

Review of the *Zonosaurus aeneus* species group, with resurrection of *Zonosaurus subunicolor* (BOETTGER 1881)

(Reptilia: Squamata: Gerrhosauridae)

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With 6 figures and 3 tables

Abstract

A taxonomic revision of the *Zonosaurus* species with three supralabials anterior to the subocular (hitherto *Z. aeneus*, *Z. rufipes*, and *Z. brygooi*; here named *Z. aeneus* group) demonstrated the validity of the taxon *Gerrhosaurus rufipes* var. *subunicolor* BOETTGER 1881, which is resurrected as *Zonosaurus subunicolor*. This species occurs sympatrically with *Z. rufipes* and can be distinguished by various colouration characters, and by habitat preferences. *Z. subunicolor* can also be distinguished from the available material of *Zonosaurus brygooi* by having a lower number of femoral pores, a higher number of scales around midbody and lamellae under the fourth toe, and by the presence of a (small) interparietal scale.

Z. aeneus and *Z. brygooi* can be distinguished by colouration and by the conformation of the first supralabial scale posterior to the subocular, which is divided in *brygooi* and entire in *aeneus*. *Z. aeneus* has generally distinct and continuous light dorsolateral stripes, whereas these stripes are absent or reduced to an inconspicuous series of light spots in *Z. brygooi*. The latter species lives in the lowlands of the Malagasy east coast, whereas *Z. aeneus* is found in eastern mid-altitude localities. The type locality of *Z. brygooi*, Nosy Be in north-western Madagascar, lacks recent confirmation.

Introduction

The rather large lizards of the genus *Zonosaurus* are endemic to the Malagasy region. Most species are restricted to Madagascar and its offshore islands; only *Z. madagascariensis* also occurs as subspecies *insulanus* on the Glorieuse and Cosmoledo islands (BRYGOO 1985a). Following the most recent revision (BRYGOO 1985a) the gerrhosaurid genus *Zonosaurus* BOULENGER 1887 contains 10 species: *Z. aeneus* (GRANDIDIER 1872), *Z. boettgeri* STEINDACHNER 1891, *Z. karsteni* (GRANDIDIER 1869), *Z. laticaudatus* (GRANDIDIER 1869), *Z. madagascariensis* (GRAY 1831), *Z. maximus* BOULENGER 1896, *Z. ornatus* (GRAY 1831), *Z. quadrilineatus* GRANDIDIER 1867, *Z. rufipes* (BOETTGER 1881), *Z. trilineatus* ANGEL 1939. An additional species, *Z. brygooi*, was described by LANG & BÖHME 1990, and one subspecies (*Z. madagascariensis havaldmeieri* BRYGOO

& BÖHME 1985) given specific rank as *Z. havaldmeieri* (MEIER 1989, LANG 1990, RAXWORTHY & NUSSBAUM 1994, GLAW & VENCES 1994).

Within *Zonosaurus* several species groups can be distinguished (LANG 1990, GLAW & VENCES 1994). *Z. trilineatus* and *Z. quadrilineatus* are very similar allopatric forms of southern Madagascar, whereas *Z. karsteni* and *Z. laticaudatus* occur sympatrically in western Madagascar. An additional group of related *Zonosaurus* species is characterized by the presence of generally three supralabials anterior to the subocular (a character shared with the genus *Tracheloptychus*), 2-3 well-defined mite pockets within the antehumeral fold (LANG & BÖHME 1990), and the relatively small size. This character combination is found in *Z. aeneus*, *Z. rufipes*, and *Z. brygooi* (LANG &

