in the paratype series due to incomplete data.

Diagnosis. *Lycodryas juergmeieri* sp. nov. is assigned to the genus *Lycodryas* based on molecular phylogenetic relationships (Fig. 1) and morphological similarity to *L. granuliceps* and *L. pseudogranuliceps*. It differs from other genera of Malagasy nocturnal tree snakes with vertical pupils as follows: from all species of *Phisalixella* (*P. arctifasciata*, *P. variabilis*, and *P. tulearensis*) by a lower number of scales around midbody (17 versus usually 21, exceptionally 19–25), divided subcaudals (versus undivided), and coloration; from *Parastenophis betsileanus* by a lower number of scales around midbody (17 versus 23), presence of one loreal scale (versus absence), different eye coloration (light versus black iris), different body

coloration (beige with 51–53 distinct dark brown crossbands versus dark brown to beige with 41–52 white narrow crossbands), and much smaller size (total length up to 702 mm versus 1290 mm).

Within the genus *Lycodryas*, the new species differs as follows: From the Comoran species and subspecies, *L. maculatus maculatus* (Günther, 1858), *L. maculatus comorensis* (Peters, 1874), *L. cococola cococola* and *L. cococola innocens* Hawlitschek, Nagy & Glaw, 2012 by a lower number of scales around midbody (17 versus usually 19), and very different dorsal coloration (dorsally beige with 51–53 distinct, dark brown crossbands on body and 14–20 crossbands on tail versus dorsal coloration uniformly beige to brown in females or with usually poorly distinct dorsal pattern in males, see Hawlitschek et al. 2012); from *L. capuroni* (considered as valid species without formal revalidation by Burbrink et al. 2019: fig. 2) by lower number of ventrals (220–240 vs. 257), smaller body size (SVL up to 560 mm vs. 892 mm), and lower number of dark crossbands (up to 88 vs. 100); from *L. guentheri* (Boulenger, 1896) by a distinctly higher number of ventrals (220–240 versus 185–209) and coloration; from *L. gaimardii* (Schlegel, 1837) by lower number of ventrals (220–240 vs. 266–284) and smaller body size (SVL up to 560 mm vs. 675 mm), *L. citrinus* (Domergue, 1995) (bright yellow body with 50–58 distinct black crossbands), *L. inopiniae* (Domergue, 1995) (usually with moderately distinct spot-like crossbands on body and tail), and *L. inornatus* (Boulenger, 1896) (uniformly light without dark crossbands) by very different coloration.

Lycodryas juergmeieri sp. nov. differs from *L. granuliceps* by a lower number of dark crossbands (> 65–88 vs. 97–113) which in many specimens are broader and more regularly shaped (vs. more irregular), by a lower number of ventrals in most individuals (220–240 vs. 224–249; Mann-Whitney U test, $P=0.037$), and possibly a slightly smaller body size (up to 560 mm vs. up to 785 mm); it differs from *L. pseudogranuliceps* (not considering specimens here considered as *L. sp. aff. pseudogranuliceps*) by a lower number of dark crossbands in most individuals (> 65–88 vs. 82–117; Mann-Whitney U test, $P=0.005$) which in many specimens are broader and more regularly shaped (vs. more irregular).

Description of the holotype

Adult male in good state of preservation. Sex determination by partly everted hemipenes. Snout–vent length 560 mm, tail length 142 + ? mm (incomplete; 20.2 % of total length; 25.4 % of snout–vent length). Head length 17.3 mm (tip of snout to the angle of the jaws), largest head width 10.6 mm (at temporal region). Distance between tip of snout and posterior

edge of parietals 14.1 mm. Body laterally compressed and head very distinct from neck. Pupil vertically elliptic, iris dark grey in preservative. Eye large, horizontal diameter 3.4 mm, slightly smaller than the distance between anterior margin of eye and posterior edge of nostril (3.5 mm) but smaller than distance between anterior margin of eye and tip of snout (5.1 mm). Distance between the eyes at mideye level 6.3 mm. Distance between nostrils 3.3 mm.

