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A NEW SPECIES OF *MABUYA* FITZINGER (SQUAMATA:
SCINCIDAE: LYGOSOMINAE) FROM NORTHERN
MADAGASCAR

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ABSTRACT.—A new species of the lygosomine, scincid genus *Mabuya* Fitzinger is described from a small area of extreme northern Madagascar. The new species, *Mabuya tavaratra*, is tentatively assigned to the *aureopunctata*-Group of Madagascan mabuyas, based on the rectangular shape of the subocular scale. The latter character distinguishes it from the three species (*M. elegans*, *M. gravenhorstii*, *M. madagascariensis*) of the *elegans*-Group, all of which have a trapezoidal subocular scale. *Mabuya tavaratra* is most similar to another northern species, *M. lavarambo*, but differs from it in having a shorter tail, a larger transparent disk in the lower eyelid, more scale rows around the body, and generally shorter toes and fingers with fewer subdigital lamellae. These two species also differ slightly in coloration. *Mabuya tavaratra* occurs in both rainforest and forests of drier aspect, ranging in elevation from 50 to 900 m. It requires relatively open habitats and may enter rainforest only along corridors of disturbance. *Mabuya tavaratra* is known from five isolated localities (Analamera, Ankarana, Daraina, Montagne d'Ambre, Montagne des Français), three of which are reserves, and it is relatively common at three of these sites where it occurs in somewhat degraded habitats as well as in undisturbed areas. Therefore, although it is restricted to a small geographic area, it does not appear to be in immediate danger of extermination.

Key words: Reptilia, Squamata, Scincidae, Lygosominae, *Mabuya*, new species, taxonomy, Madagascar

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INTRODUCTION

Recent field work in Madagascar yielded several new species of *Mabuya* found in a variety of habitats over a broad range of elevations throughout the island. Four species were described since 1994, and an additional four species remain to be described, bringing the total number of known species of *Mabuya* endemic to Madagascar to 14.

A non-endemic species, *Mabuya maculilabris*, occurs on Nosy Tanikely, a near-shore island in northwestern Madagascar (Nussbaum and Raxworthy, unpublished). *M. maculilabris* occurs throughout much of Africa and adjacent islands. The form on Nosy Tanikely is identical to the subspecific form described from the Comoro Islands, and it seems likely that it was introduced in recent times to Nosy Tanikely via the frequent boat traffic between the nearby Comoros and this region of Madagascar.

Madagascan mabuyas are tentatively assigned to two species-groups (Nussbaum and Raxworthy, 1994, 1995). The *elegans*-Group, consisting of *M. elegans*, *M. gravenhorstii*, and *M. madagascariensis*, has remained stable since the Madagascan mabuyas were reviewed by Brygoo (1981, 1983), but the *aureopunctata*-Group has proven to be far more speciose than previously believed. The latter group formerly comprised three species (*M. aureopunctata*, *M. betsileana*, *M. boettgeri*), to which Nussbaum and Raxworthy (1994, 1995, 1998a-b) added four new forms (*M. vato*, *M. dumasi*, *M. lavarambo*, *M. nancycoutuae*). Four undescribed species are also provisionally assignable to the *aureopunctata*-Group. Three of these are restricted to the more xeric western and southern environments of Madagascar. The fourth, which we describe in this paper, occurs in the more mesic lowland forests of extreme northern Madagascar. It is the obvious sister-species of *M. lavarambo*, another northern species, which is restricted to the lowland rainforests on the satellite island of Nosy Be.

METHODS AND MATERIALS

Field survey methods are described in Raxworthy and Nussbaum (1994). Specimens were euthanized by injection with chlorotone, fixed in 10% buffered formalin, soaked in water to remove the formalin, and stored in a final solution of 75% ethanol. Snout-vent and tail lengths were measured with a ruler to the nearest 1.0 mm; other measurements were done with dial calipers and recorded to the nearest 0.1 mm. Adult versus juvenile condition was determined by direct examination of the gonads. Specimens are identified by catalog numbers of the Museum of Zoology, The University of Michigan (UMMZ) and by field numbers (RAN).

Mabuya tavaratra n. sp.

(Fig. 1)

Holotype.-UMMZ 208950 (RAN 38787), mature female, collected 13 January 1992, at Betsimanefa, along trail to Ankorefo, Montagne d'Ambre, 12° 28.0' S, 49° 08.5' E, 550 m elevation, Antsiranana Fivondronana, Antsiranana Province, Madagascar, by Achille Raselimanana.

Paratypes(30).-UMMZ 208946 (RAN 38288), 30 November 1991, between Station des Roussettes and Joffreville, Montagne d'Ambre, 900 m,

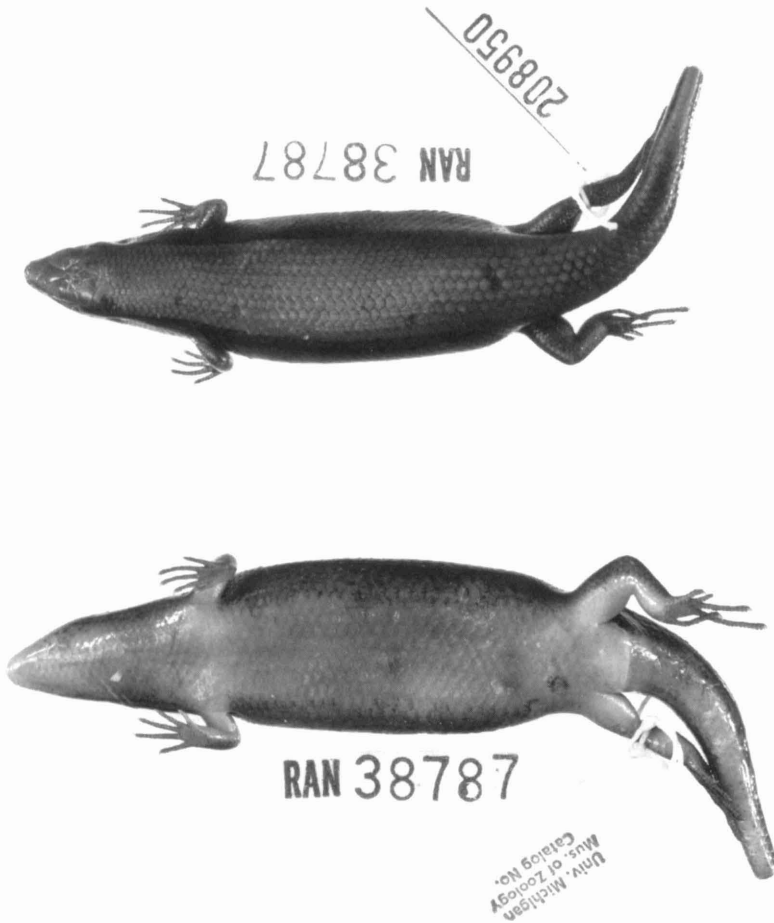


Fig.1. (A) dorsal and (B) ventral views of the holotype (UMMZ 208950) of *Mabuya tavaratra* n. sp.

