

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

(Reptilia: Squamata: Gerrhosauridae)

MIGUEL VENCES, JOACHIM MÜLLER-JUNG, FRANK GLAW & WOLFGANG BÖHME

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. brygoi*; 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 brygoi* 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. brygoi* can be distinguished by colouration and by the conformation of the first supralabial scale posterior to the subocular, which is divided in *brygoi* 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. brygoi*. 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. brygoi*, 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. brygoi*, was described by LANG & BÖHME 1990, and one subspecies (*Z. madagascariensis haraldmeieri* BRYGOO

& BÖHME 1985) given specific rank as *Z. haraldmeieri* (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 *Trachelopteryx*), 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. brygoi* (LANG &

Authors' address:

MIGUEL VENCES, JOACHIM MÜLLER-JUNG, FRANK GLAW, WOLFGANG BÖHME, Zoologisches Forschungsinstitut und Museum A. Koenig, Sektion Herpetologie, Adenauerallee 160, D-53113 Bonn.

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	Antsingy		-	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 (Institut Royal des Sciences naturelles, Bruxelles), MHNP (Muséum 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 supraciliary 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; ventrally 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. SHUP 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-

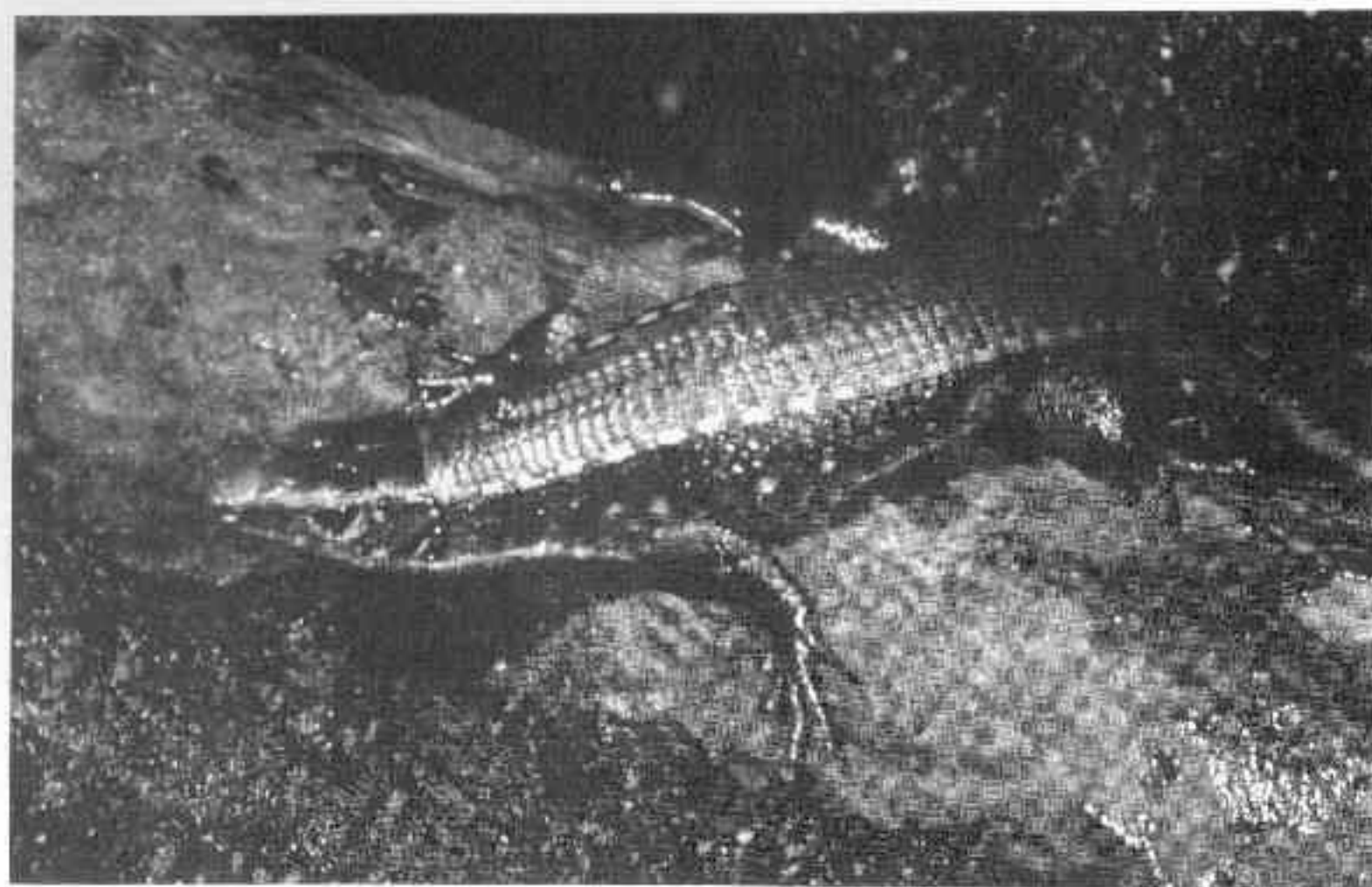


Fig. 2. *Zonosaurus brygooi*, specimen from Nosy Mangabe. — PHOTO FRANCO ANDREONE.