Supralabials 8/9, 4th and 5th in contact with the eye. 7th supralabial on right side divided. Infralabials 10, 1st pair in contact behind mental and the first 5 infralabials touching the anterior inframaxillaries. Rostral broader than high (3.1 mm vs. 1.5 mm), barely visible from above. Nasal divided below nostril, touching 1st and 2nd supralabial. One loreal present, wider than high (1.7 mm vs. 1.0 mm), touching 2nd and 3rd supralabial. Preocular 1, in contact with frontal. Postoculars 3. Temporals according to formula 2 + 3.

Upper surface of head with typical colubrid scalation consisting of 9 large shields. One pair of internasals (scale length 1.7 mm; suture 1.4 mm), one pair of prefrontals (scale length 2.8 mm; suture 2.5 mm). Frontal longer than broad (5.0 mm vs. 3.8 mm), longer and broader than supraoculars, and longer than distance between its anterior margin and posterior margin of rostral (5.0 mm vs. 4.0 mm). One pair of parietals (scale length 5.9 mm; suture 4.5 mm) bordered by 9 scales (without supraoculars, postoculars, and frontal). Two pairs of inframaxillaries, the anterior ones longer (4.7 mm vs. 3.4 mm) and broader (1.9 mm vs. 1.4 mm), the posterior pair in contact with each other. Six gulars between mental groove and first ventral. Anteriormost gulars enlarged, giving the appearance of a third pair of inframaxillaries. 240 ventrals, no prefrontals. Anal scute divided. Subcaudals at least 91 (large part of tail lost in life), mostly divided (exact formula: $1/1 + 5[\text{undivided}] + 1/1 + 2[\text{undivided}] + 82/82$). Dorsal scales smooth, with two apical pits along the body, in 17–17–15 straight rows (counted at tenth ventral, at midbody, and at tenth ventral before vent, respectively). Dorsal scales gradually increasing in size towards paravertebral and vertebral row, the latter a little larger than the former, both wider than long at midbody.

Dorsal scale row reduction according to formula:

$$19 \frac{3+4(7)}{3+4(6)} 17 \frac{3+4(152)}{4+5(147)} 15(240)$$

Dorsocaudal scales smooth with mostly 2 apical pits along tail. Dorsocaudal scale row reduction scheme as follows:

$$12 \frac{2+3(4)}{2+3(3)} 10 \frac{4+5(10)}{4+5(10)} 8 \frac{3+4(23)}{3+4(24)} 6 \frac{2+3(47)}{2+3(48)} 4(91)$$

Coloration and pattern (in preservative): Dorsal ground colour pale brown. Body with 53, tail with 20 dark brown crossbands and some isolated dark dorsolateral blotches. Width of body crossbands at vertebral row equalling ca. 2.5–3.5 dorsal scales, interspaces ca. 1–1.5 dorsal scales. Bands tapering laterally, touching the outer margins of 1–1.5 ventral plates and mostly running forward or backward obliquely, most likely due to the fusion with alternating dark dorsolateral blotches. Anteriormost dark band on neck reaching posteriormost margin of parietals. Width of tail crossbands at vertebral row equalling 3 dorsolateral scales, interspaces 1.5 dorsolateral scales, bands touching the subcaudals.

Head ground colour same as body. All scales and plates, most prominently parietals and frontal, with distinct dark borders. 4th and 5th supralabial nearly immaculate whitish. Uppermost secondary temporal of both sides completely dark.

Underside of head and body immaculate whitish except contact points of body crossbands with ventrals and a few faint small grey dots. Subcaudals whitish with dark brown crossbands alternating with the dorsocaudal tail bands.

Description of the paratype

Adult female in good state of preservation. Sex determination by incision. Snout–vent length 544 mm, tail length 111+? mm (incomplete; 16.9% of total length; 20.4% of snout–vent length). Head length 18.8 mm (tip of snout to the angle of the jaws), largest head width 12.8 mm (at temporal region). Distance between tip of snout and posterior edge of parietals 15.3 mm. Body laterally depressed and head very distinct from neck. Pupil vertically elliptic, iris in preservative dark grey. Eye large, horizontal diameter 3.3 mm, smaller than the distance between anterior margin of eye and posterior edge of nostril (3.6 mm) and than the distance between anterior margin of eye and tip of snout (5.5 mm). Interorbital distance at mideye level 6.9 mm. Distance between nostrils 3.5 mm.