Antsiranana Fivondronana, Antsiranana Province. UMMZ 208951 (RAN 38852), 22 January 1992, Montagne des Français, 50 m elevation, Antsiranana Fivondronana, Antsiranana Province. UMMZ 208952 (RAN 38876), 30 January 1992, trail to Lac Vert, Ankarana Special Reserve, 100 m elevation, Ambilobe Fivondronana, Antsiranana Province. UMMZ 209011 (RAN 38954), 30 January 1992, Ankarana Special Reserve, 100 m elevation, Ambilobe Fivondronana, Antsiranana Province. UMMZ 221316 (RAN 54794), UMMZ 221317 (RAN 54796), UMMZ 221318 (RAN 54800), 17 April 1996; UMMZ 221319 (RAN 54844), UMMZ 221320 (RAN 54845), 18 April 1996; UMMZ 221321 (RAN 54878), UMMZ 221322 (RAN 54880), UMMZ 221323 (RAN 54881), 20 April 1996, at Ampijoroana camp, Analamera Special Reserve, Antsiranana Fivondronana, Antsiranana Province. UMMZ 221324 (RAN 54941), UMMZ 221325 (RAN 54942), 22 April 1996, Ampongy forest, Analamera Special Reserve, Antsiranana Fivondronana, Antsiranana Province. UMMZ 221326 (RAN 54997), 26 April 1996, Lac Vert, 100 m elevation, Ankarana Special Reserve, Ambilobe Fivondronana, Antsiranana Province. UMMZ 221327 (RAN 54999), UMMZ 221328 (RAN 55283), 26 April 1996, at Campement des Anglais, Ankarana Special Reserve, Ambilobe Fivondronana, Antsiranana Province. UMMZ 221329 (RAN 55200), UMMZ 221330 (RAN 55202), UMMZ 221331 (RAN 55268), UMMZ 221332 (RAN 55283), 1-3 May 1996, near Andranovelona village, Daraina Forest, Iharana Fivondronana, Antsiranana province. UMMZ 221333 (RAN 55343), 25 April 1996, near Barrière village, about 800 m elevation, Montagne d'Ambre, Antsiranana Fivondronana, Antsiranana Province. UMMZ 221334 (RAN 55365), UMMZ 221335 (RAN 55366), UMMZ 221336 (RAN 55367), UMMZ 221337 (RAN 55371), UMMZ 221338 (RAN 55372), UMMZ 221339 (RAN 55373); UMMZ 221340 (RAN 55374), UMMZ 221341 (RAN 55375), 10 May 1996, Montagne des Français, 50 m elevation, Antsiranana Fivondronana, Antsiranana province.

Other specimens.-None.

Identification.-A *Mabuya* with a large, undivided, transparent disk on the lower eyelid, the length of which is twice the length of the field of opaque palpebral scales in front of it on the lower eyelid; subocular (5th supralabial) rectangular; scales of soles aspinous; subdigital scales acarinate; 34-38 scale rows around midbody; 50-58 ventral scales; head, neck, body, and tail with a broad, nearly uniform brown, dorsal band bordered dorsolaterally by very faint, light brown lines disappearing posteriorly at about midbody, below which on each side is a wide, dark brown, lateral band extending from nostril, through eye, ending above hindlimb or fading out on base of tail; lateral dark band bordered below by a narrow, white line extending from supralabials, across ear opening, to groin;

ventrolateral coloration below lateral white line, light brown, fading to dirty white or cream ventral coloration.

Description of Holotype.-Specimen (Fig. 1) in good condition; tail partially regenerated and broken (tip missing); a small incision on left side of abdomen. Right ovary slightly anterior relative to left ovary; 3 yolked (yellowish) oocytes and 6 smaller (1.5 mm) unyolked (white) oocytes in right ovary; 2 yolked and 8 unyolked oocytes in left ovary; 2 yolked oocytes in left ovary measure 5.9 x 5.7 and 5.7 x 5.2 mm.

Body form stout; short-limbed; head relatively small, narrower than neck and body, sides converging to a rounded snout; body wider than high; forelimb laid anteriorly barely reaches past eye; hindlimb laid forward reaches to midbody; appressed limbs fail to meet at midbody by about 5 mm. Tail rounded at base, tapering sharply to broken end. Measurements and counts are given in Tables 1 and 2.

Supranasals barely separated, in contact with anterior loreal; frontonasal in contact with rostral and frontal; nostril above suture between rostral and 1st supralabial; small postnasal above 1st supralabial, contacting neither rostral nor 2nd supralabial; anterior loreal rectangular, taller than long, placed above 1st and 2nd supralabials; posterior loreal longer than tall, positioned above 2nd and 3rd supralabials; 4 supralabials in front of the rectangular subocular; 4 supraoculars, 2nd largest; frontal contacts 2nd and 3rd supraoculars; 2 frontoparietals, each contacting respective supraoculars 3 and 4; 2 preoculars superimposed after 2nd loreal, larger above 3rd supralabial, smaller contacts larger and 1st superciliary; interparietal subdiamond-shaped; parietals in contact behind interparietal; 2 carinate nuchals; ear opening small, diameter slightly less than half length of eye, bearing 2 small lobules at anterior border; 11 right upper ciliaries, 12 left; 15 right lower ciliaries, 13, left; 4 lower ciliaries contact ocular disk; window in lower eyelid large, 1.7 mm long by 1.0 mm tall, about twice as long as field of palpebral scales in front of it; postmental adjacent to 1st and half of 2nd infralabials; 2 pairs of gulars, 1st pair in contact along medioventral axis, 2nd pair separated by 1st ventral scale; dorsal scales of neck, body, and tail cycloid, imbricate, and carinate; dorsal and lateral scales of neck strongly carinate; scales of upper limbs carinate; upper scales of hands, fingers, and toes acarinate; upper scales of feet carinate; subdigital scales acarinate; palms and soles aspinous.

Coloration after 3 years and 8 months in alcohol as follows. Dorsal surface of head, body, and tail brown, separated from lateral dark brown band by light brown dorsolateral line that fades and disappears at midbody. Lateral dark brown band $1/2 + 3 + 1/2$ scales wide, bordered below by white line $1/2 + 1/2$ scales wide, begins behind nostril, passes across ear, above insertion of forelimb, ending at groin. Ventrolateral body be-

Table 1. Measurements (mm) of holotype and paratypes of *Mabuya tavaratra* n. sp. from Montagne d'Ambre, Ankarana, and Daraina.