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 (93–120 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), Betampana, 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).

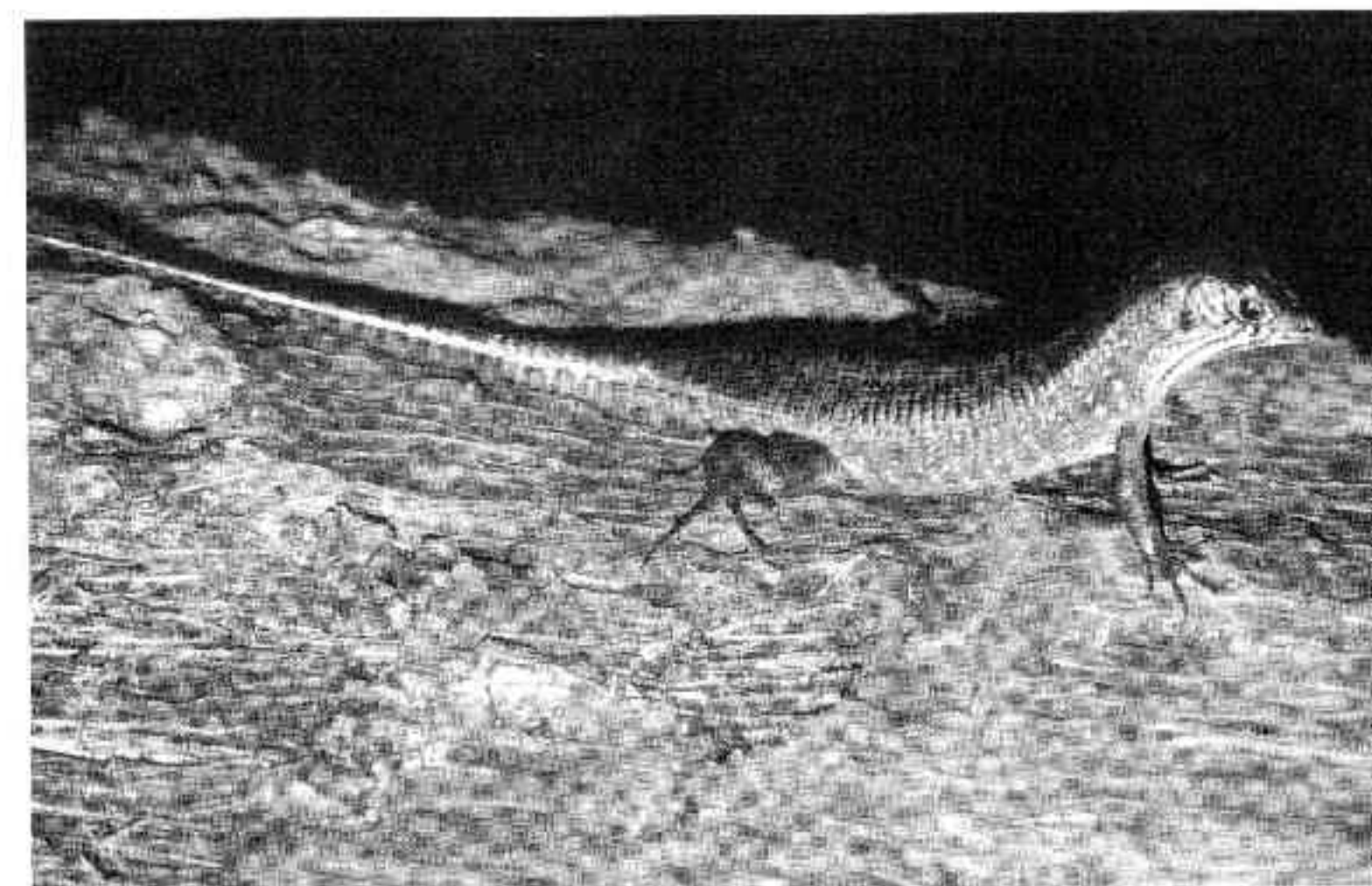


Fig. 3. *Zonosaurus rufipes*, specimen from Nosy Be.

