

Species delimitation methods put into taxonomic practice: two new *Madascincus* species formerly allocated to historical species names (Squamata, Scincidae)

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Abstract

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phylogeny

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biogeography

In a previous study, Miralles & Vences (2013) compared seven different methods of species delimitation applied to the genus *Madascincus*. While focusing on methodological aspects their study involved an extensive data set of multilocus DNA sequences and of comparative morphology. On this basis they emphasized the need of revising the taxonomy of *Madascincus*, and revealed the existence of at least two well-supported candidate species. The present paper provides formal descriptions of these two taxa: (1) *M. miafina* sp. n., a species from dry areas of northern Madagascar, morphologically very similar to *M. polleni* (although both species are not retrieved as sister taxa), and (2) *M. pyrurus* sp. n., a montane species occurring >1500 m above sea level, endemic to the central highlands of Madagascar (Ibity and Itremo Massifs). Phylogenetically, *M. pyrurus* is the sister species of *M. igneocaudatus*, a taxon restricted to the dry littoral regions of the south and south-west of Madagascar in lowlands <500 m above sea level. To facilitate future taxonomic work, we furthermore elaborated an identification key for species of *Madascincus*. Finally, some aspects of the biogeographic patterns characterising the different main clades within the genus *Madascincus* are provided and discussed for the first time in the light of a robust phylogenetic framework.

Introduction

The genus *Madascincus* represents a monophyletic group of skinks endemic to Madagascar (Crottini et al. 2009, Miralles and Vences 2013). These lizards likely have diversified during the early Oligocene (Miralles et al. 2015), giving rise to a dozen currently known species. In a recent study dealing with methodological aspects of species delimitation, Miralles and Vences (2013) applied and compared seven methods of delimitation to this genus, combining different approaches: (1) ITAX, the *Integrative Taxonomic approach*, which is based on the integration of as many lines of evidence as available to delimit

species (cf. Dayrat 2005, DeSalle et al. 2005, Padial et al. 2010, Miralles and Vences 2013); (2) MTMC, the *Mitochondrial Tree – Morphological Character approach*, which is based on the combination of evidence from DNA sequences and morphological data, considering as species those morphologically diagnosable units that are revealed by a mtDNA tree (cf. Riedel et al. 2013, Miralles and Vences 2013); (3) WP, the *Wiens and Penkrot protocol*, which is based on the identification of non-recombining molecular phylogenetic units (cf. Wiens and Penkrot 2002); (4) BAT, the *Bayesian Assignment Test*, which is based on the combination of population genetic and genealogical patterns across multiple loci, recognizing species

according to concordance between mtDNA clades and patterns of nuclear population structure (cf. Weisrock et al. 2010); (5) HW, the *Haplweb approach*, which is based on haplotype networks with additional connections between haplotypes found co-occurring in heterozygous specimens (haplowebs) to delineate species boundaries (cf. Doyle 1995, Flot et al. 2010); (6) BSD, the *Bayesian Species Delimitation*, which is based on coalescence theory, and uses bipartitions of specimens in gene trees that are shared across loci to infer species-level lineages (cf. Rannala and Yang 2003, Yang and Rannala 2010); and (7) GMYC, the *Generalized Mixed Yule-coalescent approach* which is based on a statistical model testing for the predicted change in branching rates at the species boundary of a single-locus phylogenetic tree (cf. Pons et al. 2006, Fontaneto et al. 2007, Monaghan et al. 2009). For details on each of the methods and their application to *Madascincus*, see Miralles and Vences (2013).

Miralles and Vences (2013) concluded that the taxonomy of the genus is in need of revision. Despite relevant incongruences between the various species delimitation approaches assessed, all of them agreed in suggesting at least two divergent lineages representing undescribed species: (1) a lineage referred to as *polleni*-N, with specimens morphologically very similar to *M. polleni* but phylogenetically more closely related to two morphologically distinct species, namely *M. arenicola* and *M. stumpffi*; and (2) a lineage referred to as *igneocaudatus*-C inhabiting the highland of central Madagascar, with specimens morphologically and ecologically distinguishable from *M. igneocaudatus* sensu stricto, its sister species endemic to the dry coast of southern and western Madagascar. Following up on the compelling evidence for a species status of these two lineages (Miralles and Vences 2013), the main aim of the present study is to provide their formal taxonomic description. We also took the opportunity of this work to discuss several aspects of biogeography and origins of this genus in a phylogenetic context.

Material and methods

Morphology. The comparative morphology approach mostly relies on the data-set previously published by Miralles and Vences (2013). It involved morphological data composed of a total of 168 preserved specimens used in their molecular analyses, completed by 40 additional specimens having not been sequenced and complementary data previously published by Andreone and Greer (2002), Glaw and Vences (2007) and Miralles et al. (2011a). Specimens examined also included all the type specimens known for this genus, with exception of the types of *M. minutus* (UMMZ 192705) and *M. vulsini* (MCZ R-11869), both being unambiguously members of the *M. melanopleura* clade. All the examined specimens are deposited in the Muséum National d'Histoire Naturelle, Paris (MNHN), Museo Regionale di Scienze Naturali, Torino (MRSN), National Histo-

ry Museum, London (NHM), Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main (SMF), Université d'Antananarivo, Département de Biologie Animale (UADBA), and Zoologische Staatssammlung München (ZSM). In addition, where applicable, we also give for the specimens their respective field numbers, using the abbreviations: FGZC, FG/MV, MV, and MgF referring to Frank Glaw, Miguel Vences and Madagascar Frontiers field numbers (cf. Supplementary file 1). Some specimens deposited at UADBA have not yet been formally catalogued in that collection; we refer to these specimens as UADBA uncatalogued, followed by the respective field number which allows an unambiguous identification of the specimens in this collection. More specifically, the description of the two new species herein proposed involved the record of meristic, mensural and categorical morphological characters routinely used in the taxonomy of Scincidae, such as scale counts, presence or absence of homologous scale fusions, or color patterns (cf. Andreone and Greer 2002, Miralles et al. 2011a, b, c). The ventral scales are counted in a single row from the postmentals to the preanal scales which both are included in the count, while the mental scale is excluded. The paravertebrals are counted in a single row from the first scale posterior to a line connecting the posterior edges of the thighs held normal to the long axis of the body anteriorly to and including the nuchals. Nuchal scales (*sensu* Miralles 2006) are defined as enlarged scales of the nape, occupying transversally the place of two or more rows of dorsal cycloid scale. The frontal scale is considered *hourglass-shaped* when constricted by first supraocular, *bell-shaped* otherwise. Measurements of specimens were recorded to the nearest 0.1 mm using a dial caliper. Ranges are given for each meristic and mensural character, followed by the mean \pm the standard deviation, with sample size in parentheses. For some bilateral characters, the sample size has been noted as the number of sides rather than specimens (indicated after sample size).

Phylogenetic analyses. All molecular analyses of the present paper were directly taken and adapted from the work of Miralles and Vences (2013), i.e., the separate Bayesian analyses of the nuclear DNA (nDNA) data set (segments of the genes BDNF, CMOS, PDC and RAG2) and of the mitochondrial DNA (mtDNA) data set (segments of the genes ND1 and 16S) (Fig. 1) and the haplotype network reconstruction generated by TCS 1.21 (Clement et al. 2000) for the phased haplotypes of the four nuclear gene segments (Fig. 2). Additionally, uncorrected p-distances were estimated with MEGA 6 (Tamura et al. 2013) for the 16S and ND1 mtDNA segments to provide an overview of the genetic divergence among taxa (Table 3). See Miralles and Vences (2013) for detailed descriptions of all the molecular procedures, GenBank accession numbers, phylogenetic analyses and haplotype network reconstruction methods. The respective figures shown herein have been updated for species names and integrative species delimitation conclusions.

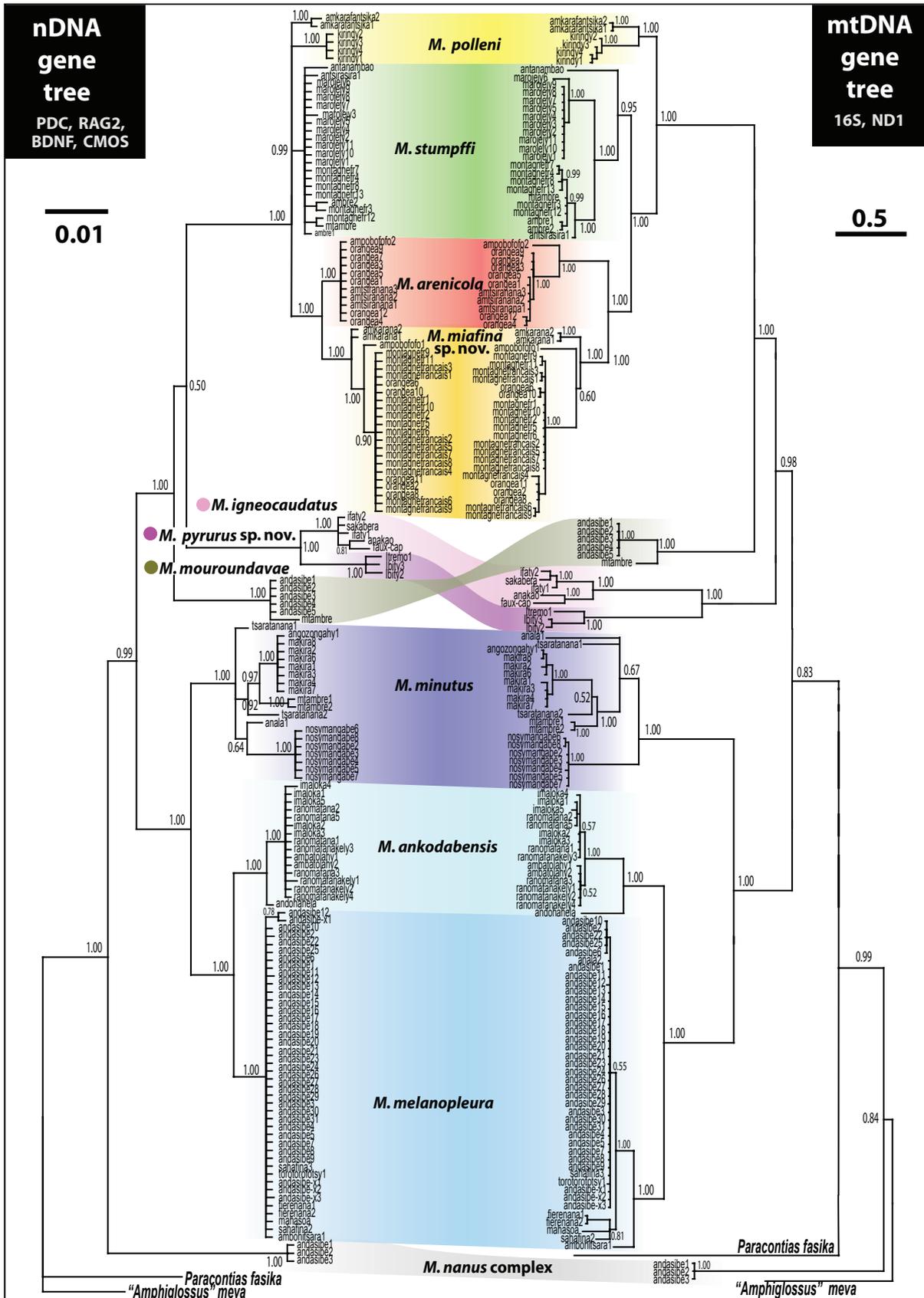


Figure 1. Comparison of phylogenetic trees of the genus *Madascincus* based on nDNA and mtDNA sequences (modified from Miralles and Vences 2013). Nuclear DNA tree inferred from BI analysis of concatenated BDNF, CMOS, PDC and RAG2 sequences compared to the mitochondrial DNA inferred from ND1 and 16S sequences (unpartitioned data set, posterior probabilities indicated for each node, see Miralles and Vences 2013 for details of analysis methods).