	Montagne d'Ambre			Ankarana			Daraina	
	Holotype		221333	Paratypes				
	UMMZ	208950		208946	221326	221328	221329	221330
Sex	female	female	female	male	female	male	male	male
Maturity	mature	mature	mature	mature	juv	mature	mature	mature
Snout-vent length	62	55	58	55	34	57	48	54
Tail length	30*	53*	96	86*	54	18*	85	91
Tail width ¹	7.8	7.2	7.1	8.0	4.0	8.2	6.4	7.9
Tail depth ¹	8.0	5.4	6.1	7.4	3.7	7.5	6.3	7.4
Head length ²	11.5	10.2	10.7	10.7	8.0	10.7	10.3	10.4
Head width	8.4	7.0	7.7	7.8	5.6	8.9	7.5	7.8
Head depth	6.9	5.5	6.2	6.7	4.1	6.3	5.6	6.8
Snout length	5.3	4.3	4.6	4.8	3.4	4.8	4.5	4.5
Internarial distance	2.4	2.0	2.3	2.3	1.9	2.4	2.3	2.3
Interocular distance	5.7	5.0	5.3	5.4	3.9	5.8	5.3	5.6
Orbit length	3.1	2.6	2.9	2.9	2.5	3.2	3.4	2.9
Eye-naris distance	3.4	2.7	2.7	3.0	2.2	3.3	2.9	2.8
Eye-ear distance	4.0	3.7	3.7	3.8	2.8	3.9	2.9	3.7
Ear opening (vert.)	1.0	0.8	1.4	1.2	0.8	0.9	1.1	1.1
Ear opening (horiz.)	0.9	0.8	0.9	0.9	0.7	0.8	0.9	0.9
Frontal length	3.4	3.2	3.3	3.4	2.3	3.7	3.1	3.4
Interparietal length	2.6	2.5	2.2	2.4	1.7	2.2	2.3	2.3
Axilla-groin length	34	30	34	28	17	30	25	29
Forelimb length	14	14	15	14	9	15	14	14
Hindlimb length	23	21	22	20	14	22	21	22
Finger II length	3.3	2.7	3.0	2.7	2.0	3.1	2.7	2.5
Finger III length	3.9	3.4	3.5	3.4	2.4	4.0	3.0	3.4
Finger IV length	4.4	3.8	3.7	3.8	2.4	4.2	3.5	3.4
Toe III length	5.6	5.7	4.7	4.7	3.5	5.2	4.7	5.1
Toe IV length	7.5	7.0	6.7	6.3	4.5	7.7	6.7	6.4
Toe V length	5.0	3.9	3.4	3.8	2.6	4.8	4.2	4.1

* tail incomplete (part missing or partly regenerated)

¹ at base² snout-ear distance

Table 2. Meristic variation in holotype and paratypes of *Mabuya tavaratra* n. sp. from Montagne d'Ambre, Ankarana, and Daraina.

Characters	Montagne d'Ambre				Ankarana			Daraina	
	UMMZ	Holotype			Paratypes				
		208950	208946	221333	221326	221328	221329	221330	221331
Frontoparietals	2	2	2	2	2	2	2	2	2
Supraocular scales (L,R)	4-4	4-4	4-4	4-4	4-4	4-4	4-4	4-4	4-4
Superciliary scales (L,R)	4-4	4-3	4-4	4-4	4-4	4-4	4-4	4-4	4-4
Supralabials (L,R)*	4-4	4-4	4-4	4-4	4-4	4-4	4-4	4-4	4-4
Infralabials (L,R)	6-6	6-6	6-6	6-6	6-6	6-6	6-6	7-6	6-6
Scale rows around midbody	35	36	34	35	—	36	37	36	36
Ventral scales**	57	58	54	57	56	54	54	55	55
Number of keels on middorsal scales	6(7)	5	6	6(8)	3	6(7)	5(6)	6	6
Sdm II (L,R)#	10-10	9-9	9-10	9-10	9-9	9-10	10-9	9-9	9-9
Sdm III (L,R)	13-13	12-11	11-11	13-13	10-9	12-12	11-11	11-12	11-12
Sdm IV (L,R)	14-14	11-11	13-13	13-13	11-9	13-11	13-12	12-11	12-11
Sdm V (L,R)	8-7	7-7	8-8	8-7	8-8	8-7	8-8	7-7	7-7
Sdp I (L,R)##	7-7	-5	7-8	6-7	6-	7-7	8-7	7-7	7-7
Sdp II (L,R)	-11	-9	11-12	10-11	10-	12-11	12-11	10-12	10-12
Sdp III (L,R)	15-15	-14	14-15	13-14	12-	14-14	15-14	14-12	14-12
Sdp IV (L,R)	18-18	-17	18-18	16-16	15-	16-16	16-17	-17	-17
Sdp V (L,R)	12-13	-10	12-11	11-11	10-	12-11	11-11	10-10	10-10

* Supralabial counts include only those anterior to the subocular scale.

** Ventral scales counted along a midventral line between the postmental scales and the cloaca.

Subdigital scales of the manus (Sdm) on fingers II-V, left and right.

Subdigital scales of the pes (Sdp) on toes I-V, left and right; missing data results from missing toes or entire limb.

low white line light brown fading to white ventral coloration. Upper surfaces of limbs brown, lower surfaces white. Supralabials white with irregular black spotting. Upper and lower ciliaries uniform brown, not differentiated in color from surrounding scales. Borders of throat and lower surface of tail with brown spots or streaks, faint dark band across throat, otherwise ventral surfaces of head, neck and tail white.

Variation.—Aspects of meristic and morphometric variation among paratypes are summarized in Tables 3-7. In general, geographic, sexual, and ontogenetic variation in morphometric characters and coloration is slight. The holotype, a mature female, is more robust than most of the paratypes.

Mature individuals range in size from 48 to 62 mm SVL, whereas available juveniles are 23 to 37 mm SVL. The size (SVL) ranges of adult males ($n = 9$) and adult females ($n = 6$) are 48-59 mm and 53-62 mm, respectively. Although the largest individual is a female, the difference in size between the sexes is small and not significant with available sample sizes. Geographic variation in size is also not evident. There is no variation associated with ontogeny, sex, and geography in the length of the tail. Individually, the range of the ratio of tail length to snout-vent length for 11 individuals with intact tails is 1.35 to 1.83. The shape of the ear opening varies noticeably from circular to vertically oval, but this variation depends neither on sex nor locality. All specimens except three paratypes (from three localities) have 4-4 superciliary scales: one has 4-3, one 3-4, and another 4-5. The two interparietals are partially fused in one paratype from Montagne des Français, but otherwise there is little noteworthy variation in configuration of head scales. The number of scale rows ranges from 34 to 38 with no evident geographic and sexual variation. Ventral scale rows vary from 50 to 58 with no geographic component, but larger samples may show that females have more ventral scale rows than males. There is neither geographic nor sexual variation in the number of subdigital lamellae, and individual variation is minimal.

Many of the paratypes differ in one aspect of coloration from the holotype. The latter has a uniformly colored, brown middorsal band whereas a majority of paratypes has a few bicolored (black and white) scales on the dorsum, which are always arranged in three or five longitudinal rows. The intensity of these small bicolored spots varies individually, and in one individual from Ankarana, the five rows of spots are longer, reaching posteriorly to the tail. The number of rows of middorsal spots depends on the presence or absence of the two lateral-most rows of spots, and this variation depends neither on population nor sex. One paratype from Montagne d'Ambre has small, black spots on its throat, which are lacking in other specimens. Ontogenetic variation in color is scarcely evident

Table 3. Measurements (mm) of paratypes of *Mabuya tavaratra* n. sp. from Montagne des Français.