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 inconspicuous 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

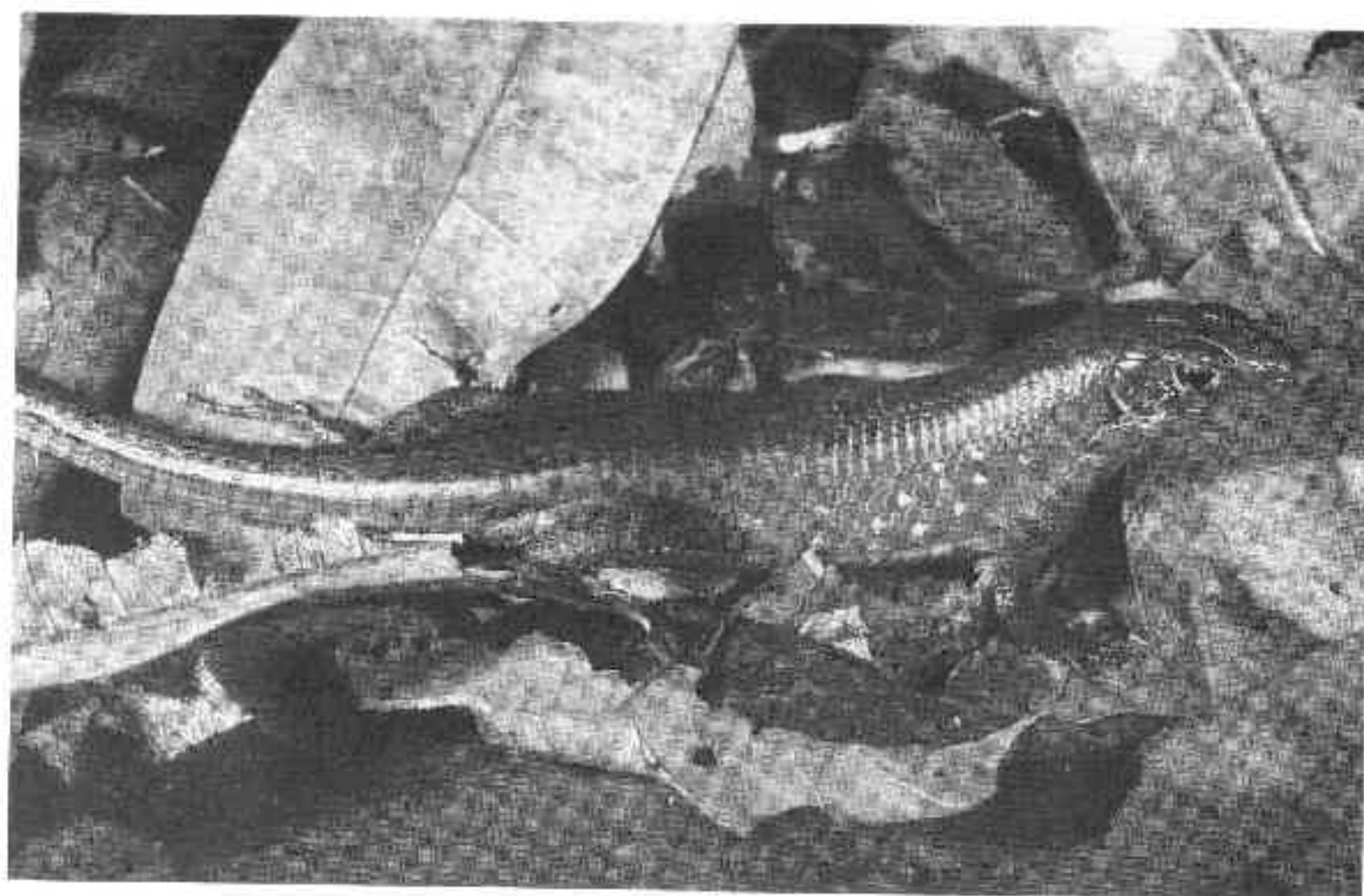


Fig. 4. *Zonosaurus subunicolor*, specimen from Nosy Be.

observations of *Zonosaurus* on Nosy Be. The data clearly show that *Z. rufipes* was mainly found at shaded places near forest brooks.

Active *Z. rufipes* were observed during the day, but also in the early evening. Main activity was recorded between 17 and 19 h pm. On the contrary, activity of the syntopic *Z. madagascariensis* was highest around 12 h pm, when sunlight best reaches the forest floor (MÜLLER 1993). A mating pair was observed during early afternoon in February. One female deposited eggs (size 8 x 13 mm), also in February.

Beside the type locality Nosy Be, we found the species at Benavony and in the Reserve Intégrale Marojejy (Camp 1, about 300 m above sea level). The locality "Marojejy" is already mentioned by BRYGOO (1985a: quoting GUILAUMEY et al. 1975). The specimen BM 95.10.29.12 was collected by R. BARON with the locality information Imerina (Central Madagascar). We believe that BRYGOO (1985a) is right considering this locality as erroneous, since all other locality records are from low altitudes.

Zonosaurus subunicolor (BOETTGER 1881)
bona species

Lectotype: SMF 41051.