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Date/ Collection Nr.	Locality	Fem.Por	IP	SVL	TaL	Mid.Bod.	CH-CL	4.Toe
<i>Zonosaurus aeneus</i>								
MHNP* 7634	Malaimbandy?	14	-	32	53	20		20
MHNP 1965-312	Anosibe	16	-	65	(-)	20		20
MHNP 1984-400	Moramanga	16	-	67	112	19		19
MHNP 1984-401	Moramanga	13	+	70	(89)	18		17
MHNP 1933-165	Moramanga	13	-	56	81	21		17
MHNP 1933-164	Moramanga	15	-	51	93	19		19
MHNP 1930-310	Ivohibe	17	-	72	(-)	21		20
MHNP 1994-1741	Ivohibe		-	40	63			20
MHNP 1994-1740	Ivohibe		-	39	(-)			20
MHNP 1930-311	Ikongo	18	-	37	(-)			21
MHNP 1907-84			-	28	42			
MHNP 1994-1739	Ivohibe		-	38	(-)			17
MHNP 1994-1738	Ivohibe		-					17
MHNP 1984-403	Andasibe		-	32	41			
MHNP 1983-886	Mandraka		-	32	(-)			
<i>Zonosaurus brygooi</i>								
ZFMK 46789*	Nosy Be	19/19	-	76		22	44	18
ZFMK 46790#	Nosy Be	17/17	-	63		21	43	19
ZFMK 46792#	Nosy Be	16/16	-	51	94	23	45	17
ZFMK 46793#	Nosy Be	19/17	-	55				18
ZFMK 46794#	Nosy Be	17/16	-	45	84	21	46	18
ZFMK 46795#	Nosy Be	16/17	-	49	75	20	48	18
ZFMK 48165#	Nosy Boraha	16/16	-	74		22	45	18
IRSNB 2.534#	Nosy Be	17/17	-	74		22	45	18
ZMB 19018#	Sakana	16/17	-	69	92	21	45	17
SMF 41053#	Nosy Be	17/17	-	68		21	47	19
MHNP 1984-402	Manompana	17	-	58	(-)	21		19
MHNP 1937-15	Betampona	16	-	55	81	21		17
MHNP 1937-14	Betampona	15	-	53	97	21		16
MHNP 1983-598	Manompana	15	-	71	125	21		16
MHNP 1983-601	Nosy Mangabe		-	36	(-)			
MHNP 1983-599	Nosy Mangabe		-	36	(-)			
MHNP 1983-602	Tampolo		-	33	(-)			
MHNP 1983-600	Nosy Mangabe		-	34	(-)			
MHNP 1950-311	Fenerive-Tampolo	16	-	52	(-)	22		19
MHNP 1950-312	Manjabe		-					17
MHNP 1984-404	Autsingy		-	33	(-)			18
<i>Zonosaurus rufipes</i>								
19.01.92	Nosy Be	12/12	+	35	62	22		
19.01.92	Nosy Be	13/13	+	35	63	22		
08.02.92	Nosy Be	11/12	-	37	64	24	46	20
08.02.92	Nosy Be	9/9	-	35	64	24	49	20
08.02.92	Nosy Be	10/10	+	35		25	47	21
08.02.92	Nosy Be	8/8	+	36	69	24	46	21
08.02.92	Nosy Be	11/12	+	34		26	50	19
08.02.92	Nosy Be	11/11	-	40		23	45	21
08.02.92	Nosy Be	11/12	+	41	75	24	49	19
11.02.92	Nosy Be	12/12	+	70	127	24	48	22
ZFMK 53978	Nosy Be	10/11	-	77	135	22	47	20
ZFMK 53979	Nosy Be	8/9	+	69	102	24	48	20
ZFMK 53980	Nosy Be	8/8	+	70	128		47	19
ZFMK 53981	Nosy Be	9/10	+	30	49	22	49	20
ZFMK 53983	Nosy Be	10/11	+	31	59		49	19
SMF 40743*	Nosy Be	13/13	-	85		25		22
<i>Zonosaurus subunicolor</i>								
28.01.92	Nosy Be	11/11	+	77	139	25	48	22
31.01.92	Nosy Be	11/13	+	75	143	25	49	19/20
21.02.92	Nosy Be	9/11	+	68	120	22		20
ZFMK 53984	Nosy Be	12/11	+	86	143	24	48	21
ZFMK 53985	Nosy Be	11/12	+	73		22	45	20
ZFMK 53986	Nosy Be	9/10	+	63	123		48	19
ZFMK 53987	Nosy Be	11/11	+	75	135		46	20
ZFMK 53988	Nosy Be	8/9	+	31		22	48	20
SMF* 41051	Nosy Be	10/10	+	45	97		46	22
SMF# 41052	Nosy Be	11/11	+	38		25	45	20

Table 1. Meristic and morphometric values of the studied specimens belonging to the *Z. aeneus* group. - Abbreviations used: Fem.Por. = number of femoral pores (separately for both femurs); IP = interparietal (+ present [but always very small], - absent); SVL = snout-vent length; TaL (tail length); Mid.Bod. = number of scales around midbody; CH-CL number of scales between chin and cloaca (including mental scale); 4. Toe = number of lamellae under fourth toe; * = Lectotype/Holotype; # = Paralectotype/Paratype. - Due to different reasons, mainly bad state of conservation or difficulties caused by small size, some measurements and counts were not taken from all specimens. Values of 4. Toe and Fem.Por. were sometimes taken on both legs. When only one value is given, this refers only to one leg. An autotomized tail is recorded as (-) in the tail length column, length of clearly regenerated tails is given in brackets. Data of IRSNB 2.534, ZMB 19018, SMF 41051-41053 from LANG & BÖHME (1990).

Böhme 1990). We will refer to this group as the *Zonosaurus aeneus* group, named after the oldest of the included taxa.

Fieldwork between 1991 and 1995 revealed problems in the differential diagnosis of these taxa, and showed the need of critical revision of the preserved material belonging to this group. Furthermore, intensive surveys on the small Malagasy island Nosy Be demonstrated the existence of an additional species of this group which corresponds well with the type material of *Gerrhosaurus rufipes* var. *subunicolor* BOETTGER 1881, presently synonym of *Zonosaurus rufipes*. GLAW & VENCES (1992, 1994) already considered *Zonosaurus subunicolor* a valid species, but referred to unpublished data. The formal resurrection of this taxon, and the detailed discussion of this taxonomic conclusion, are the aim of the present paper.