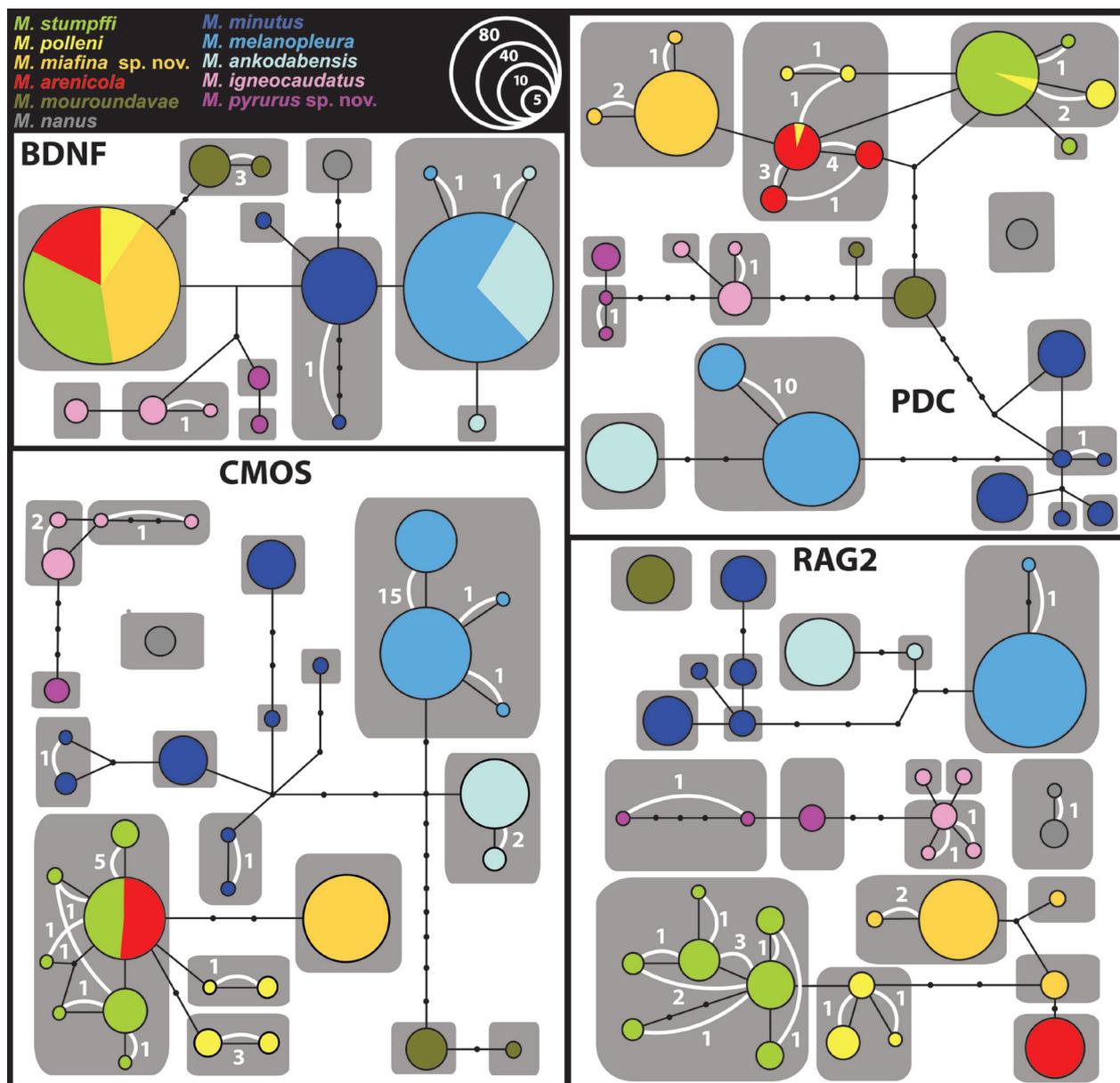


Figure 2. Haplotype network reconstructions for the four nuclear genes (BDNF, PDC, CMOS and RAG2). For each marker, circles represent haplotypes (size proportional to the number of individuals), black lines represent mutational steps and black dots missing haplotypes, white curves represent connections between haplotypes found co-occurring in heterozygous individuals, and white numbers represent the number of individuals in which the respective haplotypes were found co-occurring. Single locus fields of recombination (pools of co-occurring haplotypes) are represented by grey rectangles (redrawn from Miralles and Vences 2013).

Taxonomic background. The definition of the genus *Madascincus* herein follows previous molecular work (Schmitz et al. 2005, Crottini et al. 2009, Miralles et al. 2011c, Miralles and Vences 2013), encompassing all species of an exclusively four-legged clade that is sister to the legless genus *Paracontias*. The term “*Madascincus nanus* complex” designates a putative complex of species encompassing *M. nanus*, *M. macrolepis* and a candidate species previously referred as *Madascincus* sp. “baeus” by Glaw and Vences (2007). *Madascincus macrolepis* and *M. nanus* are very rarely encountered animals for which no topotypic molecular samples have so far become available. The three forms in the complex are almost certain-

ly closely related due to numerous morphological similarities, and we here provisionally follow Miralles and Vences (2013) in merging *M. sp.* “baeus” with *M. nanus*. The candidate species *Madascincus* sp. “vitreus”, known from a single juvenile individual from Kirindy (Glaw and Vences 2007) is here tentatively regarded as a juvenile specimen of *M. igneoicaudatus* sensu stricto, pending molecular data and collection of further specimens for a more reliable assignment. For consistency we hereafter refer to the different species-level units as clades, following Miralles and Vences (2013) who used these provisional names to refer to units forming distinct clades in the mtDNA and nDNA tree. We also avoid the term “lineage”

which in other studies we have regularly used to refer to such species-level evolutionary units. We apply the same clade names as in Miralles and Vences (2013) and then assign Linnean names to them by either formally describing new taxa (two new species) or arguing for their conspecificity with previously described species. Concerning the usage of unscientifically and unethically erected taxon names we follow the recommendations of “censuring taxonomic vandals”, as proposed by Kaiser et al. (2013).

Results

Despite numerous conflicts among the seven methods of species delimitation (ITAX, MTMC, WP, BAT, HW, BSD and GMYC) applied on *Madascincus* by Miralles and Vences (2013), all of them were in agreement on the specific distinctiveness of the two clades named *igneocaudatus-C* and *polleni-N* in that study. Some of these methods suggested a further splitting of these two units: BAT, BSD and GMYC recognized respectively two, two and three species within the *polleni-N* clade, whereas GMYC identified two species within *igneocaudatus-C* clade, corresponding to the population of Ibity and the population of Itremo. However, as argued by Miralles and Vences (2013) these approaches led to obvious oversplitting in several other *Madascincus* species, including objective errors such as assigning haplotypes co-occurring in the same population to different species, despite originating from specimens without differences in morphology or nuclear genes. We therefore do not propose a further subdivision of the *igneocaudatus-C* and *polleni-N* clades and consider each of them as one species in need of formal description.

Considering an integrative taxonomic approach, the distinctiveness of the two clades *igneocaudatus-C* and *polleni-N* is supported by the following independent lines of evidence. All results in the following are from Miralles and Vences (2013), with the exception of the genetic distances which have been newly calculated herein:

- Both clades represent monophyletic units fully supported by both the nDNA and the mtDNA data set (posterior probabilities of 1.00 for each clade and for each data set, cf. Fig. 1).
- The *igneocaudatus-C* clade possesses exclusive alleles for the four nuclear markers analysed and the *polleni-N* clade has exclusive alleles in three markers, only sharing one nuclear allele with *M. arenicola*, *M. stumpffi* and *polleni-S* for the very conserved BDNF segment (Fig. 2), suggesting no recent gene exchanges between these clades and their respective sister clades.
- Both clades are unambiguously morphologically diagnosable from their respective sister clade and from all the other species of *Madascincus* (Figs 3, 4, Tables 1, 2).
- The genetic distance values between these two clades and their respective sister clades are relatively high, with p-distances ranging from 7.3 to 9.0% (16S) and 16.2 to 17.7% (ND1) between *igneocaudatus-C* and *igneocaudatus-S*, and 2.5 to 3.4% (16S)

and 8.1 to 10.2% (ND1) between *polleni-N* and *M. arenicola*. These distances are consistent with inter-specific divergences observed between the other recognized species of *Madascincus* (Table 3), whereas intragroup divergence remains relatively low: 0.0 to 2.2% (16S) and 0.4 to 5.1% (ND1) within *igneocaudatus-C*, and 0.0 to 2.0% (16S) and 0.0 to 6.4% (ND1) within *polleni-N*.

Madascincus miafina sp. n.

<http://zoobank.org/DAC928B3-73CF-4653-B8A3-B7A4E17DFF50>

Figs 3B, 4J, K

Holotype. ZSM 1562/2008 (FGZC 1658), adult male, from near Petit Tsingy, 12°57'25"S, 49°07'06"E, 90 m above sea level, Ankarana Special Reserve, Antsiranana province, north Madagascar, collected on 16 February 2008 by M. Franzen, F. Glaw, J. Köhler and Z. Nagy.

Paratypes (n=23, all from Antsiranana province, northern Madagascar). ZSM 242/2004 (FGZC 474), 245/2004 (FGZC 480), Montagne des Français, 12°19'34"S, 49°20'09" E, 334 m a.s.l., coll. on 23 and 24 February 2004 by F. Glaw, M. Puente and R.D. Randrianiaina; UADBA uncatalogued (FGZC, 1788, 1789), Montagne des Français, coll. by Frontier staff at unknown date; ZSM 1571/2008 (FGZC 1766), 1572/2008 (FGZC 1844), Baie des Sakalava (ca. 5 km SE Ramena), 12°16.371'S, 49°23.338'E, 28 m a.s.l., coll. on 22 and 26 February 2008 by S. Megson; ZSM 1573–1577/2008 (FGZC 1678, 1680, 1687, 1836, 1838), UADBA uncatalogued (FGZC 0481, 1677, 1684, 1762, 1763, 1835), Montagne des Français (pitfall lines 1, 2 & 5, no coordinates available), coll. on 19 and 25 February 2008 by N. D’Cruze and local collectors; ZSM 259/2004, Montagne des Français, coll. on 18–28 February 2004 by F. Glaw, M. Puente, R.D. Randrianiaina and A. Razafimanantsoa; ZSM 1570/2008 (FGZC 1917), Ampombofofo region, 12°05.571'S, 49°19.035'E (trapsite 5), coll. on 23 February 2007 by S. Megson; ZSM 1563/2008 (FGZC 1827), same data as holotype, but collected by a local assistant on 24 February 2008; UADBA uncatalogued (FGZC 1742, 1768, 1840), Orangea, coll. in February 2008 by S. Megson.

Other specimens examined. (n=2, not sequenced). MNHN 1897.31, Diego Suarez; MNHN 1980.1169, Bemanevika, Plateau Bealanana.

Chresonyms.

Scelotes intermedius – Brygoo (1981, *partim*);
Amphiglossus intermedius – Brygoo (1984, *partim*);
Madascincus intermedius – Glaw & Vences (2007, *partim*);
Madascincus polleni “clade 1” – Miralles et al. (2011b);
Madascincus polleni “*polleni-N* clade” – Miralles & Vences (2013);
Madascincus sp. “*polleni*” northern clade – Miralles et al. (2015).