Supralabials 8, 4th and 5th in contact with the eye. Infralabials 9, 1st pair in contact behind mental and first 4 infralabials touching anterior inframaxillaries. Rostral broader than high (3.5 mm vs. 1.4 mm), barely visible from above. Nasal divided below the nostril, touching 1st and 2nd supralabial. One loreal present, wider than high (2.1 mm vs. 0.9 mm), touching 2nd and 3rd supralabial. Preocular 1 in contact with the frontal. Postoculars 3/2. Temporals according to formula 2+2/2+3.

Upper surface of head with typical colubrid scalation consisting of 9 large shields. One pair of internasals (scale length 2.0 mm; suture 1.7 mm),

one pair of prefrontals (scale length 3.0 mm; suture 2.7 mm). Frontal longer than broad (5.2 mm vs. 3.9 mm), longer and broader than supraoculars, and longer than distance between its anterior margin and posterior margin of rostral (5.2 mm vs. 4.4 mm). One pair of parietals (scale length 6.5 mm; suture 4.8 mm) bordered by 11 scales (without supraoculars, postoculars and frontal). Two pairs of inframaxillaries, the anterior ones longer (4.7 mm vs. 3.5 mm) and broader (2.4 mm vs. 1.5 mm), the posterior pair in contact with each other. Four gulars between mental groove and prefrontal. One prefrontal and 227 ventrals present. Anal scute divided. Subcaudals at least 65/65 (large part of tail lost in life), all divided.

Dorsal scales smooth, with two apical pits along body, in 18–17–15 straight rows (counted at tenth ventral–midbody–tenth ventral before vent). Dorsal scales gradually increasing in size towards paravertebral and vertebral row, the latter a little larger than the former, both wider than long at midbody.

Dorsal scale row reduction according to formula:

$$19 \frac{3+4(8)}{3+4(11)} 17 \frac{3+4(151)}{4+5(154)} 15(227)$$

Dorsocaudal scales smooth with mostly 2 apical pits along tail. Dorsocaudal scale row reduction scheme as follows:

$$12 \frac{2+3(3)}{2+3(3)} 10 \frac{4+5(7)}{4+5(8)} 8 \frac{3+4(16)}{3+4(15)} 6 \frac{2+3(37)}{2+3(38)} 4(65)$$

Colour and pattern: Closely resembling that of the holotype. 51 dark body cross bands and 14 tail crossbands. Pale interspaces covering 1–1.5 dorsal scales, some dark bands up to 4 dorsal scales wide. Venter somewhat greyish caudally.

Etymology. The species is dedicated to Prof. Dr. Jürg Meier, in recognition of his contribution to research and biodiversity conservation via the BIOPAT program. The species epithet is a patronym in the genitive case.

Distribution, habitat and conservation status.

Based on molecular data, *Lycodryas juergmeieri* sp. nov. is known from (i) the type locality, Andohahela National Park, and (ii) Malahelo forest in extreme southeastern Madagascar (Burbrink et al. 2019), (iii) Isalo National Park (Cocca et al. 2018), and (iv) Kirindy Mitea National Park (Burbrink et al. 2019) (Fig. 1). Recently published records from Sainte Luce (Hyde Roberts et al. 2025) also belong to this species based on genetic data (not included in Fig. 1). In addition, we assign various localities in the area encompassed by the genetically confirmed sites, based on historical voucher specimens from the MNHN collection and listed by Vences et al. (2004) to *L. juergmeieri* (Table 1): (v) Befaisitra at the Mandrare river (MNHN-RA-1901.392, collected by Descorse), (vi) Toliara (MNHN-RA-1899.401 and

MNHN-RA-1906.119), and (vii) Fiherenana valley (MNHN-RA-1929.177). An additional record from the Ifotaka North Protected Area (INPA) in the Mandrare river valley northwest of Tolagnaro, identified as *L. pseudogranuliceps* by Theisinger & Ratianarivo (2015), likely refers to this species as well. A record on iNaturalist from the Andohahela region (24.9448°S, 46.6305°E), based on a photograph (<https://www.inaturalist.org/observations/232855359>) and identified as *Lycodyras gaimardii* most likely belongs to *L. juergmeieri* as well, and the same is true for photographs from Andavadoaka (22.07493°S, 43.24264°E, 10 m a.s.l.) taken by Arne Hartig (pers. comm.). A further potential locality in need of confirmation is the lower Onilahy river valley in the South where *L. cf. gaimardii* has been recorded (D'Cruze et al. 2009), the true *L. gaimardii* being restricted to eastern Madagascar.