Material and methods

Field observations on specimens referred to the *Zonosaurus aeneus*-group were made at the following localities: Nosy Boraha (*Z. brygooi*), Nosy Mangabe (*Z. brygooi*), Andasibe (*Z. aeneus*), Antorotorofotsy, north of Andasibe (*Z. aeneus*), Marojejy (*Z. rufipes*), Benavony (*Z. rufipes*), Nosy Komba (*Z. subunicolor*), Nosy Be (*Z. subunicolor*,

Z. rufipes). For a more exact location of these sites see GLAW & VENCES (1994).

Morphological data were taken from both preserved museum material and from living, successively released, specimens in the field. All specimens studied are listed in Table 1. Used museum acronyms are: AMNH (American Museum of Natural History, New York), BM (Natural History Museum, London), CAS (California Academy of Sciences, San Francisco), IRSNB (Institute Royale des Sciences naturelles, Bruxelles), MHNP (Museum National d'Histoire Naturelle, Paris), NMW (Naturhistorisches Museum, Wien), SMF (Senckenberg-Museum, Frankfurt am Main), ZFMK (Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn), ZMB (Zoologisches Museum der Humboldt-Universität, Berlin). For specimens measured in the field we give the date at which they were captured. For abbreviations of measurements see Table 1.

Statistical analyses were carried out with the software package SPSS for Windows. Species were pairwise compared with Student's t-tests and with non-parametrical Mann-Whitney-U-tests. Significance values found with these two methods did not differ substantially from each other. All statistical information in the following sections refers to comparisons of the data listed in Table 1 with U-tests.

Results

Zonosaurus aeneus (GRANDIDIER 1872)

Type: MHNP 7634. The holotype is a juvenile specimen in bad state of preservation. Attribution of adult specimens to the taxon *aeneus* is therefore rather problematic and will be discussed below. Several characters of the type are provided by BRYGOO (1985a). There are no paratypes. No type locality is mentioned in the original description. MOCQUARD (1895) states that it is Malaimbandy ("Pays des Sakalaves") in western Madagascar, without giving his source of information. The locality is therefore somewhat doubtful and, following BRYGOO (1985b), may be due to confusion with the type locality of *Euprepes sakalava*, (currently synonym of *Mabuya elegans*).

Other material: Examination of the preserved material labelled as *Z. aeneus* in the MHNP clearly revealed the existence of two different forms included in the taxon. One group of specimens collected at mid-altitude localities of eastern Madagascar has distinct continuous narrow dorsolateral stripes which continue on the anterior half of the back until they fade. The second

group of individuals, from different lowland localities on the east coast, have no continuous dorsolateral stripes. Either these lack completely, or exist only in form of rows of isolated light spots. Only one meristic character was found to be in all cases diagnostic between these two forms: In specimens with dorsolateral stripes the first supralabial posterior to the subocular was undivided, whereas this scale was divided in specimens without dorsolateral stripes. We did not observe the undivided state of this character in any other *Zonosaurus* species.

Identity of *Z. aeneus*: The taxon *aeneus* was historically the first described *Zonosaurus* species with 3 supralabials anterior to the subocular. Because of the bad conservation state of the holotype and its juvenile colouration only meristic characters remain to attribute a *Zonosaurus* form to *aeneus*. The first supralabial posterior to the subocular is undivided in the type; we therefore consider specimens with this character, which also share narrow dorsolateral stripes as *Z. aeneus*. This definition