Table 1. Comparison of the most relevant morphological characters, plus additional data on the altitudinal distribution and reproductive mode of *Madascincus* species. Ranges are given for meristic and mensural characters, followed by the mean \pm the standard deviation, with sample size in parentheses. For some bilateral characters, the sample size was noted as the number of sides rather than specimens. Data from Andreone and Greer 2002, Glaw and Vences 2007, Miralles et al. 2011a, Miralles and Vences 2013.

	igneocaudatus clade		melanopleura clade		mouroundavae	nanus complex	polleni clade						
	igneocaudatus	pyrurus (C)	minutus (N)	melanopleura (C)			ankodabensis (S)	arenicola	miafina (N)	polleni (S)	stumpffi		
N lamellae under 4th finger	min-max:	8-11	8-11	5-7	5-8	5-8	8-11	3-5	6-7	7-8	6-9	6-9	
	mean \pm SD: n sides:	9.0 \pm 0.9 (50)	9.1 \pm 0.9 (14)	6.0 \pm 0.8 (13)	7.0 \pm 0.6 (40)	6.3 \pm 1.0 (9)	6.3 \pm 1.0 (9)	9.8 \pm 0.7 (16)	3.9 \pm 0.6 (8)	6.4 \pm 0.5 (11)	7.6 \pm 0.5 (22)	7.5 \pm 0.7 (26)	7.3 \pm 0.8 (27)
N lamellae under 4th toe	min-max:	15-22	15-18	9-13	12-16	12-15	16-20	5-8	16-19	18-23	16-22	15-20	
	mean \pm SD: n sides:	18.1 \pm 1.4 (54)	16.4 \pm 1.3 (13)	11.3 \pm 1.5 (10)	14.1 \pm 1.2 (52)	13.8 \pm 1.1 (12)	13.8 \pm 1.1 (12)	17.5 \pm 1.2 (15)	6.8 \pm 1.3 (9)	17.5 \pm 0.8 (13)	20.6 \pm 1.3 (20)	18.5 \pm 1.5 (22)	17.9 \pm 1.2 (28)
N ventral scale rows	min-max:	68-83	73-78	55-63	56-61	59-63	63-66	52-60	75-80	65-73	74-78	70-88	
	mean \pm SD: n:	76.7 \pm 4.4 (21)	75.7 \pm 1.8 (7)	58.3 \pm 3.0 (7)	58.8 \pm 1.2 (27)	60.2 \pm 1.5 (6)	60.2 \pm 1.5 (6)	64.3 \pm 1.0 (8)	57.6 \pm 3.3 (5)	77.9 \pm 1.6 (7)	68.7 \pm 2.1 (14)	75.8 \pm 1.2 (12)	81.3 \pm 4.0 (16)
N paravertebral scale rows	min-max:	69-80	71-79	57-65	51-62	52-62	60-65	50-57	74-81	65-79	71-81	76-88	
	mean \pm SD: n:	74.7 \pm 3.0 (26)	74.6 \pm 3.7 (7)	59.7 \pm 3.4 (7)	55.9 \pm 2.9 (28)	57.7 \pm 3.1 (7)	57.7 \pm 3.1 (7)	62.6 \pm 2.1 (8)	53.6 \pm 2.5 (5)	79.0 \pm 2.3 (7)	68.7 \pm 3.3 (14)	77.9 \pm 2.6 (13)	82.7 \pm 3.2 (15)
N longitudinal scale rows at midbody	min-max:	24-26	22-24	22-26	24-26	22-26	28-30	18-20	26	24-26	24-26	30-32	
	mean \pm SD: n:	24.2 \pm 0.6 (28)	23.3 \pm 1.0 (7)	24.0 \pm 1.2 (7)	24.1 \pm 0.4 (27)	23.7 \pm 1.5 (6)	23.7 \pm 1.5 (6)	29.0 \pm 4.2 (8)	19.6 \pm 0.9 (5)	26.0 \pm 0 (7)	24.1 \pm 0.5 (14)	25.4 \pm 0.9 (13)	31.6 \pm 0.8 (16)
Enlarged nuchal scales	absent:	-	-	-	-	-	-	-	-	-	-	-	
	one row:	-	-	-	2%	7.1%	100%	40.0%	42.9%	92.3%	56.3%	81.3%	
	two rows:	23.2%	21.4%	28.6%	50%	35.8%	-	20.0%	57.1%	7.7%	37.5%	18.7%	
	three rows:	71.4%	78.6%	57.1%	48%	57.1%	-	40.0%	-	-	6.2%	-	
Postnasal	four rows:	5.4%	-	14.3%	-	-	-	-	-	-	-	-	
	n sides:	(56)	(14)	(14)	(58)	(14)	(14)	(16)	(14)	(14)	(26)	(22)	(32)
Frontal and interparietal	present:	100%	100%	100%	100%	100%	100%	100%	-	89.3%	100%	94.4%	
	absent:	-	-	-	-	-	-	-	100%	10.7%	-	5.6%	
Frontal	n sides:	(56)	(14)	(14)	(58)	(14)	(16)	(10)	(14)	(28)	(26)	(36)	
	fused:	-	-	-	-	-	87.5%	-	-	-	-	-	
Snout-vent length (mm)	separated:	100%	100%	100%	100%	100%	12.5%	100%	100%	100%	100%	100%	
	n:	(28)	(14)	(7)	(28)	(7)	(7)	(8)	(10)	(7)	(14)	(13)	(16)
Frontal	bell-shaped:	100%	100%	-	-	-	100%	-	100%	100%	100%	47.2%	
	hour-glass shaped:	-	-	100%	100%	100%	100%	100%	-	-	-	52.8%	
Snout-vent length (mm)	n:	(23)	(12)	(14)	(29)	(14)	(8)	(10)	(7)	(14)	(13)	(18)	
	max:	73.0	54.2	47.4	53.5	50.5	50.5	68.5	33.6	81.7	61	75	114.0
Snout-vent length (mm)	mean \pm SD:	56.3 \pm 11.6 (9)	52.3 \pm 2.1 (4)	42.0 \pm 5.1 (7)	49.5 \pm 2.5 (21)	48.0 \pm 2.4 (5)	48.0 \pm 2.4 (5)	60.1 \pm 9.6 (7)	27.8 \pm 8.2 (6)	72.3 \pm 6.1 (7)	54.9 \pm 3.1 (14)	66.0 \pm 7.1 (13)	89.6 \pm 10.8 (14)
	n:	(9)	(4)	(7)	(21)	(5)	(5)	(7)	(6)	(7)	(14)	(13)	(14)

	igneocaudatus clade		melanopleura clade			mouroundavae	nanus complex	polleni clade				
	igneocaudatus	pyrusus (C)	minutus (N)	melanopleura (C)	ankodabensis (S)			arenicola	miafina (N)	polleni (S)	stumpffi	
Supraciliaries												
five:	–	7.1%	7.1%	–	–	–	–	–	–	–	–	–
six:	98.2%	92.9%	57.1%	8.6%	35.7%	93.8%	66.6%	92.9%	100%	87.5%	–	–
seven:	1.8%	–	35.8%	79.3%	50.0%	6.2%	33.3%	7.1%	–	12.5%	–	n/a
eight:	–	–	–	12.7%	14.3%	–	–	–	–	–	–	–
n sides:	(56)	(14)	(14)	(58)	(14)	(16)	(6)	(14)	(2)	(8)	–	–
Subocular												
third SL:	1.8%	–	–	–	7.1%	–	100%	–	3.6%	–	–	–
Fourth SL:	98.2%	100%	100%	100%	92.9%	100%	–	100%	96.4%	100%	–	100%
n sides:	(56)	(14)	(14)	(58)	(14)	(24)	(10)	(14)	(28)	(24)	–	(32)
Lower eyelid window	spectacled	spectacled	spectacled	spectacled	spectacled	scaly	scaly	scaly	scaly	scaly	scaly	scaly
Reproduction	viviparous	oviparous	?	oviparous?	?	oviparous	?	?	?	?	?	?
Altitudinal range	≤ 500 m	≥ 1500 m	≤ 1000 m	≤ 1000 m	≤ 1000 m	≤ 1000 m	500–1500 m	≤ 500 m	≤ 500 m	≤ 500 m	≤ 500 m	≤ 500 m

Table 2. Summary of the most relevant morphological characters differentiating each pair of species of *Madascincus*. Only objective and unambiguous diagnostic characters (e.g. fixed character states for qualitative characters or non-overlapping values for meristic characters) are reported; see complete data in Table 1. F: number of lamellae under 4th finger; T: number of lamellae under 4th toe; VR: number of ventral scale rows; PR: number of paravertebral scale rows; MR: number of longitudinal scale rows at midbody; N: number of enlarged nuchal scales; PN: presence or absence of postnasal scales; FS: shape of the frontal scale; SO: position of the subocular scale; EW: aspect of the lower eyelid window; R: reproduction mode (oviparity vs. viviparity).

	<i>nanus</i> complex	<i>igneocaudatus</i>	<i>pyrurus</i>	<i>mouroundavae</i>	<i>minutus</i>	<i>melanopleura</i>	<i>ankodabensis</i>	<i>miafina</i>	<i>polleni</i>	<i>stumpffi</i>
<i>M. arenicola</i>	F, T, VR, PR, MR, PN, FS, SO	F, N, PN, EW	F, MR, N, PN, EW	F, VR, PR, MR, PN, FS, EW	T, VR, PR, N, PN, FS, EW	VR, PR, PN, FS, EW	T, VR, PR, PN, FS, EW	VR	PN	MR
<i>M. nanus</i>	–	F, T, VR, PR, MR, FS, EW	F, T, VR, PR, MR, FS, SO, EW	F, T, VR, PR, MR, SO	T, MR, SO, EW	T, MR, SO, EW	T, MR, EW	F, T, VR, PR, MR, FS	F, T, VR, PR, MR, FS, SO	F, T, VR, PR, MR, SO
<i>M. igneocaudatus</i>	–	–	R	VR, PR, MR, N, FS, EW, R	F, T, VR, PR, FS	VR, PR, FS	VR, PR, FS	N, EW	EW	MR, N, EW
<i>M. pyrurus</i> sp. n.	–	–	–	VR, PR, MR, N, FS, EW	F, T, VR, PR, FS	VR, PR, FS	VR, PR, FS	N, EW	EW	MR, N, EW
<i>M. mouroundavae</i>	–	–	–	–	F, T, MR, N, EW	VR, MR, EW	T, MR, EW	MR, FS	VR, PR, MR, FS	VR, PR
<i>M. minutus</i>	–	–	–	–	–	none	none	T, VR, N, FS, EW	T, VR, PR, FS, EW	T, VR, PR, MR, N, EW
<i>M. melanopleura</i>	–	–	–	–	–	–	none	T, VR, PR, FS, EW	VR, PR, FS, EW	VR, PR, MR, EW
<i>M. ankodabensis</i>	–	–	–	–	–	–	–	T, VR, PR, FS, EW	T, VR, PR, FS, EW	VR, PR, MR, EW
<i>M. miafina</i> sp. n.	–	–	–	–	–	–	–	–	VR	MR
<i>M. polleni</i>	–	–	–	–	–	–	–	–	–	MR

Table 3. Genetic divergences among *Madascincus* species: mean of the uncorrected p-distances for the ND1 (above diagonal) and the 16S (below diagonal) mtDNA segments estimated between and within the different species. The genetic distance values obtained between the two newly described species and their respective sister clades (in bold) are consistent with interspecific divergences observed between the other recognized species of *Madascincus*.