	Montagne des Français							
	UMMZ	208951	221335	221336	221337	221338	221339	221340
Sex		female	female	male	male	male	male	female
Maturity		mature	juv	juv	juv	mature	mature	juv
Snout-vent length		53	34	37	35	52	52	36
Tail length		60*	46	63	63	78*	26*	66
Tail width ¹		6.7	3.7	3.5	4.3	7.1	7.6	4.5
Tail depth ¹		6.4	3.6	4.0	4.1	6.7	7.3	4.1
Head length ²		10.0	7.7	8.0	7.9	10.3	10.1	8.3
Head width		7.5	5.1	5.8	5.9	7.4	7.6	5.7
Head depth		6.5	4.2	4.1	4.6	6.2	6.6	4.3
Snout length		4.5	3.1	3.4	3.3	5.0	4.9	3.4
Internarial distance		2.1	1.5	1.7	1.7	2.1	2.2	1.7
Interocular distance		5.2	3.4	3.9	4.5	5.4	5.6	4.2
Orbit length		2.8	2.7	2.7	2.6	3.0	2.9	2.6
Eye-naris distance		2.8	2.0	2.2	2.3	2.9	3.1	2.3
Eye-ear distance		3.5	3.0	2.8	2.7	3.9	3.9	2.8
Ear opening (vert.)		1.2	0.7	1.0	1.0	1.1	1.1	0.7
Ear opening (horiz.)		0.6	0.8	0.8	0.8	0.8	1.0	0.7
Frontal length		3.3	2.3	2.1	2.4	3.4	3.5	2.4
Interparietal length		2.4	1.5	1.5	1.9	2.3	2.5	1.5
Axilla-groin length		27	17	19	17	26	27	19
Forelimb length		12	9	9	9	14	14	9
Hindlimb length		19	13	13	13	20	20	15
Finger II length		2.6	1.9	1.8	1.9	2.5	2.6	2.0
Finger III length		3.5	2.7	2.5	2.7	3.5	3.4	2.6
Finger IV length		3.8	2.7	2.7	3.0	3.7	3.5	2.9
Toe III length		5.3	3.8	3.1	3.6	4.5	4.5	4.0
Toe IV length		6.6	4.9	4.4	4.7	6.1	5.4	5.0
Toe V length		3.9	2.8	2.7	2.6	4.0	3.4	3.0

* tail incomplete (part missing or partly regenerated)

¹ at base

² snout-ear distance

with the exception that the bicolored scales on the middorsal band are weakly expressed or not visible in juveniles.

Etymology.-The name "*tavaratra*" ("tuh var' ut cha") is Malagasy for "northern race" and is used as a noun in apposition in reference to the "northern mabuya".

Habitat.-All specimens of *Mabuya tavaratra* were collected during the daytime, usually between 0800 and 1800 hr, and most were found on the ground. At Montagne d'Ambre, specimens were observed in open areas covered with low herbaceous plants, one next to a trail and another on the trail through rainforest on the lower slopes of Montagne d'Ambre near to the transition to dry forest. Specimens from Analamera, Ankarana,

Table 4. Meristic data of paratypes of *Mabuya tavaratra* n. sp. from Montagne des Français.

Characters	Montagne des Français						
	UMMZ 208951	221335	221335	221337	221338	221339	21340
Frontoparietals	2	2	2	2	2	2	2
Supraocular scales (L,R)	4-4	4-4	4-4	4-4	4-4	4-4	4-4
Superciliary scales (L,R)	4-4	4-4	4-4	4-4	4-4	4-4	3-4
Supralabials (L,R)*	4-4	4-4	4-4	4-4	4-4	4-4	4-4
Infralabials (L,R)	6-6	7-7	6-6	6-6	6-6	6-7	6-6
Scale rows around midbody	34	34	35	35	34	34	35
Ventral scales**	57	56	55	55	50	50	55
Number of keels on middorsal scales	5	3	3	3	5	5	4
Sdm II (L,R)#	9-8	10-11	9-9	9-10	9-9	9-9	10-10
Sdm III (L,R)	11-11	12-12	11-12	-11	11-11	10-12	12-12
Sdm IV (L,R)	13-12	14-14	13-12	-12	11-10	11-12	14-14
Sdm V (L,R)	7-7	7-8	8-8	7-7	7-7	7-7	7-7
Sdp I (L,R)##	7-7	7-7	7-7	7-7	6-7	7-6	7-7
Sdp II (L,R)	11-10	11-12	10-10	10-10	10-10	10-10	11-11
Sdp III (L,R)	12-12	14-14	14-14	13-12	12-12	13-13	13-14
Sdp IV (L,R)	16-16	18-16	17-17	17-16	16-16	16-17	18-18
Sdp V (L,R)	10-10	10-11	11-11	10-11	11-11	11-11	12-12

* Supralabial counts include only those anterior to the subocular scale.

** Ventral scales were counted along a midventral line between the postmental scales and the cloaca.

Subdigital scales of the manus (Sdm) on fingers II-V, left and right.

Subdigital scales of the pes (Sdp) on toes I-V, left and right; missing data results from missing toes or entire limb.

Daraina, and Montagne des Français were found mostly in forest-edge habitats. They seem to be rare or absent in grassland and highly degraded areas far from the forest edge. One exception is an individual from Montagne des Français that was found basking on the ground at 1300 hr in a dry, open, grassy area with scattered brush close to relict forest on rocky slopes. Another exception is a specimen from Ankarana Reserve that was taken in dry forest on tsingy rock at 1200 hr.

At all five sites, the vegetation is transitional between mid-altitude rainforest and dry, deciduous, western forest. At Montagne d'Ambre, the rainforest on the lower slopes becomes progressively drier at lower elevations and has a very different herpetofauna compared to the higher elevations (Raxworthy and Nussbaum, 1994). The canyon systems in the calcareous massifs of Montagne des Français and Ankarana harbor forests of a more mesic type than in the surrounding areas. Annual rainfall in the region of these "dry" northern forests is 1200-2400 mm, compared to 600-1200 mm for much of southern and western Madagascar (Donque,

Table 5. Measurements (mm) of paratypes of *Mabuya tavaratra* n. sp. from Analamera.

		Analamera								
		UMMZ	221316	221317	221318	221319	221320	221321	221324	221325
Sex		male	male	male	male	female	female	male	male	
Maturity		mature	juv	juv	juv	mature	mature	mature	mature	
Snout-vent length		54	37	32	37	59	55	51	59	
Tail length		18*	67	55	56*	61*	19*	85	84*	
Tail width ¹		7.6	4.5	3.6	4.0	7.8	8.0	7.5	7.6	
Tail depth ¹		7.6	4.5	3.7	4.2	7.0	7.3	6.8	7.5	
Head length ²		11.1	8.5	7.6	8.0	10.2	10.6	10.2	10.8	
Head width		8.6	6.1	5.2	6.0	7.6	7.9	7.6	8.2	
Head depth		7.1	4.7	4.1	4.3	6.0	5.8	6.1	6.7	
Snout length		5.0	3.6	3.0	3.1	5.0	4.7	4.7	4.8	
Internarial distance		2.4	1.8	1.6	1.7	2.3	3.6	2.3	2.3	
Interocular distance		5.2	4.3	3.8	4.3	5.6	5.3	5.2	5.9	
Orbit length		3.0	2.4	2.5	2.5	3.0	3.0	2.7	3.1	
Eye-naris distance		3.1	2.4	2.2	2.3	2.9	2.7	2.8	2.9	
Eye-ear distance		3.7	3.0	2.5	3.3	3.2	3.0	3.6	4.0	
Ear opening (vert.)		1.4	0.8	0.7	0.9	1.1	1.1	1.3	1.3	
Ear opening (horiz.)		1.1	0.7	0.7	0.7	0.6	0.9	0.8	0.9	
Frontal length		3.6	2.6	1.9	2.4	3.3	3.3	3.2	3.3	
Interparietal length		2.1	1.8	1.4	1.6	2.4	3.0	1.9	2.4	
Axilla-groin length		28	18	16	19	32	29	28	32	
Forelimb length		14	9	7	9	14	15	14	15	
Hindlimb length		22	15	12	15	20	21	20	22	
Finger II length		2.4	2.0	1.7	1.7	2.7	2.8	3.1	2.7	
Finger III length		3.5	3.0	2.3	2.6	3.6	3.6	3.8	3.4	
Finger IV length		3.6	3.2	2.4	2.8	3.7	4.0	4.0	4.0	
Toe III length		4.8	4.4	3.5	3.8	4.7	5.6	5.4	5.5	
Toe IV length		6.2	5.4	4.3	5.2	6.5	6.4	6.7	7.0	
Toe V length		4.1	3.5	2.4	3.0	3.5	4.4	4.0	4.1	