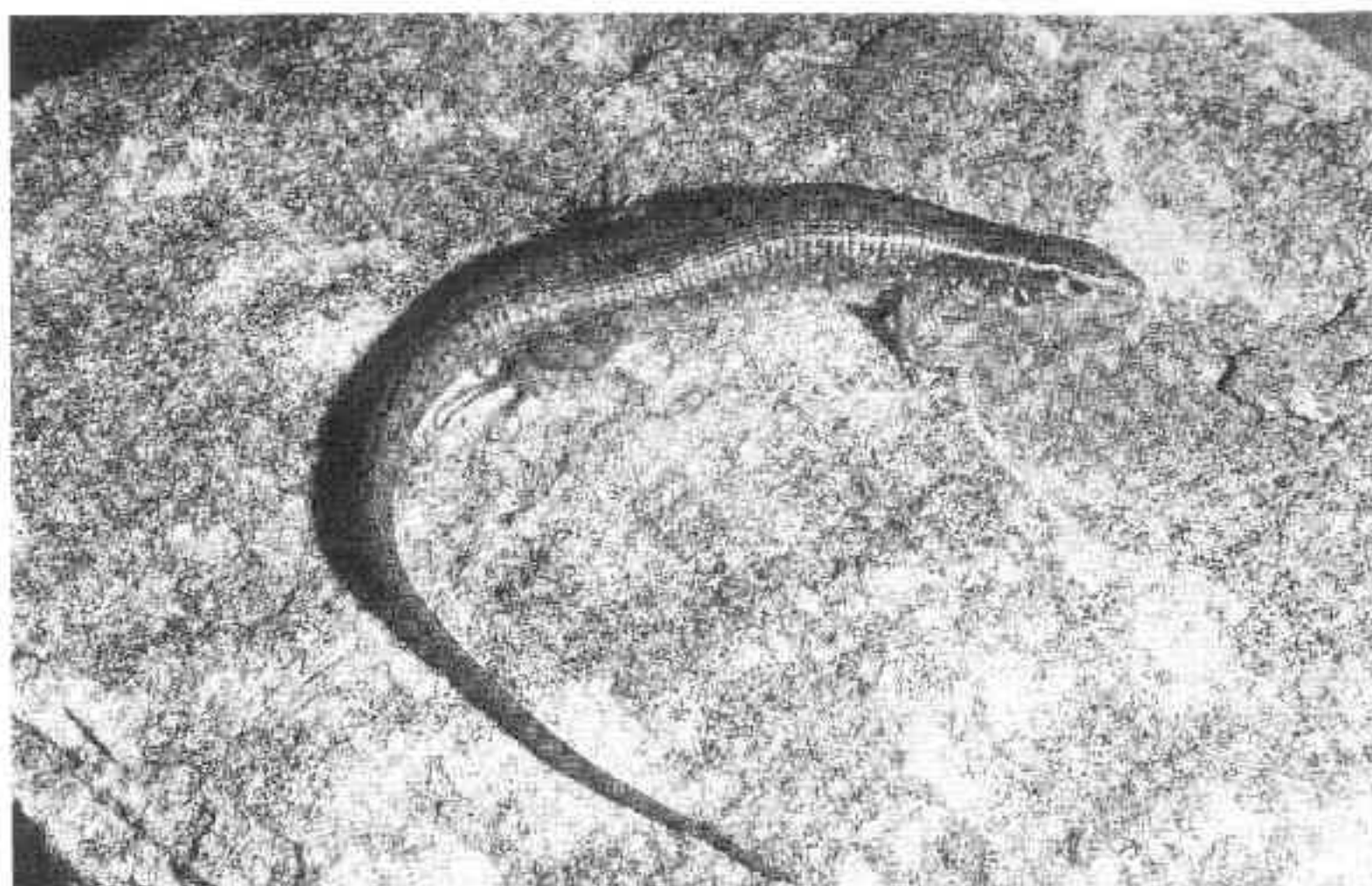


Fig. 1. *Zonosaurus aeneus*, specimen from Andasibe.

applies to the specimens listed as *aeneus* in Table 1, as well as to ZFMK 14365 (Nosy Be), 21272 (Fianarantsoa), 59784 (Andasibe), 62321 (Andasibe) and 59798 (near Tolagnaro). One specimen from Andasibe (figured by GLAW & VENCES 1994) had a bluish throat, another specimen a yellowish throat. This difference is probably due to sexual dimorphism, but we did not study the sex of these specimens.

Diagnosis: *Z. aeneus* differs from the other members of the *Z. aeneus*-group by the presence of continuous dorsolateral stripes which begin on the head and continue at least on the anterior third of the body; it differs from all other *Zonosaurus* by the undivided first supralabial behind the subocular. According to LANG (1990) its tongue is not totally dark pigmented; however we did not check this character in all specimens included in the present study. Relative tongue pigmentation is difficult to evaluate in specimens not in good state of preservation. A differentiation of *Z. aeneus* by additional meristic characters is clearly possible from *Z. rufipes* and *Z. subunicolor*; and partly from *Z. brygooi*; data will be mentioned in the diagnoses of these species.

By general appearance it is easy to mistake *Z. aeneus* for subadult *Z. madagascariensis*, which also have continuous (although often somewhat broader) dorsolateral stripes. In most cases the number of supralabials anterior to the subocular (3 in *aeneus*, 4 in *madagascariensis*) is diagnostic. However, single *madagascariensis* specimens with aberrant supralabial numbers are known. 68 out of 80 specimens studied by BRYGOO (1985) had 4 supralabials anterior to the subocular on both sides of the head; however, one specimen also showed a number of 3 on both sides. We found one subadult *Z. madagascariensis* on Nosy Be (ZFMK 53989) with 3/4 supralabials on either side of the head.

Redescription: Since the type of *Z. aeneus* is a juvenile specimen in bad state of preservation we give a redescription of the species based on ZFMK 59784. The specimen is in good state of preservation, and was collected in December 1993 by M. VENCES in the vicinity of Andasibe, central eastern Madagascar. The tail is fixed on the body but is regenerated for its largest part. The posterior third of the tail is broken into two separate pieces. The tail is rather abruptly constricted just posterior to the sacral region, whereafter it is vertically compressed. Lateral fold continuous from tympanum to cloaca, not very well developed. There are three mite pockets in the antehumeral fold. Tongue with some dark pigment.

Ventral scales are arranged in 8 longitudinal rows. 56 scales between chin and cloaca. 19 lamellae under fourth toe. 15 femoral pores on right hindlimb, 13 on left hindlimb. 18 midbody scale rows between the lateral folds. Outermost midbody scales on flanks (3 rows on each side) semicircular, with a rounded or pointed posterior edge. Remaining midbody scales on flanks and back (5 rows on each side) squarish, with a straight posterior edge. The median (vertebral) midbody scales (2 rows) triangular and intercalating. Ventral scales smooth; lateral, dorsal and vertebral scales slightly keeled, with 8–10 very small keels of similar size on each scale.