	Inter-specific distances (%)										Intra-specific distances (%)		
	<i>aren.</i>	<i>nanu.</i>	<i>pyru.</i>	<i>igne.</i>	<i>anko.</i>	<i>mela.</i>	<i>minu.</i>	<i>mour.</i>	<i>poll.</i>	<i>miaf.</i>	<i>stum.</i>	16S	ND1
<i>M. arenicola</i>	-	19.8	17.9	19.2	17.5	16.6	17.3	16.9	12.5	9.0	10.5	0.1	1.1
<i>M. nanus</i>	10.1	-	21.1	21.2	21.3	19.0	21.3	20.0	21.1	21.2	20.5	0.0	0.0
<i>M. pyrurus</i> sp. n.	8.2	10.1	-	17.0	18.9	17.3	18.3	20.8	19.5	19.2	19.3	1.5	3.5
<i>M. igneocaudatus</i>	9.3	9.9	8.3	-	20.5	19.3	20.1	18.8	19.3	20.0	19.3	2.5	5.9
<i>M. ankodabensis</i>	8.3	10.9	9.8	11.2	-	8.2	14.7	17.5	16.5	17.9	16.2	0.5	1.0
<i>M. melanopleura</i>	8.5	10.6	9.7	11.6	3.4	-	12.3	17.1	15.9	16.1	15.2	0.5	0.7
<i>M. minutus</i>	8.7	11.3	10.9	12.5	8.5	8.0	-	17.0	17.7	18.1	16.6	3.1	5.7
<i>M. mouroundavae</i>	7.0	8.6	9.2	8.7	9.9	9.9	10.6	-	15.8	17.6	15.6	0.7	1.3
<i>M. polleni</i>	3.4	9.8	8.7	10.0	8.4	9.2	9.2	6.8	-	10.5	9.5	1.2	3.1
<i>M. miafina</i> sp. n.	2.8	10.1	9.2	10.0	9.2	9.3	10.3	7.1	3.4	-	8.9	0.5	1.5
<i>M. stumpffi</i>	3.4	8.7	9.1	9.4	7.6	8.6	9.3	6.7	3.0	3.8	-	1.1	2.7

Diagnosis. A member of the genus *Madascincus* based on its molecular phylogenetic relationships (see Fig. 1). Within the genus *Madascincus*, *M. miafina* is distinguishable from all its congeners by the following combination of characters: medium body size with a maximum snout-vent length (SVL) of 61.0 mm (versus, in smaller species, a maximum SVL of 33.6 mm in *M. nanus* complex, 47.4

mm in *M. minutus*, 50.5 mm in *M. ankodabensis*, 53.5 mm in *M. melanopleura*); 65–79 rows of paravertebral scales (versus 51–62 in *M. melanopleura*, 57–65 in *M. minutus*, 52–62 in *M. ankodabensis*, 60–65 in *M. mouroundavae*, and 50–57 in *M. nanus* complex); 65–73 rows of ventral scales (versus 55–63 in *M. minutus*, 56–61 in *M. melanopleura*, 52–60 in *M. nanus* complex, 59–63 in

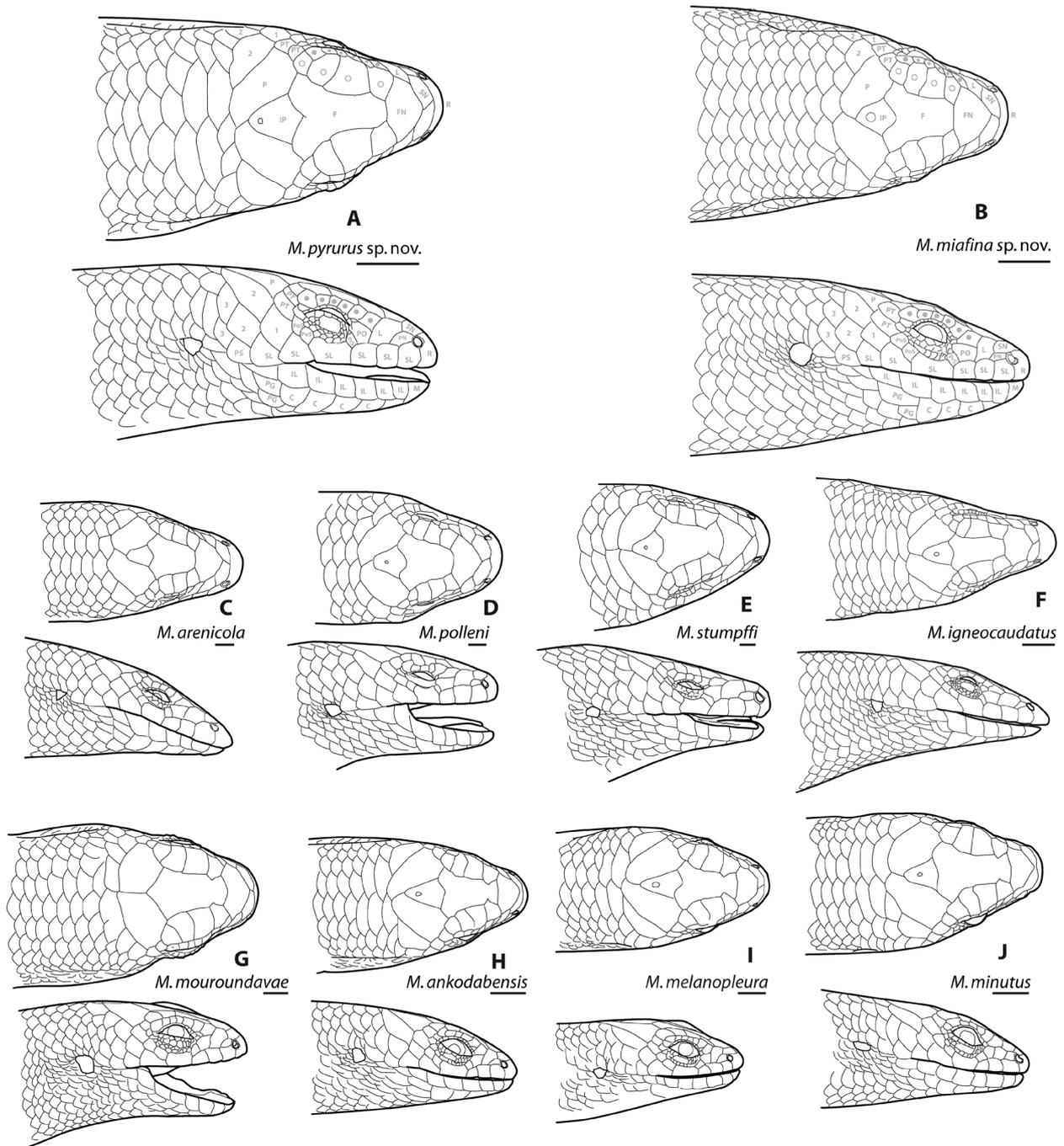


Figure 3. Drawings of the lateral and dorsal views of the heads of most of the species of *Madascincus*, including the holotypes of the two new species described herein. **A:** *Madascincus pyrurus* sp. n., holotype ZSM 520/2001 (MV 2001-445), Mont Ibity; **B:** *M. miafina* sp. n., holotype ZSM 1562/2008 (FGZC 1658), Ankarana Special Reserve; **C:** *M. arenicola*, holotype ZSM 1565/2008 (FGZC 1703), Baie des Sakalava; **D:** *M. polleni*, holotype MNHN 1895.210, “Mouroundava” (= Morondava); **E:** *M. stumpffi*, holotype SMF 16019, “Nossibé” (=Nosy Be); **F:** *M. igneocaudatus*, ZSM 1600/2010 (ZCMV 12888), Anakao; **G:** *M. mouroundavae*, ZSM 13/2005 (ZCMV 2254), Andasibe; **H:** *M. ankodabensis*, ZSM 355/2006 (ZCMV 2907), Ranomafana; **I:** *M. melanopleura*, ZSM 20/2005 (ZCMV 2266), Andasibe; **J:** *M. minutus*, ZSM 400/2005 (ZCMV 2166), Nosy Mangabe. Dwarf species of *Madascincus*, namely *M. nanus* and *M. macrolepis*, not represented. Scale bars = 2 mm. Abbreviations used for indication of scales (**A**, **B**) follow those defined by Miralles et al. (2011b).

M. ankodabensis, 63–66 in *M. mouroundavae*, 73–78 in *M. pyrurus*, 74–78 in *M. polleni* and 75–80 in *M. arenicola*); 18–23 subdigital lamellae under the fourth toes (versus 5–8 in *M. nanus* complex, 9–13 in *M. minutus*,

12–15 in *M. ankodabensis*, 12–16 in *M. melanopleura* and 15–18 in *M. pyrurus*); 24–26 rows of scales around midbody (versus in *M. nanus* complex, 28–30 in *M. mouroundavae*, 22–24 in *M. pyrurus* and 30–32 in *M. stumpf-*

fi); pentadactyl forelimbs (versus 3–5 digits in *M. nanus* complex); and most often (89.3%) the presence of postnasal scales (always absent in *M. arenicola*). The frontal is bell-shaped (versus hourglass-shaped in *M. nanus*, *M. minutus*, *M. melanopleura*, *M. ankodabensis*, *M. mouroundavae*, and in half (52.8%) of the specimens examined of *M. stumpffi*); the frontal is always separated from the interparietal (versus most often (87.5%) fused in *M. mouroundavae*). The lower eyelid window is scaly (versus spectacled in *M. igneocaudatus*, *M. pyrurus*, *M. minutus*, *M. melanopleura* and *M. ankodabensis*); absence in most specimens (92.3%) of a single row of enlarged nuchal scales (versus presence of at least two rows in *M. igneocaudatus*, *M. pyrurus* and *M. minutus*). More generally, *M. miafina* can be distinguished from all the other species (with exception of *M. polleni*) by its apparently very conserved pattern of coloration, characterized by a single pair of lateral dark brown stripes relatively large and well-defined anteriorly, then progressively breaking up into two parallel very thin dashed lines posteriorly to forelimbs, hardly distinguishable from the rest of the dots covering the body.

Madascincus miafina differs from its sister species *M. arenicola* by a paler coloration, with lateral lines well defined anteriorly, becoming one – or two parallel – very thin dashed line posteriorly to forelimbs (versus a very contrasted coloration in *M. arenicola*, characterized by the presence of a pair of two-scale wide dark lateral lines extending from snout to hindlimbs, well defined all along the body) and by a relatively shorter snout, rounded in lateral aspect (versus a relatively long snout, acute in lateral aspect, in *M. arenicola*). It also differs by a lower number of ventral scales (65–73 vs. 75–80 in *M. arenicola*). Moreover, *M. miafina* is one of the few species (together with *M. pyrurus* and *M. igneocaudatus*) in which the tail might be bright red in some specimens (see also Tables 1 and 2). Morphologically, the species most similar to *M. miafina* is *M. polleni* (including its junior synonym *M. intermedius*); this species is identical in coloration, body shape, and body size to *M. miafina* despite not being the direct sister species, differing only by the number of ventrals (see above).