* tail incomplete (part missing or partly regenerated)

¹ at base

² snout-ear distance

1972) where the truly dry forests occur. It therefore appears that *Mabuya tavaratra* is adapted to the northern, relatively dry, low elevation rainforests, transitional forests, and open dry forests. The presence of this species at forest edge and in disturbed habitats at Montagne d'Ambre and Montagne des Français suggests it has some tolerance to habitat modification.

Distribution.-*Mabuya tavaratra* is known from only five isolated localities in northern Madagascar: Analamera, Ankarana, Daraina, Montagne d'Ambre, and Montagne des Français (Fig. 2).

Remarks.-*Mabuya tavaratra* is known to be sympatric only with *M. elegans*, a species with which it is not likely to be confused in the field because of obvious differences in coloration. *M. tavaratra* is superficially most simi-

Table 6. Meristic data of paratypes of *Mabuya tavaratra* n. sp. from Analamera.

Characters	UMMZ	Analamera							
		221316	221317	221318	221319	221320	221321	221324	221325
Frontoparietals		2	2	2	2	2	2	2	2
Supraocular scales (L,R)		4-4	4-4	4-4	4-4	4-4	4-4	4-4	4-4
Superciliary scales (L,R)		4-4	4-4	4-4	4-4	4-4	4-4	4-4	4-4
Supralabials (L,R)*		4-4	4-4	4-4	4-4	4-4	4-4	4-4	4-4
Infralabials (L,R)		6-6	6-6	6-6	6-6	6-6	7-6	7-7	6-6
Scale rows around midbody		36	36	36	36	36	38	35	36
Ventral scales**		53	53	53	54	56	58	53	55
Number of keels on middorsal scales		5	4	3	3	6	6	5	6
Sdm II (L,R)#		8-8	8-8	9-9	9-9	9-9	10-11	10-10	9-9
Sdm III (L,R)		10-10	11-11	11-11	11-11	11-11	12-12	12-14	11-11
Sdm IV (L,R)		12-12	11-11	11-11	12-12	13-13	14-13	13-14	14-14
Sdm V (L,R)		7-7	7-7	8-7	7-7	8-8	7-8	8-8	7-7
Sdp I (L,R)##		7-6	7-7	7-7	7-7	6-8	8-8	7-7	7-7
Sdp II (L,R)		11-10	10-10	11-10	11-11	10-11	10-11	11-11	10-12
Sdp III (L,R)		12-12	13-13	12-12	12-12	13-12	13-14	15-14	15-14
Sdp IV (L,R)		16-15	16-15	17-16	15-15	17-16	18-18	19-19	16-17
Sdp V (L,R)		12-11	10-11	10-10	11-10	11-11	11-11	11-11	10-10

* Supralabial counts include only those anterior to the subocular scale.

** Ventral scales were counted along a midventral line between the postmental scales and the cloaca.

Subdigital scales of the manus (Sdm) on fingers II-V, left and right.

Subdigital scales of the pes (Sdp) on toes I-V, left and right; missing data results from missing toes or entire limb.

Table 7. Morphometric (mm) and meristic variation among juvenile paratypes of *Mabuya tavaratra* n. sp.

	Analamera		Ankarana			Daraina	Mt. des Français	
	UMMZ	221322	221323	208952	209011	221327	221332	221334
Snout-vent length	29	37	27	23	29	30	33	30
Tail length	18*	39*	30*	30*	43	5*	18*	32*
Axilla-groin distance	15	17	12	10	15	15	17	15
Forelimb length	7	10	—	—	7	9	8	5
Hindlimb length	12	15	—	—	11	14	14	12
Frontoparietals	2	2	2	2	2	2	2	2
Supraocular scales (L,R)	4-4	4-4	4-4	4-4	4-4	4-4	4-4	4-4
Superciliary scales (L,R)	4-4	4-4	4-4	4-4	4-4	4-5	4-4	4-4
Supralabial scales (L,R)	4-4	4-4	4-4	4-4	4-4	4-4	4-4	4-4
Infralabial scales (L,R)	7-7	6-6	7-7	6-6	7-6	7-7	6-6	7-7
Scale rows around body	36	35	—	37	34	37	34	34
Ventral scale rows	51	53	—	—	52	—	52	54
Number of keels on middorsal scales	3	5	3	3	3	3	3	3

* Regenerated tail.

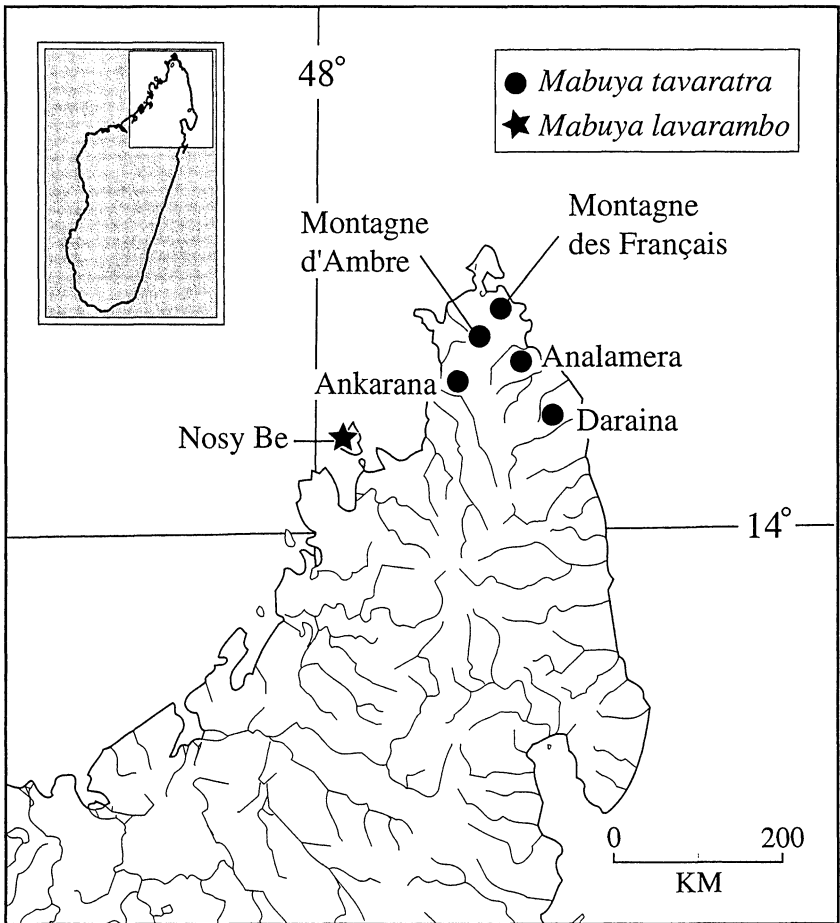


Fig. 2. Distribution of *Mabuya tavaratra* n. sp. and its apparent sister-species, *Mabuya lavarambo*, in northern Madagascar.