Snout-vent length 68 mm, tail length 70 mm. Maximum head width 11.3 mm, maximum head depth 8.4 mm, maximum body diameter about 11 mm, distance between insertion point of fore- and hindlimbs 31 mm. Forelimb length 19 mm, length of hindlimb 35 mm, length of third forelimb toe 5.5 mm, forelimb toe 3 and 4 of same lengths, length of fourth hindlimb toe 12.8 mm.

Mental in contact with postmentals and first supralabials on each side. Posterior edge of mental straight. Postmentals largely contact each other. Post-postmentals

Table 2. Differential characters in the species of the *Z. aeneus* group. Meristic and morphometric data from Table 1 except for maximum total length of *Z. brygooi* (refers to ZFMK 53152). Values are given as range (mean \pm standard deviation).

	<i>Z. aeneus</i>	<i>Z. brygooi</i>	<i>Z. rufipes</i>	<i>Z. subunicolor</i>
Throat colour	somet. yellow or blue	sometimes blue?	whitish	somet. blue with orange
Throat pattern	none	none	longitudinal stripes	none
Flank colour	dark brown	dark brown	reddish	light brown
- relative to back	darker	mostly darker	mostly lighter	mostly lighter
Light dorsolateral stripes				
- on anterior back	continuous	row of spots/absent	row of spots/absent	indistinct/absent
- on posterior back/anterior tail	absent/indistinct	mostly absent	absent	present
First labial posterior to subocular	entire	divided	divided	divided
Interparietal	mostly absent	absent	mostly present	present
Maximum total length as SVL+TaL	67+112 mm	76+122 mm	77+135 mm	86+143 mm
Femoral pores	13-18 (14.9 \pm 1.6)	15-19 (16.4 \pm 1.1)	8-13 (10.6 \pm 1.4)	8-13 (11.2 \pm 1.3)
Scales around midbody	18-21 (19.7 \pm 1.1)	20-23 (21.4 \pm 0.8)	22-26 (23.8 \pm 1.2)	22-25 (23.5 \pm 1.6)
Lamellae under fourth toe	17-21 (18.9 \pm 1.4)	16-19 (17.7 \pm 1.1)	19-22 (20.3 \pm 0.9)	19-22 (20.3 \pm 0.8)

not in contact with each other; post-postmentals entire on both sides. One small scale interposed between post-postmentals; contacts both postmentals and post-postmentals.

There are three supralabials anterior to the subocular. One large subocular. One supralabial posterior to the subocular (= supralabial posterior to the subocular not divided), thus a total of five scales between rostral and tympanum. There are four supraocular and four supra-ciliary scales. Two large parietal scales; no frontoparietal scales. Interparietal absent. Nasal scales not in median contact, separated by a frontonasal scale. Two loreals. Pre-frontals separated by frontal-frontonasal contact. One small postocular scale, and 2+2 large temporal scales.

Colour in preservative dorsally brown; flanks dark brown with white spots which cover one or two scales. Vertebral scales dark brown on anterior back, forming a continuous dark median stripe to the level of hindlimb insertion. Head dorsally brown with several dark brown markings. Temporal region dark brown. A white dorsolateral stripe runs from behind the eye onto the sacral region; it is continuous and distinct on the anterior back and begins to fade on the posterior back. It is formed by white colour on one dorsal scale row. The white stripe is a sharp border to the dark flank colour; vertebrally it is also bordered by dark brown colour which is irregularly present on two dorsal scale rows. The regenerated part of the tail is uniformly light brown. Fore- and hindlimbs are dorsally brown with indistinct light spots. The ventral side is uniformly whitish.

Habits and distribution: Few ecological data on *Z. aeneus* are available in the literature. We found specimens at Andasibe and Antorotorofotsy (near Andasibe) at the edge of primary rainforest, or on sunny patches in the forest. Beside the type locality, another somewhat doubtful locality for *Z. aeneus* is Nosy Be. One specimen from this island (ZFMK 14365) must be referred to this species. Despite intensive surveys we were not able to find *Z. aeneus*

at this locality. However, our observations around Andasibe have shown that the species can locally be quite common, but very rare at other neighboured plots. Such a mosaic distribution could explain why we were not able to confirm the Nosy Be locality, but the record certainly needs confirmation. One subadult specimen probably belonging to *aeneus* (ZFMK 59798) is known from the Tolagnaro region, and one specimen (ZFMK 21272) from Fianarantsoa (probably forested regions around Fianarantsoa). Other *Z. aeneus* localities are (see Table 1): Andasibe, Moramanga, Mandraka, Anosibe, Ikongo, Ivohibe.

Zonosaurus brygooi LANG & BÖHME 1990

Holotype (ZFMK 46789): Collected in April 1987 by R. SHIFF at Loucoubé (= Lokobe, Nosy Be). Specimen in good condition. Detailed measurements and meristic data are given in the original description.