Description of the holotype (Fig. 3B). ZSM 1562/2008 (FGZC 1658). Adult male, with both hemipenes everted. Good state of preservation, with exception of a little circular sampling incision on the left flank (ca. 5 mm of diameter). SVL (57.0 mm) 7.5 times head length (7.6 mm), almost as long as tail (79.1 mm, apparently entire and not regenerated). Limbs relatively short: SVL 5.6–5.8 times front limb length (9.9–10.2 mm) and 3.2–3.3 times hind limb length (17.3–18.0 mm). Snout relatively short and rounded on lateral aspect, with a rostral tip bluntly rounded in dorsal aspect. Rostral wider than high/long, contacting first supralabials, nasals, and supranasals. Paired supranasals in median contact, contacting loreals. Frontonasal roughly triangular, wider than long, contacting loreals, first supraciliaries and first supraoculars. Prefrontals absent. Frontal approximately as wide as long, wider

posteriorly, in contact with frontonasal, supraoculars, parietals and interparietal. Supraoculars four, all of them in contact with frontal; subequal in size, except for the posteriormost pair that is significantly smaller; the first pair not constricting frontal (frontal bell-shaped sensu Andreone and Greer 2002). Frontoparietals absent. Interparietal longer than wide, well separated from supraoculars; parietal eyespot present with parietal eye evident. Parietals contact posterior to interparietal. Absence of enlarged nuchals. Nasals just slightly larger than nostrils; contacting rostral, first supralabials, postnasals and supranasals. Postnasals present, separating supranasals from first supralabials, and nasals from loreals. Loreal single, slightly higher than long. Preocular trapezoidal, longer than high, single. Presubocular roughly square, single. Six supraciliaries on both sides, in continuous row; first and last pairs significantly larger and longer than the intermediate ones; last pair projecting onto supraocular shelf. Upper palpebrals small except for last which projects dorsomedially. Pretemporals two, both contacted by parietal. Postsuboculars two; upper contacting lower pretemporal; both contacting penultimate supralabial. Lower eyelid moveable, scaly; lower palpebrals small, longer than high, interdigitating with large polygonal scales of central eyelid. Contact between upper palpebrals and supraciliaries seemingly direct but flexible, i.e. palpebral cleft narrow. Primary temporal single. Secondary temporals two; upper long, contacting lower pretemporal anteriorly and overlapping lower secondary temporal ventrally. Two tertiary temporals bordering lower secondary temporal. Supralabials six, with the fourth being the enlarged subocular, contacting scales of the lower eyelid. Postsupralabial single. External ear opening round, without lobules. Mental wider than long, posterior margin convex. Postmental wider than long, contacting first two pairs of infralabials. Infralabials six. Three pairs of large chin scales, both members of first pair in contact, both members of second pair separated by a single median scale, and members of third pair separated by three scale rows. No scales extending between infralabials and large chin scales; two asymmetrical postgenials posterolaterally in contact with the third pair of chin scales. Gulars similar in size and outline to ventrals. All scales, except head shields and scales on palms, soles, and digits, cycloid, smooth, and imbricate; longitudinal scale rows at midbody 24; paravertebrals 68, similar in size to adjacent scales; ventrals 68. Inner preanals overlapped by outer. Both pairs of limbs pentadactyl; fingers and toes relatively short, clawed; relative length of toes in the following order: I<II<V<III<IV. Subdigital lamellae smooth, single, with 8 under right fourth finger and 7 under left fourth finger, 18 under right fourth toe, and 20 under left fourth toe.

Coloration of the holotype in preservative with a pair of lateral dark brown stripes (about two scales wide on the neck) relatively large and well defined anteriorly (overlapping rostral, mental, first four supralabials, loreals, and presuboculars), then progressively breaking up into two parallel very thin dashed lines posteriorly



Figure 4. Photographic plate showing most of the recognized species of *Madascincus* (picture not available for *M. macrolepis*), highlighting the chromatic polymorphism (red tail and brown tail morphs) for *M. miafina* sp. n., *M. pyrurus* sp. n. and *M. igneocaudatus*. Picture I depicts the sole specimen known from Kirindy that in Glaw and Vences (2007) was assigned to a candidate species *M. sp.* “vitreus”, and O depicts a specimen that these authors assigned to a candidate species *M. sp.* “baeus”.

to forelimbs, hardly distinguishable from the rest of the dots covering the body. Dorsum and dorsal sides of forelimbs, hindlimbs and tail light bronze. The bronze dorsal field and flanks are covered by numerous little dark dots, each of them in the middle of a dorsal scale, in contact with its posterior edge; resulting in many thin dash lines (14 to 16 at midbody, including the dark lateral stripes), darker and more contrasted in the posterior part of the dorsum, then posteriorly becoming progressively indistinguishable from the background coloration of tail, and laterally, becoming progressively indistinguishable from the light coloration of the ventral field. No distinct border

between the background coloration of the dorsal and the ventral sides. Immaculate whitish ventral field extending from lower side of head (mental excluded), throat, lower side of limbs and venter, to the ventral side of tail. Palms and soles barely darker than venter. Coloration in life was almost identical to the coloration in preservative, with the only significant difference being the presence of iridescent glints of scales and a venter with some violet-pinkish tint (*cf.* Figs 4J, K).

Variation. For variation in measurements and scale characters see Table 1. Some variation is evident with respect

to overall dorsal and tail coloration. The paratype from Ankarana was more or less similar to the holotype described above, with a bronze dorsal color predominating the dorsum and tail. At Montagne des Français, specimens were generally darker, with a bronze-brown dorsal coloration and a reddish brown tail dorsally and red-orange tail ventrally.

Etymology. The specific epithet *miafina* is the Malagasy word for “secretive”. The name refers to the secretive habits of the species, as all specimens were exclusively trapped by pitfalls and never observed in situ, as well as to the fact that this species was hidden behind several other taxon names in use and could only be discovered by an integrative taxonomic approach. The name is treated as an invariable noun in apposition.

Distribution, habitat and habits. The species is known from northernmost Madagascar including at least four localities (see localities of type specimens above and Fig. 5) with karstic outcrops and sandy soils. The species apparently has nocturnal and secretive habits, as all specimens were exclusively caught by pitfall trapping overnight in forest or shrub areas. The species can therefore be considered to represent a leaf litter dweller. The new species occurs in sympatry with *M. arenicola* and *M. stumpffi*. Hence, it appears to tolerate a rather wide range of habitat conditions, whereas *M. arenicola* exclusively occurs on sandy soils and *M. stumpffi* seems to be restricted to forests. Nothing else is known on the natural history of the new species.

Madascincus pyrurus sp. n.

<http://zoobank.org/2A2D2E29-6FE3-4964-A17D-624BAEF8C842>

Figs 3A, 4D, E

Holotype. ZSM 520/2001 (MV 2001-445), adult male from Mont Ibity, approximately at 20°14'S, 47°03'E, 1700–1800 m above sea level, Fianarantsoa province, central Madagascar, collected on 10 March 2001 by M. Vences, D.R. Vieites, L. Raharivololoniaina and D. Rakotomalala.

Paratypes (n=7). MNHN 1980-1217, Mont Ibity, Fianarantsoa province, central Madagascar, coll. by Y. Thérézien and R. Capuron; ZSM 518–519/2001 (MV 2001-441, 2001-444), UADBA uncatalogued (MV2001.442 and 443), same data as holotype; ZSM 521/2001 (MV 2001-611), UADBA uncatalogued (MV2001.610), Itremo (camp, 20°36'08"S, 46°34'16"E, 1648 m a.s.l.), Fianarantsoa province, coll. on 10 March 2001 by M. Vences, D.R. Vieites, L. Raharivololoniaina and D. Rakotomalala.

Chresonyms.

Scelotes igneocaudatus – Blanc (1967), Brygoo (1981, *partim*);

Amphiglossus igneocaudatus – Brygoo (1984, *partim*), Whiting et al. (2004), Schmitz et al. (2005);

Madascincus igneocaudatus – Glaw and Vences (2007, *partim*), Crottini et al. (2009; *partim*), Miralles et al. (2011a, c, *partim*; 2011b);

Madascincus igneocaudatus “*igneocaudatus*-C clade” – Miralles and Vences (2013);

Madascincus sp. “*igneocaudatus*” central clade – Miralles et al. (2015).

Diagnosis. A member of the genus *Madascincus* based on its molecular phylogenetic relationships (see Fig. 1). Within the genus *Madascincus*, *M. pyrurus* is distinguished from all its congeners by the following combination of characters: medium body size with a maximum snout-vent length (SVL) of 54.2 mm (versus, in smaller species, a maximum SVL of 33.6 mm in *M. nanus* complex); 71–79 rows of paravertebral scales (versus 51–62 in *M. melanopleura*, 57–65 in *M. minutus*, 52–62 in *M. ankodabensis*, 60–65 in *M. mouroundavae*, and 50–57 in *M. nanus* complex); 73–78 rows of ventral scales (versus 55–63 in *M. minutus*, 56–61 in *M. melanopleura*, 52–60 in *M. nanus* complex, 59–63 in *M. ankodabensis*, 65–73 in *M. miafina*, 63–66 in *M. mouroundavae*); 15–18 subdigital lamellae under the fourth toes (versus 5–8 in *M. nanus* complex, 9–13 in *M. minutus*, 18–23 in *M. miafina* and 12–15 in *M. ankodabensis*); 22–24 rows of scales around midbody (versus 18–20 in *M. nanus* complex, 28–30 in *M. mouroundavae*, 24–26 in *M. igneocaudatus* and 30–32 in *M. stumpffi*); pentadactyl forelimbs (versus 3–5 digits in *M. nanus* complex; the presence of postnasal scales (always absent in *M. arenicola*); the frontal is bell-shaped (versus hourglass shaped in *M. nanus*, *M. minutus*, *M. melanopleura*, *M. ankodabensis*, *M. mouroundavae*, and in half (52.8%) of the specimen examined of *M. stumpffi*); the frontal is always separated from the interparietal (versus most often (87.5%) fused in *M. mouroundavae*); lower eyelid window is spectacled (versus scaly in *M. arenicola*, *M. nanus*, *M. mouroundavae*, *M. polleni*, *M. miafina* and *M. stumpffi*), the presence of two (21.4%) or three (78.6%) rows of enlarged nuchal scales (versus absence or presence of a single row in *M. nanus*, *M. mouroundavae*, *M. miafina* and *M. stumpffi*). More specifically, *M. pyrurus* differs from its sister species *M. igneocaudatus* in having a shorter and rounder snout (versus a relatively long and pointed snout usually characterizing semi-fossorial species found in sandy habitat) and in being oviparous (versus viviparous). More generally, *M. pyrurus* can also be easily distinguished from all the other members of the genus *Madascincus* by its very characteristic pattern of coloration, being the only species with six well-defined very dark stripes (a pair of thin dorsal, a pair of wide upper lateral and a pair of thin lower lateral stripes) running along the body, and one of the few species (together with *M. miafina* and *M. igneocaudatus*) in which the tail might be bright red in some specimens (see also Tables 1 and 2).

Description of the holotype. ZSM 520/2001 (MV 2001-445, Fig. 3A). Adult male, with both hemipenes everted.