The habitat of the new species is remarkably variable including deciduous dry forest in the West (Burbrink et al. 2019), spiny forest in the South (Theisinger & Ratianarivo 2015), littoral forests in the Southeast at Sainte Luce (Hyde Roberts et al. 2025), and low-altitude rainforest in the Andohahela reserve (likewise in the Southeast) where the holotype has been found. In the latter habitat *L. juergmeieri* seems to be a relatively rare species as it was apparently not recorded by previous surveys in the Andohahela rainforests (Andreone & Randriamahazo 1997, Nussbaum et al. 1999, Raselimanana 2008). Conversely, this species was encountered relatively frequently at Sainte Luce, often found in the thatched roofs of human dwellings made of leaves of *Ravenala madagascariensis* (Hyde Roberts et al. 2025). These authors classified the species as arboreal and nocturnal as is typical for all *Lycodyras* species, but the holotype was discovered in the evening on the ground in primary low-altitude rainforest, just before a heavy cyclone hit the region. One individual was crawling at 19:45 along a large rock in lowland disturbed rainforest about 15 m from the river side in Andohahela NP (APR pers. obs.). At Isalo, this species was found on a small shrub at night (Cocca et al. 2018).

Due to its wide distribution range in southern Madagascar (Fig. 1), its occurrence in multiple protected areas (at least in Andohahela National Park, Sainte Luce, INPA, Isalo National Park, and Kirindy Mitea National Park) and its adaptability to human settlements, we suggest that *L. juergmeieri* qualifies as Least Concern according to IUCN Red List criteria (IUCN 2012).

Distribution and conservation status of *Lycodyras granuliceps* and *L. pseudogranuliceps*. Compared to previous distribution maps (Glaw & Vences 2007, Raxworthy & Vences 2010) our revised map (Fig. 1),

based on genetically identified specimens shows that *L. granuliceps* has a much larger extent of occurrence in northeastern Madagascar, extending southwards into the Vohemar region. It occurs in numerous protected areas (e.g., Sahamalaza National Park, Lokobe National Park, Manongarivo Special Reserve, Montagne d'Ambre National Park and Montagne des Français), and its enlarged distribution range and its ability to tolerate a variety of habitats, including disturbed environments, confirm the previous IUCN Red List assessment as Least Concern (Raxworthy & Vences 2010).

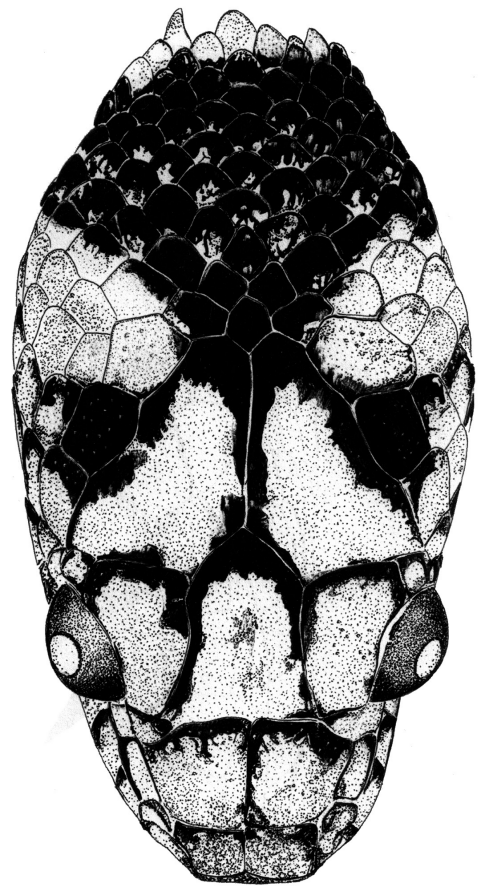
The same classification (Least Concern) also remains appropriate for *L. pseudogranuliceps*. Due to the description of *L. juergmeieri* sp. nov., its distribution range in the South has become smaller (Fig. 1) compared to the previous IUCN Red List assessment (Vences 2011). We furthermore found no support for the unconfirmed presence of *L. pseudogranuliceps* in northern Madagascar (Rakotondravony 2006, see also map in Vences 2011), suggesting that the three species do not occur in sympatry. However, *L. pseudogranuliceps* is still widespread in the Northwest and West and occurs in several protected areas, including Ankarafantsika National Park, Tsingy de Bemaraha National Park, Namoroka National Park, Beanka and Antrema (Fig. 1).