Paratypes: ZFMK 46790, 46792-95, IRSNB 2.534 all from Nosy Be, SMF 41053 and ZMB 19018 from Sakana, and ZFMK 48165 from Nosy Boraha.

Other material: MHNP specimens without continuous dorsolateral stripes, labelled as *Z. aeneus* (see above), were found to correspond in pholidosis and colouration with the type series of *Z. brygooi*. The studied specimens are listed in Table 1. An additional specimen is ZFMK 53152 from Nosy Mangabe (meristic data: 23 scale rows around midbody, no interparietal scale, 8 rows of ventral scales, forelimb toe 3 \geq forelimb toe 4, 18 lamellae under fourth toe, 16 femoral pores, SVL 76 mm, tail length 122 mm).

Diagnosis: *Z. brygooi* differs from *Z. rufipes* by the different colouration and from *Z. rufipes* and *Z. subunicolor* statistically by several meristic characters (see diagnoses of these species). From *Z. aeneus* it differs by having a divided supralabial posterior to the subocular (see above) and by lacking continuous dorsolateral stripes. Additional differences are a larger number of scale rows around mid-

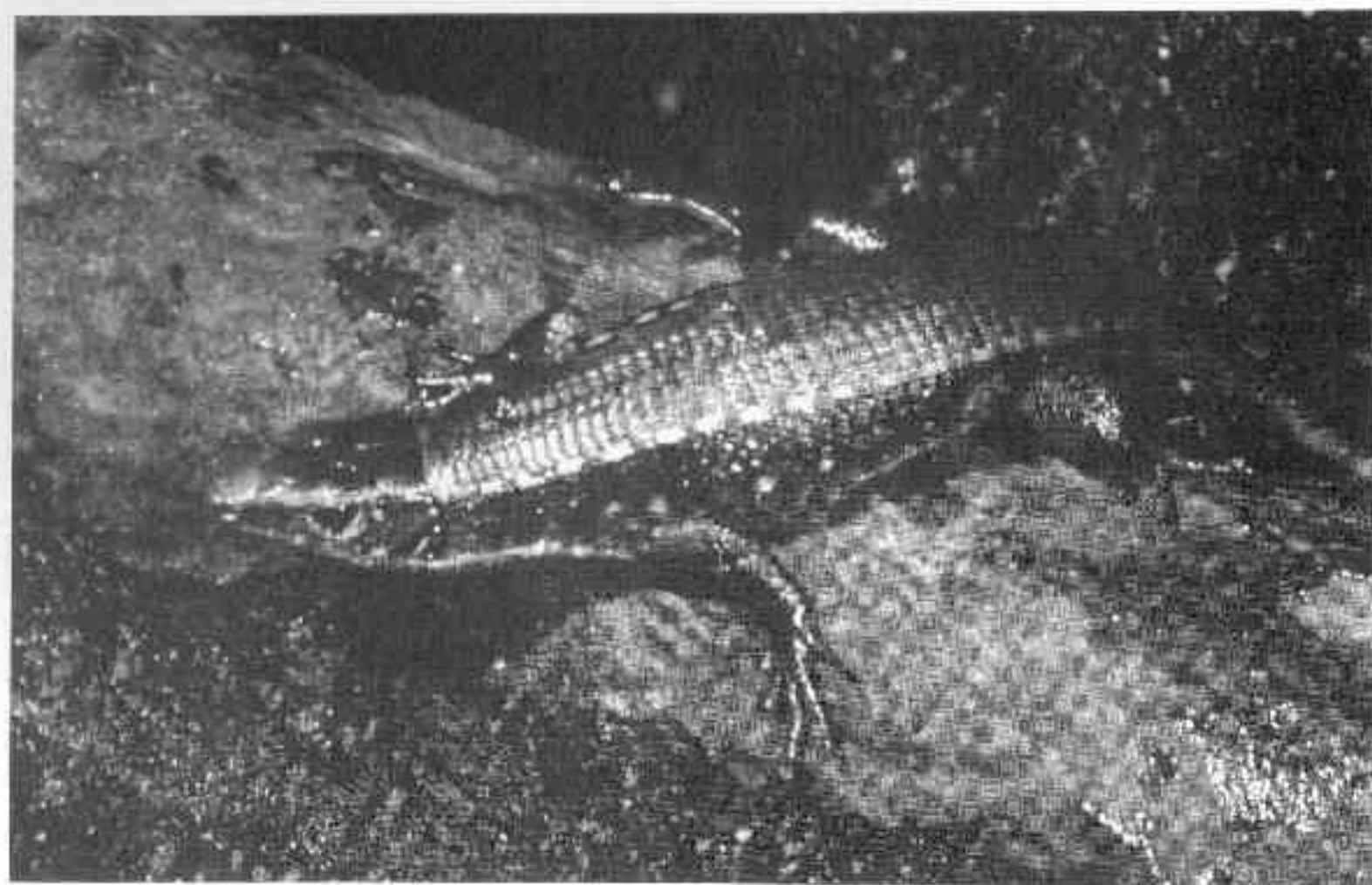


Fig. 2. *Zonosaurus brygooi*, specimen from Nosy Mangabe. — PHOTO FRANCO ANDREONE.

body (mean 21.4 in *brygooi* versus 19.7 in *aeneus*; $p < 0.01$), a lower number of lamellae under the fourth toe (mean 17.7 in *brygooi* versus 18.9 in *aeneus*; $p < 0.05$) and possibly a somewhat higher number of femoral pores (mean 16.4 in *brygooi* versus 14.9 in *aeneus*; $p < 0.1$).