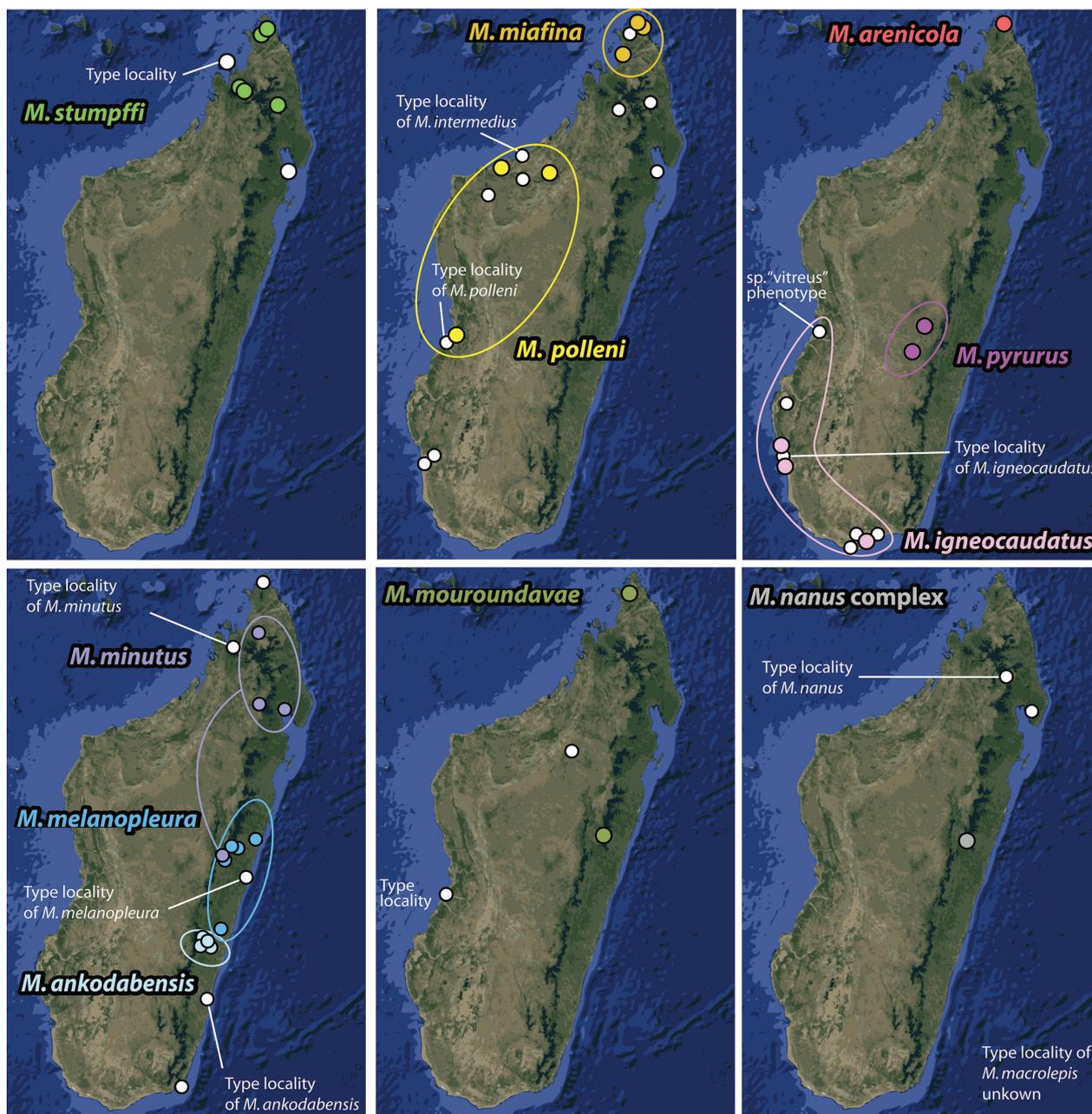


Figure 5. Distribution maps for *Madascincus* species. Colored dots are representing localities sampled in the molecular studies by Miralles and Vences (2013), whereas white dots are representing localities of specimens only identified by morphology, and/or type localities. For *M. polleni*, another locality has been added based on a recent paper from Rakotoarison et al. (2015), who have collected an additional specimen (ZCMV 14157) in Mitsinjo forest in north-western Madagascar (16°02'54.5"S, 45°47'24.1"E). The identity of this specimen is confirmed by both its morphological characteristics and its phylogenetic position inferred from a segment of the 16S rRNA gene (nested within the *M. polleni* clade, and closely related to the population of Ankarafanstika, GenBank accession number KR025911). Note that for some species, especially *M. mouroundavae*, additional verified localities exist but these are here excluded for consistency because no samples were examined in the framework of the present study.

Good state of preservation, with exception of a little incision on the right flank (ca. 10 mm). SVL (49.0 mm) 7.1 times head length (6.9 mm), shorter than the tail (58.0 mm, apparently regenerated). Limbs relatively short: SVL 6.2–6.5 times front limb length (7.5–7.9 mm) and 3.4 times hind limb length (14.4–15.0 mm). Snout relatively short and rounded on lateral aspect, with a rostral tip bluntly rounded in dorsal aspect. Rostral wider

than high/long, contacting first supralabials, nasals, and supranasals. Paired supranasals in median contact, contacting loreals. Frontonasal roughly pentagonal, wider than long, contacting loreals, and first suproculars. Pre-frontals absent. Frontal longer than wide, wider posteriorly, in contact with frontonasal, supraoculars, parietals and interparietal. Supraoculars four, all of them in contact with frontal; the second anteriormost pair larger and the

posteriormost pair significantly smaller; the first pair not constricting frontal (bell-shaped). Frontoparietals absent. Interparietal longer than wide, well separated from supraoculars; parietal eyespot present but poorly marked. Parietals contact posterior to interparietal. Two pairs of primary nuchal scales (with two cycloids scales inserted between the parietal and the first nuchal, on the right side). Nasals slightly larger than nostrils; contacting rostral, first supralabials, postnasals and supranasals. Postnasals present, separating supranasals from first supralabials, and nasals from loreals. Loreal single, as high as long. Preocular higher than long, single. Presubocular single. Six supraciliaries on both sides, in continuous row; last pair slightly larger than the others, and projecting onto supraocular shelf. Pretemporals two, both contacted by parietal. Postsuboculars two; upper contacting lower pretemporal; both contacting penultimate supralabial. Lower eyelid moveable, with a transparent and undivided disc, and one row of small scales across its dorsal edge. Contact between upper palpebrals and supraciliaries seemingly direct but flexible, i.e. palpebral cleft narrow. Primary temporal single. Secondary temporals two; the upper one elongated, contacting lower pretemporal anteriorly and overlapping lower secondary temporal ventrally. Two tertiary temporals bordering lower secondary temporal. Supralabials six, with the fourth being the enlarged subocular contacting scales of the lower eyelid. Postsupralabial single. External ear opening roughly triangular, without lobules. Mental wider than long, posterior margin straight. Postmental wider than long, contacting first two pairs of infralabials. Infralabials six. Three pairs of large chin scales, both members of first pair in contact, both members of second pair separated by a single median scale, and members of third pair separated by three scale rows. No scales extending between infralabials and large chin scales; two asymmetrical postgenials posterolaterally in contact with the third pair of chin scales. Gulars similar in size and outline to ventrals. All scales, except head shields and scales on palms, soles, and digits, cycloid, smooth, and imbricate; longitudinal scale rows at midbody 22; paravertebrals 71, similar in size to adjacent scales; ventrals 73. Inner preanals overlapped by outer. Both pairs of limbs pentadactyl; fingers and toes relatively short, clawed; relative length of toes in the following order: I<II=V<III<IV. Subdigital lamellae smooth, single, 10 under fourth finger of both left and right manus, 17 under right fourth toe, and 15 under left fourth toe.

Coloration in preservative with upper side of the head, neck, back, limbs, and tail dark bronze. Venter, lower side of head, throat, lower side of limbs, and tail whitish/cream. Lateral borders on the ventral side maculated by very small dark dots. Six very well defined very dark stripes run along the body, continuing along the first third of the tail, then abruptly ending where the tail is regenerated. Two thin blackish dorsal stripes formed by succession of contiguous dots start on the supranasal; at midbody, each dorsolateral stripe is less than one scale wide and both are separated by two rows of dorsal

scales. Two wide dark brown upper lateral stripes; margins slightly darker and very sharp; about two scales wide at midbody and overlying three rows of scales; starting from the rostral, where the stripes all meet, extending on the upper half of each supralabial, the loreals, around the eyes, above ear opening, and above forelimbs and hindlimbs. Two thin dark lower lateral stripes, starting on the last infralabials, extending through the forelimb and hindlimb insertion. At midbody, each lower lateral stripe is less than one scale wide, with irregular margin. Four very light stripes run along the body, continuing along the first third of tail, then abruptly ending where the tail is regenerated. Two whitish dorsolateral stripes separate dark dorsal stripes from the upper lateral dark stripes; about one scale wide at midbody and overlying two rows of scales. Two whitish lateral stripes separating the dark upper lateral stripes from the dark lower lateral stripes; about one scale wide at midbody and overlying two rows of scales. Regenerated part of the tail cream, maculate with many small dark dots on the dorsal side. Palms and soles darker than the ventral side.

Life coloration for the holotype has not been documented, but it is apparently very similar to the coloration in preservative, with exception of the tail which is usually bright red, or pinkish brown in some specimens (cf. Fig. 4D, E).

Variation. For variation in measurements and scale characters see Table 1. Some variation is evident with respect to tail coloration which may be bronze or reddish (cf. Fig. 4D, E) and ventral coloration which may be maculated by small black dots or uniformly whitish (Blanc and Blanc 1967).

Etymology. The specific epithet *pyrurus* is based on Greek roots *pûr* (πῦρ) and *ourá* (οὐρά), respectively meaning “fire” and “tail”. This word is here treated as invariable noun and has the same meaning as an other specific epithet in the genus, *igneocaudatus*, which is based on Latin roots. This epithet has been chosen to highlight the morphological similarity of *M. igneocaudatus* and *M. pyrurus*, both these sister species being characterized by a tail which may be red and reminding fire.

Distribution, habitat and habits. The species is known from the dry environments on two massifs in the central highlands of Madagascar, in Mont Iby and in Itremo (Fig. 5), dominated by rock outcrops and tapia woodlands (loose forests of *Uacapa bojeri* trees). This montane lizard has been found at altitudes ranging from 1648 to 1922 m a.s.l. in Itremo, and up to 2252 m a.s.l. in Iby (Brygoo 1984, present study). It can be commonly found under stones on usually somewhat sandy substrate (quartz sand especially on Mont Iby), in open areas. On Mont Iby, 6 eggs of *M. pyrurus* have been collected at the end of December which measured 18 × 12 mm, the hatched juveniles measuring 25 mm SVL (Blanc and Blanc 1967, Brygoo 1984). In contrast, in *M. igneocaudatus*, developed juveniles have been found in a female dissected from Ifaty, indicating that the sister species of *M. pyrurus*, endemic to the dry low-

lands of the western coast, is viviparous (Glaw and Vences 2007). Interestingly, the different modes of reproduction observed in these two sister species appear to be in contradiction with the trend usually observed in lizard taxa

having both oviparous and viviparous species/populations: typically, evolution to viviparity in these groups is interpreted as local adaptation to cold climates, either at high altitude or latitude (Pianka and Vitt 2003).

Synopsis and identification key

A list of the species currently recognized, including information supporting their respective taxonomic validity is presented in Table 4. To facilitate future taxonomic work, we furthermore elaborated the following identification key for species of *Madascincus*. The key is based on the selection of the features we considered to be the most diagnostic and easily observable.