Discussion

By combining all available DNA sequences of the *Lycodyras granuliceps* complex from previous studies with newly obtained sequences (Nagy et al. 2010, Hawlitschek et al. 2012, Penny et al. 2017, Cocca et al. 2018, Burbrink et al. 2019, Fulgence et al. 2022), we have herein updated the knowledge on the phylogeny, taxonomy, and biogeography of these snakes. Samples from what was previously considered to be the southern part of the range of *L. pseudogranuliceps* (e.g., Vences et al. 2004, Glaw & Vences 2007) belong to *L. juergmeieri* sp. nov., and samples from Kirindy and probably other sites in the Menabe area belong to a taxonomically still poorly understood mitochondrial lineage (*L. sp. aff. pseudogranuliceps*). Biogeographically, the *L. granuliceps* complex thus appears to consist of fully or largely allopatric or parapatric lineages, arranged from north to south in the order *L. granuliceps* – *L. pseudogranuliceps* – *L. sp. aff. pseudogranuliceps* – *L. juergmeieri*. DeBaun et al. (2023), based on the data set of Burbrink et al. (2019), tested for reticulate speciation within the Pseudoxyrhophiidae and suggested a hybrid origin of *L. pseudogranuliceps*, originating from the parental species *L. granuliceps* and *L. juergmeieri* (as *L. sp. G*), with a dominant genomic contribution of

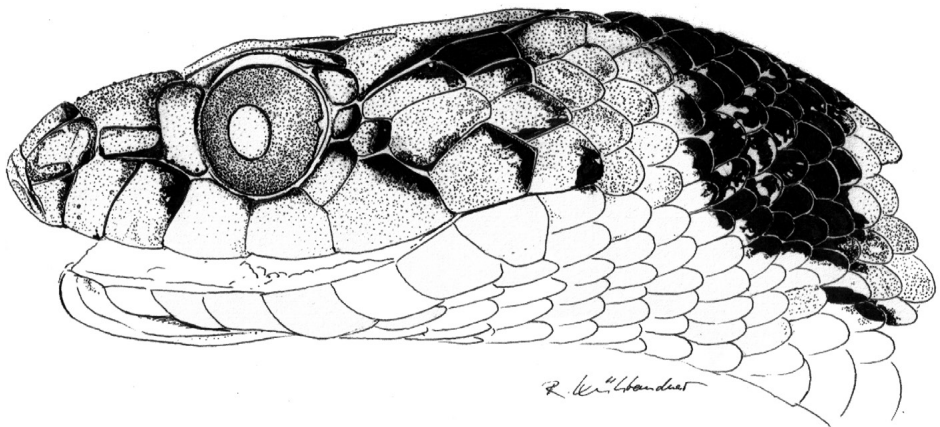
66 % from *L. granuliceps* and 34 % from *L. juergmeieri*. This suggested hybrid origin of *L. pseudogranuliceps* is in line with its geographic distribution between *L. granuliceps* in the north and *L. juergmeieri* in the south. Burbrink et al. (2019) were already aware of the mitochondrial lineage named *L. sp. aff. pseudogranuliceps* in our Fig. 1 (their sample RAX14013), but attributed this sample to *L. juergmeieri* (as *L. sp. 5* in their fig. S1 and suppl. file 6), apparently based on their genomic data. All these data indicate a poorly understood speciation process in this species complex. However, the validity of *L. juergmeieri* as a separate species is supported not only by mitochondrial data (Fig. 1), which in this case could be deemed as insufficient evidence (Wüster 2025), but also by a quasi-absence of haplotype sharing in CMOS, subtle morphological traits and most importantly, its phylogenetic position as sister to the *L. granuliceps*/ *L. pseudogranuliceps* clade in the phylogenomic tree of Burbrink et al. (2019) and the putative hybrid origin of *L. pseudogranuliceps* inferred by DeBaun et al. (2023). Nevertheless, the taxonomic status of all lineages in this complex – and of other allopatrically distributed species of reptiles in Madagascar – requires more extensive testing by rigorous phylogenomic species delimitation methods based on systematic sampling of their geographical contact zones (Vences et al. 2024a).