lar to *M. lavarambo* (restricted to Nosy Be) and *M. gravenhorstii*, which is broad-ranging in Madagascar, but has not been found as far north as *M. tavaratra*. In the hand, *M. elegans* and *M. gravenhorstii* can readily be distinguished from *M. tavaratra* by the presence of trapezoidal subocular scales in the former two species.

DISCUSSION

Mabuya tavaratra is clearly a distinctive taxon with no available name. It differs from the three species of the *elegans*-Group (*M. elegans*, *M. gravenhorstii*, *M. madagascariensis*) in having a rectangular rather than a trapezoidal subocular scale. It is assignable to the *aureopunctata*-Group

(*M. aureopunctata*, *M. betsileana*, *M. boettgeri*, *M. dumasi*, *M. lavarambo*, *M. nancykoutuae*, *M. vato*) because of its rectangular subocular, but it differs strongly from all members of this group except for *M. lavarambo*, which is its likely sister-species.

Mabuya betsileana is a problematic form known only from the holotype collected from an unknown specific locality (Brygoo, 1983; Nussbaum and Raxworthy, 1995). It is nearly indistinguishable from the west African *M. perrotetii*, and probably belongs to that species. If so, then the holotype was probably not collected in Madagascar. *M. betsileana* is nearly uniform in dorsolateral coloration and has many (73) scales between the postmentals and the cloaca. In these two characteristics, *M. betsileana* is unlike any other Madagascan mabuya. Because *M. betsileana* has not been recorded in Madagascar for nearly 100 years, it should be removed from the faunal list for Madagascar until such time that it is rediscovered.

Four other species of the *aureopunctata*-Group, *M. aureopunctata*, *M. dumasi*, *M. nancykoutuae*, and *M. vato*, and two undescribed species are southern forms that have a distinctive color pattern in which the anterior half of the body and head are darker with white spotting arranged in various patterns, and in which the posterior body and tail are lighter in coloration with fewer or no white spots. The remaining two described species of the *aureopunctata*-Group, *M. boettgeri* and *M. lavarambo*, are similar in having a dorsolateral color pattern of longitudinal stripes and bands, and no anterior white spotting. *M. boettgeri* is readily distinguished from *M. lavarambo* and *M. tavaratra* in having only three supraoculars (compared to 4), three superciliaries (compared to 4 or 5), and four narrow longitudinal black stripes in a broad middorsal light brown band (compared to nearly uniform dorsal coloration). *M. boettgeri* differs further from *M. lavarambo* in having a short tail less than twice the head and body length (cf., more than twice as long in *M. lavarambo*).

By contrast, *Mabuya tavaratra* and *M. lavarambo* are, at a glance, nearly identical. They differ in color only in that the dorsolateral longitudinal line that separates the dorsal band from the lateral darker band is distinctive in *M. lavarambo* and fainter, even disappearing posteriorly, in *M. tavaratra* (Figs. 3-4). The size of the window in the lower eyelid is obviously larger in *M. tavaratra* (Fig. 5). In *M. lavarambo*, the length of the window is equal to or slightly less than the distance from the anterior edge of the window to the anterior edge of the lower eyelid, whereas in *M. tavaratra* the window length is far greater than the remaining distance to the anterior edge of the lower eyelid. The two forms differ significantly in several other morphometric and meristic characteristics (Tables 1, 7, 8, 9). *M. tavaratra* has more scale rows around the body (34-38) than does *M. lavarambo* (28-30). In general, *M. lavarambo* has longer fingers and toes with more subdigital lamellae, compared to *M. tavaratra*. And

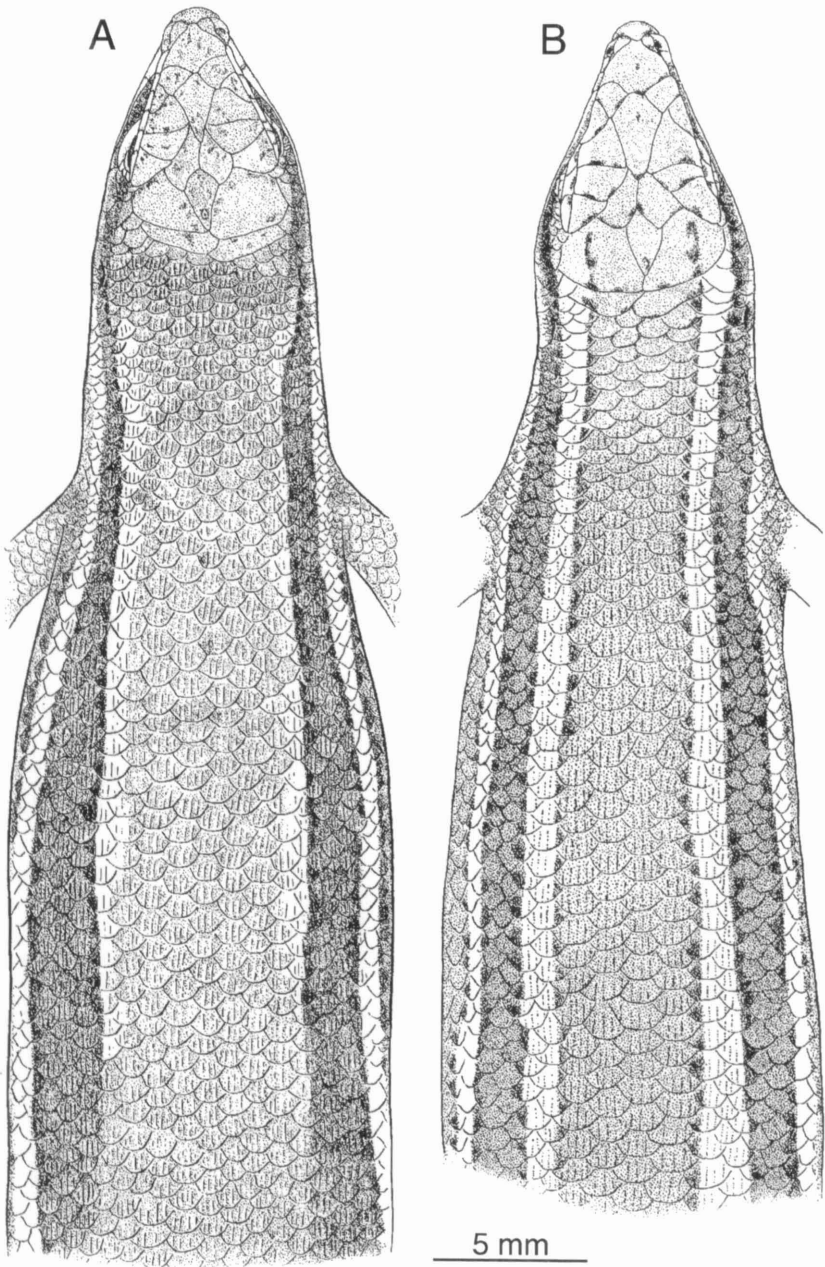


Fig. 3. Dorsal views of (A) *Mabuya tavaratra* n. sp. (paratype UMMZ 208946) and (B) *Mabuya lavarambo* (UMMZ 209151), illustrating interspecific differences in coloration as described in text.