- a postnasal always absent.....*M. arenicola*
- a' postnasal mostly present (rarely absent in *M. miafina* and *M. stumpffi*).....b
- b 28 or more scale rows at midbody.....c
- b' 26 or less scale rows at midbody.....d
- c 30–32 scale rows at midbody, 76–88 paravertebral scale rows, 70–88 ventral scale rows, frontal and interparietal separated together *M. stumpffi*
- c' 28–30 scale rows at midbody, 60–65 paravertebral scale rows, 63–66 ventral scale rows, frontal and interparietal mostly fused together*M. mouroundavae*
- d 18–20 scale rows at midbody, 8 or less lamellae under 4th toe, frequently less than 5 fingers, adult SVL < 35 mm, an atypical head shape with a short and acuminate snout and relatively large eyes *M. nanus* complex
- d' 22–26 scale rows at midbody, 9 or more lamellae under 4th toe, always 5 fingers, SVL in adult > 40 mme
- e Frontal bell-shaped, 65 or more ventral scale rows, 65 or more paravertebral scale rows, tail frequently red colored.....f
- e' Frontal hour-glass shaped, 63 or less ventral scale rows, 65 or less paravertebral scale rows, tail always brown colored.....*M. melanopleura* complex (including also *M. ankodabensis* and *M. minutus*)
- f Two lateral dark brown stripes relatively large and well defined anteriorly, then progressively breaking up into two parallel very thin dashed lines posteriorly to forelimbs, hardly distinguishable from the rest of the dots covering the body, lower eyelid scalyg
- f' Four or six well defined and brightly contrasted dark stripes running along the body, lower eyelid spectacled.....h
- g 65–73 ventral scale rows *M. miafina*
- g' 74–78 ventral scale rows *M. polleni*
- h A relatively short and rounded snout, six well defined and contrasted stripes running along the body, 22–24 scale rows around midbody..... *M. pyrurus*
- h' A relatively long and pointed snout, four well defined and contrasted stripes running along the body, 24–26 scale rows around midbody..... *M. igneocaudatus*

Discussion

Taxonomy in the genus *Madascincus*. By applying the results supported by the ITAX approach of Miralles and Vences (2013), eleven distinct species within their *Madascincus* sampling can presently be recognized for this genus. This number might be increased to 12 if *M. macrolepis* is included. It is worthwhile to remind here that we are following Miralles and Vences (2013, Supporting information 1) who synonymized *Madascincus intermedius* (Boettger, 1913) - type locality “Majunga” = Mahajanga, with *Madascincus polleni* (Grandidier, 1869) - type locality “Morondava”, both type localities unambiguously corresponding to conspecific populations of the *polleni*-S clade.

Phylogenetic relationships. In their previous work, Miralles and Vences (2013) published multilocus phylogenetic results used to delimit species but did not discuss the results from biogeographic and phylogeographic perspectives.

The different phylogenetic inferences applied (separated phylogenetic Bayesian analysis based on the

mtDNA; (Fig. 1), retrieved the monophyly of the 11 recognized species sampled in this study. These different approaches also agreed on the existence of five main clades strongly supported within the genus *Madascincus*: (1) the *M. polleni* clade (*M. arenicola*, *M. stumpffi*, *M. polleni* and *M. miafina*); (2) *M. mouroundavae*; (3) the *M. igneocaudatus* clade (*M. igneocaudatus* and *M. pyrurus*); (4) the *M. melanopleura* clade (*M. ankodabensis*, *M. melanopleura* and *M. minutus*); and (5) *M. nanus*. Their tree derived from the concatenated nuclear data set was congruent in topology with the mtDNA tree, with only two exceptions: (1) the relative positions of the *M. igneocaudatus* clade and *M. mouroundavae* clade are inverted and (2) the monophyly of *Madascincus* is recovered with exclusion of *Paracontias*. The species tree presented by Miralles and Vences (2013, Supporting information S6e), inferred by *BEAST and combining mtDNA and nDNA agreed with the mtDNA Bayesian tree.

Two of these clades reveal a relevant biogeographical component: (1) The *M. polleni* clade includes four species

Table 4. List of the species presently recognized in the genus *Madascincus*, with the different lines of evidences supporting their distinctiveness. MSD = Methods of species delimitation.

Taxa	Morphological diagnosability	Monophyly	Species delimitation methods
<i>M. arenicola</i> Miralles, Köhler, Glaw and Vences, 2011	Unambiguously diagnosable	Monophyletic (mtDNA / nDNA)	Supported by six of seven MSD, HW merging <i>M. arenicola</i> , <i>M. polleni</i> , and <i>M. stumpffi</i> into a single species.
<i>M. mouroundavae</i> (Grandidier, 1872)	Unambiguously diagnosable	Monophyletic (mtDNA / nDNA)	Supported by all seven MSD.
<i>M. stumpffi</i> (Boettger, 1882)	Unambiguously diagnosable	Monophyletic (mtDNA / nDNA)	Supported by six of the seven MSD, HW merging <i>M. arenicola</i> , <i>M. polleni</i> , and <i>M. stumpffi</i> into a single species.
<i>M. nanus</i> (Andreone and Greer, 2002)	Unambiguously distinguishable from most of the species (see below <i>M. macrolepis</i>) <i>Taxonomic comment:</i> Miralles and Vences (2013) treated <i>M. sp.</i> “baeus” provisionally as conspecific with <i>M. nanus</i> , pending molecular analysis of topotypic <i>M. nanus</i>	Monophyletic (mtDNA / nDNA)	Supported by all seven MSD.
<i>M. macrolepis</i> (Boulenger, 1888)	Unambiguously distinguishable from most of the species (see species delimitation) <i>Taxonomic comment:</i> Almost certainly closely related to <i>M. nanus</i> due to numerous morphological similarities, it seems to differ from the latter by several morphological characters (Andreone and Greer, 2002), leading us to consider both taxa as distinct pending more detailed investigations.	Not tested	Rare species so far not studied using molecular methods and therefore not included in Miralles and Vences (2013).
<i>M. polleni</i> (Grandidier, 1869)	Unambiguously distinguishable from almost all other species of <i>Madascincus</i> , but superficially very similar to <i>M. miafina</i> . Both species only differ by a single character, the number of ventral scale rows (65–73 in <i>M. miafina</i> and 74–78 in <i>M. polleni</i>) which is likely to become less diagnostic once a larger sampling will reveal the true extent of intraspecific variation of this character <i>Taxonomic comment:</i> Referred to as <i>polleni</i> -S clade in Miralles and Vences (2013). According to type examinations and/or type localities, and in application of the principles of nomenclature (ICZN 1999), the name <i>M. polleni</i> , type locality (TL) “Morondava”, is here restricted to the <i>polleni</i> -S clade. <i>Scelotes intermedius</i> Boettger, 1913, type locality “Majunga” = Mahajanga, has been considered as a subjective junior synonym of <i>M. polleni</i> by Miralles and Vences (2013).	Monophyletic (mtDNA / nDNA), not closely related to <i>M. miafina</i> despite very similar phenotypes	Supported by six of the seven MSD, HW merging <i>M. arenicola</i> , <i>M. polleni</i> , and <i>M. stumpffi</i> into a single species.
<i>M. miafina</i> sp. n.	Unambiguously distinguishable from almost all other species of <i>Madascincus</i> , but superficially very similar to <i>M. polleni</i> (see above) <i>Taxonomic comment:</i> referred as <i>polleni</i> -N clade in Miralles and Vences (2013). Herein described as a new species.	Monophyletic (mtDNA / nDNA).	Supported by all seven MSD.
<i>M. igneocaudatus</i> (Grandidier, 1867)	Unambiguously diagnosable <i>Taxonomic comment:</i> Referred to as <i>igneocaudatus</i> -S clade in Miralles and Vences (2013). The type material fits morphologically very well with the specimens sequenced from this clade, and its type locality is unambiguously nested within its distribution area (see Fig. 5). According to type examinations and/or type localities, and in application of the principles of nomenclature (ICZN 1999), the name <i>M. igneocaudatus</i> , type locality “Tuléar” (= Toliara), is here restricted to the <i>igneocaudatus</i> -S clade.	Monophyletic (mtDNA / nDNA).	Supported by all seven MSD.
<i>M. pyrusus</i> sp. n.	Unambiguously diagnosable <i>Taxonomic comment:</i> Referred as <i>igneocaudatus</i> -C clade in Miralles and Vences (2013). Herein described as a new species.	Monophyletic (mtDNA / nDNA)	Supported by all seven MSD.
<i>M. melanopleura</i> (Günther, 1877)	Species of the <i>M. melanopleura</i> complex are well diagnosable from all the other species of <i>Madascincus</i> , but the three species of this complex are apparently not diagnosable by their morphology alone (see. <i>M. ankodabensis</i> and <i>M. minutus</i>) <i>Taxonomic comment:</i> Referred as <i>melanopleura</i> -C clade in Miralles and Vences (2013). According to type examinations and/or type localities, and in application of the principles of nomenclature (ICZN 1999), the name <i>Madascincus melanopleura</i> , type locality “Anzahamaru” (close to Mahanoro in the central eastern lowlands), is here restricted to the <i>melanopleura</i> -C clade (including <i>Sepsina vulsini</i> Barbour, 1918, type locality “eastern forest between Tamatave and Tananarive”, as a junior synonym). This type locality is indeed nested very centrally within the distribution area of the C-clade, making it very probable that the type specimen of <i>Madascincus melanopleura</i> is a member of this clade predominantly present in that central region (cf. Fig. 5). It should nevertheless be highlighted that due to the presence of one outlier sample in the Miralles and Vences (2015) data set, which unambiguously clustered with the northern clade but geographically is nested within the central clade distribution area (in An’Ala, a locality relatively close to the type locality of <i>M. melanopleura</i>), we cannot totally discard the possible – past or present – sympatric occurrence of <i>M. minutus</i> at Anzahamaru.	Monophyletic (mtDNA / nDNA)	Supported by five of the seven MSD, MTMC and WP merging all the species of the <i>M. melanopleura</i> species complex (namely <i>M. melanopleura</i> , <i>M. ankodabensis</i> and <i>M. minutus</i>) into a single species. Miralles and Vences (2013) have nevertheless found evidence supporting the distinctiveness of these three taxa (e.g., absence of gene flow between <i>M. melanopleura</i> and <i>M. minutus</i> despite their sympatric occurrence in An’Ala).

Taxa	Morphological diagnosability	Monophyly	Species delimitation methods
<i>M. ankodabensis</i> (Angel, 1930)	Species of the <i>M. melanopleura</i> complex are well diagnosable from all the other species of <i>Madascincus</i> , but the three species of this complex are apparently not diagnosable by their morphology alone (see. <i>M. melanopleura</i> and <i>M. minutus</i>)	Monophyletic (mtDNA / nDNA)	Supported by five of the seven MSD (see discussion on <i>M. melanopleura</i> above).
	<i>Taxonomic comment:</i> Referred as <i>melanopleura</i> -S clade in Miralles and Vences (2013). In application of the principles of nomenclature (ICZN 1999), the name <i>Madascincus ankodabensis</i> , type locality “Ankodabe”, is here applied to the <i>melanopleura</i> -S clade based on the fact that (1) the morphology of the type material fits remarkably well with the sequenced specimens of this clade and (2) the S clade is the most southern one put into evidence by Miralles and Vences (2013) and therefore the only one fitting with this type locality (see Fig 5).		
<i>M. minutus</i> (Raxworthy and Nussbaum, 1993)	Species of the <i>M. melanopleura</i> complex are well diagnosable from all the other species of <i>Madascincus</i> , but the three species of this complex are apparently not diagnosable by their morphology alone (see. <i>M. ankodabensis</i> and <i>M. melanopleura</i>)	Monophyletic (mtDNA / nDNA)	Supported by five of the seven MSD (see discussion on <i>M. melanopleura</i> above). In contrast with other species of the <i>M. melanopleura</i> species complex, the taxonomy of the <i>melanopleura</i> -N clade remains insufficiently understood. The ITAX approach suggested the existence of at least two genetically distinct but morphologically cryptic species within this group, whereas other approaches suggested up to six cryptic species, all occurring in allopatry but partly in close spatial proximity. A more complete sampling (both in terms of number of localities and number of samples per population) is required to investigate more into detail the taxonomy of this species complex.
	<i>Taxonomic comment:</i> Referred to as <i>melanopleura</i> -N clade in Miralles and Vences (2013). Due to sampling gaps, Miralles and Vences (2013) were unable to assign the name <i>M. minutus</i> (Raxworthy and Nussbaum, 1993), type locality “Manongarivo”, to one of these identified clades and therefore proposed conservatively to consider the whole <i>melanopleura</i> -N group as a single species <i>M. minutus</i> , pending a more detailed taxonomic revision.		

apparently restricted to the western and northern regions of Madagascar, and a diversification concentrated in the northern tip of the island (Fig. 5). All species in this clade inhabit leaf-litter of dry deciduous forests or shrubs, or in more open and sandy areas. On the contrary, (2) the *M. melanopleura* clade, which includes at least three species morphologically extremely similar, is mostly restricted to the eastern part of Madagascar, with species essentially inhabiting rainforest leaf litter.