Habits and distribution: We carried out some systematic observations on the *Z. brygooi* population of Nosy Mangabe, a small offshore island on the Malagasy east coast which is nearly entirely covered with primary rainforest. *Z. brygooi* here occurs syntopically with the larger *Z. madagascariensis*. Line transect data were collected on 5 consecutive days in March 1991. The transect had a length of 660 m, reaching from the base camp at sea level to the summit at about 200 m above sea level. A total of 47 *Zonosaurus* observations were made: 15 of *Z. brygooi*, 11 of *Z. madagascariensis*, and 21 of undetermined juvenile specimens. Few *Zonosaurus* were observed at the base camp, but no one on the first 100 m of the transect. Most observations of *Z. madagascariensis* ($n=6$) were made at two small sun-exposed spots in the forest; the other observations clustered around a transect part between 180 and 260 m (95–120 m altitude). *Z. brygooi*, on the other hand, was more evenly distributed, although specimens clustered also at the same places. Rather large parts of the transect seemed not to be populated by adult *Zonosaurus* at all (only juveniles between 470 and 610 m). These observations agree with those of R. SEIPP (pers. comm.), who collected all ZFMK specimens of the *Z. brygooi* type series at one single, not very shaded, locality in the forest of Nosy Be. At other localities on Nosy Be he saw only specimens of *Z. rufipes*.

The only record of *Z. brygooi* from Nosy Be refers to a large part of the type series of the species; all these specimens were provided by the same collector (R. SEIPP). One specimen from Sakana (SMF 41053; collected in 1905

by A. VOELTZKOW) was erroneously cited with the locality Nosy Be by LANG & BÖHME (1990). During our own intensive surveys on Nosy Be we were unable to detect the species. The species is also known from a number of east coast localities. These are (see Table 1): Nosy Mangabe, Fenoarivo (Tampolo), Betampona, Nosy Boraha, Manjabe forest, Manompana. The exact location of the locality Sakana can unfortunately not be traced (see GLAW & VENCES 1994). ANGEL (1942) located Sakana in eastern Madagascar, LANG & BÖHME (1990) speculate that it may be in coastal north-eastern Madagascar, coinciding with the travel routes of the collector VOELTZKOW. A record exists also for western Madagascar (Antsingy, see Table 1), but only a juvenile specimen is known from this locality, and its specific identity is not certain.

Zonosaurus rufipes (BOETTGER 1881)

Lectotype: The original description refers to a syntype series of 12 specimens. MERTENS (1967) designated the specimen SMF 40743 (probably a female after BOETTGER) as lectotype.

Paralectotypes: SMF 40744–40748 as well as NMW 23350.1 and 23350.2 and ZMB 10097 and 49640. All types are from Nosy Be.

Other material: Specimens preserved in the ZFMK, as well as specimens which we observed in the field, correspond well with the lectotype (Table 1). Measurements and meristic values for several other specimens assigned to *Z. rufipes* are given by LANG & BÖHME (1990). We did not study these specimens again for the present paper, so it can not be excluded that some of them may belong to *Z. subunicolor*. These specimens are: AMNH 24769; BM 86.2.25.8, 86.2.25.9, 87.12.5.13, and 95.10.29.12; CAS 156896 and 156897; NMW 12243, 12245.1, 12245.2, 12246.1, 12246.2, 12247.1, 12247.2, 20097.1, 20097.2, 23350.1, and 23350.2; SMF 40744–40748; ZMB 10097 (2 specimens).