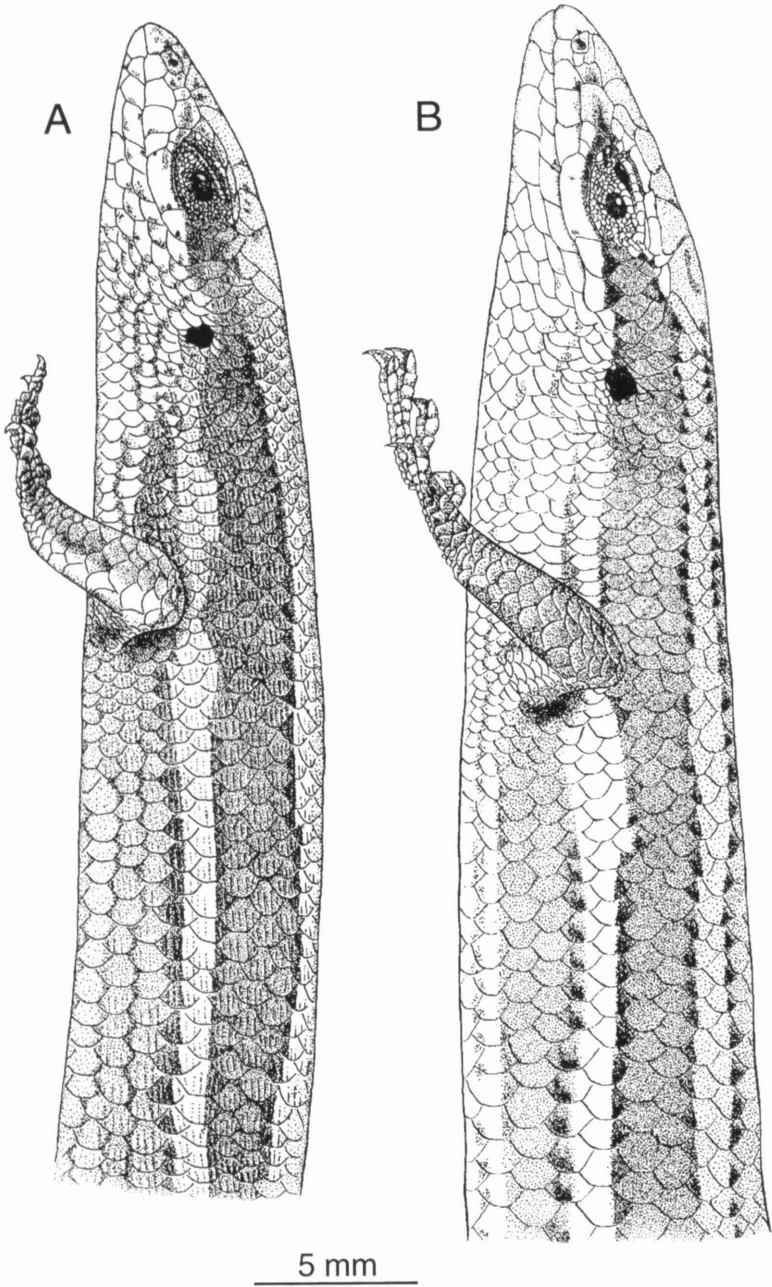


Fig. 4. Lateral views of (A) *Mabuya tavaratra* n. sp. (paratype UMMZ 208946) and (B) *Mabuya lavarambo* (UMMZ 209151), illustrating differences in coloration as described in text.

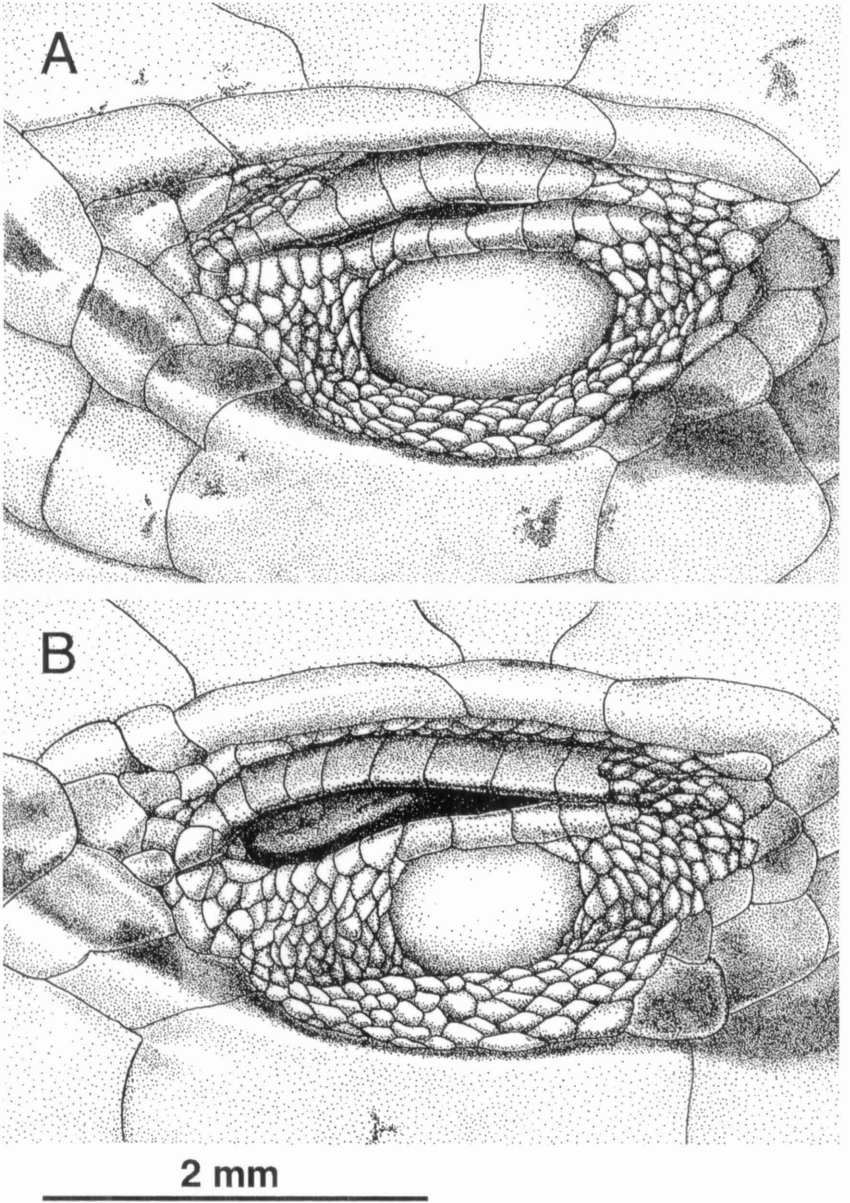


Fig. 5. Left lateral eyes of (A) *Mabuya tavaratra* n. sp. (paratype UMMZ 208951) and (B) *Mabuya lavarambo* (UMMZ 209151), demonstrating difference in size of the palpebral window.