The phylogenetic tree inferred herein (Fig. 1), along with the phylogenomic tree of Burbrink et al. (2019), provides indications for additional, taxonomically not yet revised lineages of *Lycodryas*. Burbrink et al. (2019) included two deep genetic lineages forming a clade with *L. guentheri* (*L. sp. 1*



A

Ruth K. Kuhbandner



B

R. K. Kuhbandner



Fig. 4 Head drawings of *Lycodryas juergmeieri* sp. nov. (holotype, ZSM 113/2004). **A.** Dorsal view; **B.** lateral view. Scale bars: 5 mm. Drawings by Ruth Kühbandner.

and 2), plus a lineage affiliated to *L. gaimardii* and *L. capuroni* (named *L. sp. 3*) and a further one sister to *L. citrinus* (*L. sp. 4*). Our tree (Fig. 1) includes two samples from Marojejy in the Northeast of Madagascar, one of which clusters with *L. citrinus* and one with the Comoran taxa (which were not included in the tree of Burbrink et al. 2019). Also, the identity of *L. capuroni* from the Ankarana Massif, considered as synonym of *L. granuliceps* by Vences et al. (2004) but treated as valid species by Burbrink et al. (2019: fig. 2), requires further study. Most of these lineages and species occur in northern Madagascar and are characterized by dark crossbands on a more or less brownish body and tail, and in-depth analysis of their morphology based on genotyped individuals will be necessary to satisfactorily revise their taxonomy.

Aside from clarifying the taxonomy of numerous lineages, and as with many other snakes of Madagascar, more data are also needed to understand their basic natural history and life history. Most species of *Lycodryas* are rarely collected and observed, and there are very few data on their reproductive mode, activity, prey, or population density. Domergue (1995) and Mertens (1955) reported ovoviviparity in *L. pseudogranuliceps* and Vences et al. (1998) characterized *L. citrinus* as live-bearing. A non-public YouTube video by Mattias Deuss shows that *L. maculatus comorensis* is giving birth to live young as well. Other *Lycodryas*, including *L. granuliceps*, were categorized as oviparous by Feldman et al. (2015), probably as default. If confirmed, this potentially could indicate differences in reproductive strategies among species of *Lycodryas*, even within the *L. granuliceps* complex, but no detailed observations of oviparity in *Lycodryas* have so far been published. This exemplifies the need for ongoing field exploration and survey work in Madagascar, including the collection of voucher specimens and the thorough documentation of natural and life history from genotyped specimens.

Acknowledgements

We are very grateful to Molly Bletz, Parfait Bora, Neil D'Cruze, Hildegard Enting, Michael Franzen, Kathrin Glaw, Timon Glaw, Oliver Hawlitschek, Angelika Knoll, Jörn Köhler, Steven Megson, P. Mitchell, Marta Puente Molins, David Prötzel, Ny Ando Rahagalala, Theo Rajoafiarison, Andolalao Rakotoarison, Roger-Daniel Randrianiaina, Fanomezana M. Ratsoavina, Delina Razafimanafa, Angeluc Razafimanantsoa, Jary H. Razafindraibe, Mark D. Scherz, Meike Teschke and David R. Vieites for their help in the field, and to Ivan Ineich and Nicolas Vidal (MNHN) and the late Gunther Köhler and Linda Mogk (SMF), for the loan of snakes under their care. Many thanks go to Ruth Kühbandner (ZSM) for her excellent head drawings of the new species and to Arne

Hartig for sharing interesting photographs. Research was carried out in the framework of an established collaboration with the UADBA. We are very grateful to the Madagascar authorities for research and export permits and to Jürg Meier for financial support of this work and his patience. The field work for this research has been supported by the European Association of Zoos and Aquaria (EAZA), the Mohamed bin Zayed Species Conservation Fund and the Volkswagen Foundation.

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Managing editor of this article: Roland R. Melzer