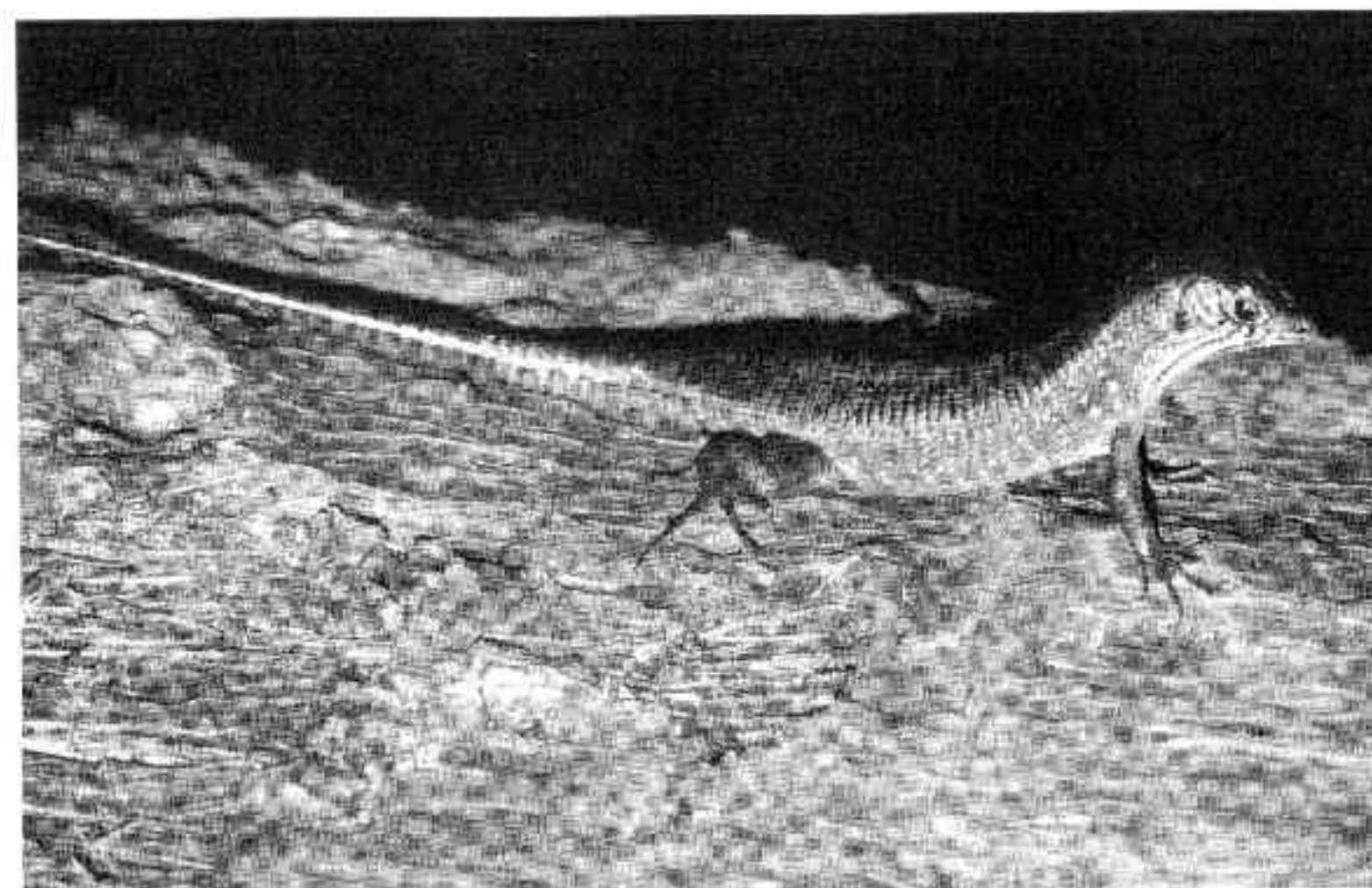


Fig. 3. *Zonosaurus rufipes*, specimen from Nosy Be.

Diagnosis: *Z. rufipes* can easily be recognized by its characteristic colouration. Several blackish longitudinal stripes run along the outer borders of the throat scales. The lateral stripes are more intense than the inner stripes. The flanks and legs are typically reddish, what explains the name *rufipes*. Light dorsolateral stripes are only present in form of incontinuous rows of spots.

Z. rufipes differs in pholidosis from *Z. brygooi* by a lower number of femoral pores (mean 10.6 versus 16.4; $p < 0.001$), a higher number of scales around midbody (mean 23.8 versus 21.4; $p < 0.001$), and a higher number of lamellae under fourth toe (mean 20.3 versus 17.7; $p < 0.001$).

Similar values differentiate *Z. rufipes* from *Z. aeneus*: a higher number of scales around midbody (mean 23.8 versus 19.7; $p < 0.001$), and a higher number of lamellae under fourth toe (mean 20.3 versus 18.9; $p < 0.001$); no

significant difference is found between *aeneus* and *rufipes* in the number of femoral pores.

Differentiation from the sympatric *Zonosaurus subunicolor* is mainly based on colouration; for characters see the diagnosis of that species.

Habits and distribution: We carried out some systematic studies on the ecology of *Z. rufipes* on Nosy Be: 120 out of 121 records of *rufipes* specimens were made in the rainforest. Only a single specimen was found in secondary forest near a coffee plantation, not far from primary forest. A 700 m transect in the rainforest was divided into 11 parts which differed by relative sun-exposition. Beside *Z. rufipes*, also *Z. madagascariensis* occurred along this transect. 111 out of 117 *Z. rufipes* records along the transect were made at shaded places (only 10 out of 45 *Z. madagascariensis* records; differences significant, $p < 0.001$, Chi-square-test). Table 3 summarizes all our

Table 3. Habitat choice of *Zonosaurus* species on Nosy Be, given as number of observed specimens in different habitat types.

Habitat	<i>Z. madagascariensis</i>	<i>Z. rufipes</i>	<i>Z. subunicolor</i>
Shaded/near brooks	14	98	0
Shaded/not near brooks	4	15	1
Sun-exposed/near brooks	64	5	0
Sun-exposed/not near brooks	54	2	11
Total	136	120	12
Not in primary forest	73	1	0