In contrast, the *M. igneocaudatus* clade does not present any obvious shared biogeographic characteristic. *Madascincus igneocaudatus* is indeed endemic to the dry lowlands of the south-western and southern coasts of Madagascar, whereas *M. pyrurus* is a montane species only known from the central highlands of Madagascar. The ranges of *M. nanus* and of *M. mouroundavae* are less accurately understood, and more studies will be necessary to better elucidate the systematics and the biogeography of these taxa. Nevertheless, both groups appear to be restricted to the rainforests and transitional forests in the northern half of Madagascar. The holotype of *M. mouroundavae* has been described by Grandidier (1872) from Morondava, on the central west coast of Madagascar, but no other specimens of this species have ever been collected subsequently in this area, suggesting that its type locality might be erroneous. Taking into account these data and the internal topology of the phylogenetic tree (Fig. 1), we hypothesize that the genus *Madascincus* has likely originated in the humid central-eastern part of Madagascar. Subsequently, diversification led to species colonizing the dry lowlands of the western, southern and northern parts of the island, where the other quadrupedal Malagasy scincine

skinks (genus *Amphiglossus* sensu stricto, and two new genera which will be described by Erens et al. in press) are absent or significantly under-represented (Glaw and Vences 2007). More specifically, the northern part of the island represents a center of diversification for the *M. polleni* species complex (sensu Miralles et al. 2011a) with a diversification trend oriented toward the north. Similar biogeographical patterns are also observed in the sister lineage of *Madascincus* (genus *Paracontias*, Miralles et al. 2016) and in several other squamates (Brown et al. 2014, 2016).

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References

- Andreone F, Greer AE (2002) Malagasy scincid lizards: descriptions of nine new species, with notes on the morphology, reproduction and taxonomy of some previously described species (Reptilia, Squamata: Scincidae). *Journal of Zoology* 258: 139–181. doi: 10.1017/S0952836902001280
- Blanc CP, Blanc F (1967) Observations biologiques (adultes, oeufs, jeunes) sur quelques Sauriens du Mont Bity. *Annales Université Madagascar (Sciences)* 5: 67–74.
- Brown JL, Cameron A, Yoder AD, Vences M (2014) A necessarily complex model to explain the biogeography of the amphibians and reptiles of Madagascar. *Nature Communications* 5: e5046. doi: 10.1038/ncomms6046
- Brown JL, Sillero N, Glaw F, Bora P, Vieites DR, Vences M (2016) Spatial biodiversity patterns of Madagascar's amphibians and reptiles. *PLoS ONE* 11: e0144076. doi: 10.1371/journal.pone.0144076
- Brygoo ER (1981) Systématique des lézards scincidés de la région malgache. IX. Nouvelles unités taxinomiques pour les *Scelotes* s. l. *Bulletin du Muséum national d'Histoire naturelle. Section A*, 3(4): 1193–1204.
- Brygoo ER (1984) Systématique des lézards scincidés de la région malgache. XV. *Gongylus igneocaudatus* A. Grandidier, 1867, et *Scelotes intermedius* Boettger, 1913. Les *Amphiglossus* du groupe *igneocaudatus*. *Bulletin du Muséum national d'Histoire naturelle. Section A*, 6(3): 779–789.
- Clement M, Posada D, Crandall K (2000) TCS: a computer program to estimate gene genealogies. *Molecular Ecology* 9(10): 1657–1660. doi: 10.1046/j.1365-294x.2000.01020.x
- Crottini A, Dordel J, Köhler J, Glaw F, Schmitz A, Vences M (2009) A multilocus phylogeny of Malagasy scincid lizards elucidates the relationships of the fossorial genera *Androngo* and *Cryptoscincus*. *Molecular Phylogenetics and Evolution* 53: 345–350. doi: 10.1016/j.ympev.2009.05.024
- Dayrat B (2005) Toward integrative taxonomy. *Biological Journal of the Linnean Society* 85: 407–415. doi: 10.1111/j.1095-8312.2005.00503.x
- DeSalle R, Egan MG, Siddal M (2005) The unholy trinity: taxonomy, species delimitation and DNA barcoding. *Philosophical Transactions of the Royal Society B* 360: 1905–1916. doi: 10.1098/rstb.2005.1722
- Doyle J (1995) The irrelevance of allele tree topologies for species delimitation, and a non-topological alternative. *Systematic Botany* 20: 574–588. doi: 10.2307/2419811
- Erens J, Miralles A, Glaw F, Chatrou L, Vences M (in press) Extended molecular phylogenetics and revised systematics of Malagasy scincine lizards. *Molecular Phylogenetic and Evolution*.
- Flot J-F, Couloux A, Tillier S (2010) Haplowebs as a graphical tool for delimiting species: a revival of Doyle's "field for recombination" approach and its application to the coral genus *Pocillopora* in Clipperton. *BMC Evolutionary Biology* 10: e372. doi: 10.1186/1471-2148-10-372
- Fontaneto D, Herniou E, Boschetti C, Caprioli M, Melone G, Ricci C, Barraclough TG (2007) Independently evolving species in asexual bdelloid rotifers. *PLoS Biology* 5: e87. doi: 10.1371/journal.pbio.0050087
- Glaw F, Vences M (2007) A field guide to the amphibians and reptiles of Madagascar. Third edition. Vences & Glaw Verlag, Cologne, 496 pp.
- Grandidier MA (1872) Description de quelques Reptiles nouveaux, découverts à Madagascar en 1870. *Annales des Sciences naturelles (Zoologie)* (5) 15 art. 20: 6–11.
- ICZN (1999) International Code of Zoological Nomenclature. The International Trust for Zoological Nomenclature, London.
- Kaiser H, Crother BI, Kelly CMR, Luiselli L, O'Shea M, Ota H, Passos P, Schleich WD, Wüster W (2013) Best practices: in the 21st Century, taxonomic decisions in herpetology are acceptable only when supported by a body of evidence and published via peer-review. *Herpetological Review* 44: 8–23.
- Miralles A (2006) A new species of *Mabuya* (Reptilia, Squamata, Scincidae) from the isolated Caribbean island of San Andrés, with a new interpretation of nuchal scales, character of systematic importance. *Herpetological Journal* 16: 1–7.
- Miralles A, Hipsley CA, Erens J, Gehara M, Rakotoarison A, Glaw F, Müller J, Vences M (2015) Distinct patterns of desynchronized limb regression in Malagasy scincine lizards (Squamata, Scincidae). *PLoS ONE* 10(6): e0126074. doi:10.1371/journal.pone.0126074
- Miralles A, Jono T, Mori A, Gandola R, Erens J, Köhler J, Glaw F, Vences M (2016) A new perspective on the reduction of cephalic scales in fossorial legless skinks (Squamata, Scincidae). *Zoologica Scripta* 45: 380–393. doi: 10.1111/zsc.12164
- Miralles A, Köhler J, Glaw F, Vences M (2011a) A molecular phylogeny of the "*Madascincus polleni* species complex", with description of a new species of scincid lizard from the coastal dune area of northern Madagascar. *Zootaxa* 2876: 1–16.
- Miralles A, Köhler J, Vieites DR, Glaw F, Vences M (2011c) Developing hypotheses on rostral shield evolution in head-first digging squamates from a molecular phylogeny and new species of the genus *Paracontias* (Scincidae). *Organisms, Diversity and Evolution* 11: 135–150. doi: 10.1007/s13127-011-0042-6
- Miralles A, Raselimanana AP, Rakotomalala D, Vences M, Vieites DR (2011b) A new large and colorful skink of the genus *Amphiglossus* from Madagascar revealed by morphology and multilocus molecular study. *Zootaxa* 2918: 47–67.
- Miralles A, Vences M (2013) New metrics for comparison of taxonomies reveal striking discrepancies among species delimitation methods in *Madascincus* lizards. *PLoS ONE* 8(7): e68242. doi: 10.1371/journal.pone.0068242
- Monaghan MT, Wild R, Elliot M, Fujisawa T, Balke M, Inward DJ, Lees DC, Ranaivosolo R, Eggleton P, Barraclough TG, Vogler AP (2009) Accelerated species inventory on Madagascar using coalescent-based models of species delineation. *Systematic Biology* 58: 298–311. doi: 10.1093/sysbio/syp027
- Padial JM, Miralles A, De la Riva I, Vences M (2010) The integrative future of taxonomy. *Frontiers in Zoology* 7: 16. doi: 10.1186/1742-9994-7-16
- Pianka ER, Vitt LJ (2003) *Lizards: Windows to the Evolution of Diversity*. University of California Press, Berkeley, 348 pp.
- Pons J, Barraclough TG, Gomez-Zurita J, Cardoso A, Duran DP, Hazell S, Kamoun S, Sumlin WD, Vogler A (2006) Sequence-based species delimitation for the DNA taxonomy of undescribed insects. *Systematic Biology* 55: 595–609. doi: 10.1080/10635150600852011
- Rakotoarison A, Erens J, Ratsoaivina FM, Vences M (2015) Amphibian and reptile records from around the Betsiboka delta area in North-Western Madagascar. *Herpetology Notes* 8: 535–543.
- Rannala B, Yang Z (2003) Bayes estimation of species divergence times and ancestral population sizes using DNA sequences from multiple loci. *Genetics* 164: 1645–1656.
- Riedel A, Sagata K, Suhardjono YR, Tänzler R, Balke M (2013) Integrative taxonomy on the fast track - towards more sustaina-

- bility in biodiversity research. *Frontiers in Zoology* 10: e15. doi: 10.1186/1742-9994-10-15
- Schmitz A, Brandley MC, Mausfeld P, Vences M, Glaw F, Nussbaum RA, Reeder TW (2005) Opening the black box: phylogenetics and morphological evolution of the Malagasy fossorial lizards of the subfamily “Scincinae”. *Molecular Phylogenetics and Evolution* 34: 118–133. doi: 10.1016/j.ympev.2004.08.016
- Tamura K, Stecher G, Peterson D, Filipinski A, Kumar S (2013) MEGA6: Molecular Evolutionary Genetics Analysis Version 6.0. *Molecular Biology and Evolution* 30: 2725–2729. doi: 10.1093/molbev/mst197
- Weisrock DW, Rasoloarison RM, Fiorentino I, Ralison JM, Goodman SM, Kappeler PM, Yoder AD (2010) Delimiting species without nuclear monophyly in Madagascar’s mouse lemurs. *PLoS ONE* 5: e9883. doi: 10.1371/journal.pone.0009883
- Whiting AS, Sites JW Jr, Bauer AM (2004) Molecular phylogenetics of Malagasy skinks (Squamata: Scincidae). *African Journal of Herpetology* 53(2): 135–146. doi: 10.1080/21564574.2004.9635506
- Wiens JJ, Penkrot TA (2002) Delimiting species using DNA and morphological variation and discordant species limits in spiny lizards (*Sceloporus*). *Systematic Biology* 51: 69–91. doi: 10.1080/106351-502753475880
- Yang Z, Rannala B (2010) Bayesian species delimitation using multilocus sequence data. *Proceedings of the National Academy of Sciences USA* 107: 9264–9269. doi: 10.1073/pnas.0913022107

Supplementary material 1

List of specimens examined morphologically

Authors: Aurélien Miralles, Jörn Köhler, Frank Glaw, Miguel Vences

Data type: Adobe PDF file

Explanation note: Specimens examined are listed including collection number, locality and collector information.

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