Table 8. Measurements (mm) of holotype and paratypes of *Mabuya lavarambo*.

	Holotype UMMZ 209152	Paratype UMMZ 209150	Paratype UMMZ 209151
Sex	female	female	female
Maturity	mature	mature	mature
Snout-vent length	52	59	61
Tail length	128	145	98*
Tail width (at base)	6.9	7.4	7.5
Tail depth (at base)	6.0	7.0	7.8
Head length (snout-ear)	11.5	12.3	12.1
Head width	8.4	8.9	8.8
Head depth	6.5	6.6	6.6
Snout length	4.8	5.1	5.4
Internarial distance	2.1	2.4	2.2
Interocular distance	4.6	5.0	5.1
Orbit length (horizontal)	3.7	3.8	3.6
Eye-naris distance	2.9	3.2	3.0
Eye-ear distance	4.0	4.2	4.2
Ear opening (vertical)	1.3	1.3	1.3
Ear opening (horizontal)	0.9	0.9	1.2
Frontal length	3.5	3.7	3.5
Interparietal length	2.8	2.6	2.5
Axilla-groin distance	26	30	32
Forelimb length	15	18	18
Hindlimb length	24	25	24
Finger III length	4.8	5.3	5.5
Finger IV length	5.2	5.7	5.5
Toe III length	6.4	6.8	6.7
Toe IV length	8.0	9.0	9.1
Toe V length	5.1	5.2	5.5

* Regenerated.

most obviously, *M. lavarambo* has a much longer tail (2.46 times SVL) than *M. tavaratra* (1.35-1.83 times SVL).

Within the *aureopunctata*-Group, *Mabuya aureopunctata*, *M. dumasi*, *M. nancykoutuae*, *M. vato*, and one undescribed species are clearly closely related forms that share a southwestern distribution in Madagascar. The unique characters of *M. boettgeri* and its occurrence in northern Madagascar set it apart from these five species, casting doubt on the naturalness of an *aureopunctata*-Group that includes *M. boettgeri* (Nussbaum and Raxworthy, 1995). The recent discovery of *M. tavaratra* and *M. lavarambo* in northern Madagascar, with unknown relationships to the southwestern forms and to *M. boettgeri*, further erodes confidence in the usefulness of the shape of the subocular scale in defining monophyletic assemblages of Madagascan mabuyas. The matter is further complicated by our very recent discovery of two additional, as yet undescribed, species of *Mabuya* in western Madagascar, both of which have rectangular subocular scales

Table 9. Meristic data of holotype and paratypes of *Mabuya lavarambo*.

	Holotype UMMZ 209152	Paratype UMMZ 209150	Paratype UMMZ 209151
Frontoparietals	2	2	2
Supraocular scales (L,R)	4-4	4-4	4-4
Superciliary scales (L,R)	4-4	5-5	5-5
Supralabials (L,R)*	4-4	4-4	4-4
Infralabials (L,R)	7-7	7-8	7-6
Scale rows around midbody	29	30	28
Ventral scales**	49	52	54
Number of keels on middorsal scales	5	5	5
Sdm I (L,R)#	7-6	7-6	7-7
Sdm II (L,R)	12-13	12-12	12-13
Sdm III (L,R)	16-15	17-17	16-16
Sdm IV (L,R)	17-17	18-18	19-18
Sdm V (L,R)	11-11	10-10	11-11
Sdp I (L,R)##	9-9	8-	9-9
Sdp II (L,R)	15-15	16-	14-15
Sdp III (L,R)	19-20	20-	21-21
Sdp IV (L,R)	23-22	25-	25-24
Sdp V (L,R)	14-13	13-	14-14

* Supralabial counts include only those anterior to the subocular scale.

** Ventral scales were counted along a midventral line between the post-postmental scales and the cloaca.

Subdigital scales of the manus (Sdm) on fingers I-V, left and right.

Subdigital scales of the pes (Sdp) on toes I-V, left and right.

and may be related to the northern species. It seems increasingly unlikely that mabuyas with rectangular suboculars form a monophyletic unit within Madagascar, as opposed to an hypothesis of independent invasion of two or more lineages with rectangular suboculars.

Because *Mabuya lavarambo* is confined to Nosy Be and *M. tavaratra* to the nearby mainland, it is necessary to infer that the two forms are specifically distinct. We believe they should be recognized as distinctive species, because the difference in the size of the window of the lower eyelid exceeds that observed between other species. Furthermore, the amount of differentiation in the number of scale rows around the body, the number of subdigital lamellae on some digits, and the tail length all exceed the variation found among some other undoubtedly distinct species of Madagascan *Mabuya*.

Only two other reptiles are thought to be endemic to the island of Nosy Be: *Typhlops madagascariensis* and a new species of *Typhlops* (Wallach, Nussbaum, and Raxworthy, unpublished). Interestingly, the new *Typhlops* appears to be the sister-species of *T. microcephalis*, a species currently known

only from Montagne d'Ambre. Therefore, this species-pair of *Typhlops* has a distributional pattern partially congruent with that of *Mabuya tavaratra* and *M. lavarambo*. Recent studies of patterns of endemism of amphibians and reptiles have revealed a close relationship between the herpetofaunas of Nosy Be and both Montagne d'Ambre and Ankarana (Raxworthy and Nussbaum, 1996, 1997).

The five populations of *Mabuya tavaratra*, while not far apart, are probably isolated by areas of highly disturbed habitat between the five massifs. We strongly suspect that prior to the human invasion of Madagascar about 2,000 years ago, the distribution of *M. tavaratra* was continuous along former lowland corridors of dry or transitional forest that linked the lower slopes of the five massifs where *M. tavaratra* currently appears to be restricted.

Mabuya tavaratra is protected within Analamera and Ankarana Réserves Spéciale, and it probably occurs in Parcel 1 and 2 of Montagne d'Ambre Réserve Spéciale, which includes transitional forest between 417 and 1143 m elevation. Montagne des Français is not a reserve, but, because of its unique aspect, it is currently being protected by government forest guards. Daraina forest is unprotected. The range of *M. tavaratra* has undoubtedly contracted over the past 2,000 years, and it is restricted to a very small area. However, because it occurs in three reserves, has some tolerance of habitat disturbance, and is relatively abundant in at least three of the five known sites, it does not appear to be immediately threatened with extinction.

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