Paralectotype: SMF 41052. Both types are juvenile specimens from Nosy Be.

Other material: We collected 8 *Zonosaurus* specimens on Nosy Be which correspond to the types of *subunicolor*. 5 of these are preserved (ZFMK 53984-53988). An additional specimen was observed on Nosy Komba. MEIER (1989: 21, Fig. 8a) showed a picture of the ventral side of a *Zonosaurus* from Nosy Be (classified as *Z. brygooi* by LANG & BÖHME 1990) which may also be *Z. subunicolor*.

Diagnosis: We were not able to detect significant differences in pholidosis when comparing a group consisting of the *subunicolor* types and our specimens with *rufipes* (data from Tab. 1; p always >0.4). Only the presence/absence of the small interparietal scale may constitute a difference: It is present (although sometimes extremely small) in all *subunicolor*, but lacks in about 25% of the examined *rufipes* specimens (11 out of 46 specimens, data from LANG & BÖHME 1990 and MÜLLER 1993).

Nevertheless, we regard *Z. subunicolor* as a valid species. This is based on the combination of several colour differences to *rufipes* which are constant and do not show intermediate states. *Z. subunicolor* has a throat which can be blue with orange (whitish with longitudinal dark stripes in *rufipes*), light brownish flanks and legs (reddish in *rufipes*), a rather light, copper-brownish back (often darker in *rufipes*), no sharp border between dorsal and ventral colour at the lateral folds (rather sharp border in *rufipes*), dorsolateral yellowish stripes which begin at the hindleg insertion and continue on the first third of the tail, and are already present on juvenile specimens (absent in *rufipes*), bluish spots on the anterior flank (absent in *rufipes*).

Z. subunicolor is superficially similar to *Z. brygooi*. When comparing statistically the meristic data of the *subunicolor* types and our specimens with those of the *brygooi* types and east coast specimens attributed to *brygooi*, we found several significant differences. *Z. subunicolor* has a higher number of lamellae under the fourth toe (mean 20.3 versus 17.7, $p < 0.001$), a higher number of scale rows around midbody (mean 23.5 versus 21.4, $p < 0.01$), and a lower number of femoral pores (mean 11.2 versus 16.4, $p < 0.001$). The interparietal scale is present in all *subunicolor* but in no *brygooi* specimens. Additionally, *Z. brygooi* lacks the dorsolateral stripes in the tail region typical for *subunicolor* (see above).

Z. subunicolor clearly differs from *Z. aeneus*. Main differences are the state of the supralabial posterior to the subocular (see diagnosis of *aeneus*), and the absence in *Z. subunicolor* of the distinct narrow dorsolateral stripes typical for *aeneus*. The dorsolateral stripes in the tail region, which are characteristic for *subunicolor*, do not occur in *aeneus*. Meristic differences are: a higher number of scales around midbody (mean 23.5 in *subunicolor* versus 19.7 in *aeneus*; $p < 0.005$), a lower number of femoral pores (mean 11.2 versus 14.9; $p < 0.001$), and a higher number of lamellae under the fourth toe (mean 20.3 versus 18.9; $p < 0.05$). The interparietal scale is present in *Z. subunicolor* but mostly absent in *aeneus*.

Redescription: Based on ZFMK 53984. Adult specimen in good state of preservation, collected 1992 by F. GLAW and J. MÜLLER-JUNG in Lokobe Strict Nature Reserve, Nosy Be, north-western Madagascar. The original tail is still fixed on body, but begins to break away about 5 ventral scales behind cloaca. A transversal cut is present on the venter, about 7 ventral scales before the cloaca. The tail is abruptly constricted just posterior to the sacral region, whereafter it is vertically compressed. Lateral fold continuous from tympanum to cloaca, very distinct and well-developed. There are three mite pockets in the antehumeral fold. Tongue with dark pigment.

Ventral scales are arranged in 8 longitudinal rows. There were 48 scales between chin and cloaca (MÜLLER 1993; some destroyed by transversal cut on venter). 21 lamellae under fourth toe. 12 femoral pores on right hindlimb, 11 on left hindlimb. 24 midbody scale rows between lateral folds. Midbody scales on flanks (6 rows on each side) semicircular, with a rounded posterior edge; midbody scales on back (5 rows on each side) square, with a straight posterior border. The median (vertebral) midbody scales (2 rows) triangular and intercalating. Some irregularities in dorsal scale rows in the inguinal region. Anterior to forelimb insertion the shape of the vertebral scales changes, becoming larger, semicircular, with a rounded posterior edge. Ventral scales smooth; lateral, dorsal and vertebral scales slightly keeled. There is one larger keel on each dorsal and vertebral scale, bordered by several smaller keels. On the lateral scales often all keels (up to 15) are similar, but sometimes the median keel is larger and bordered by up to 7 smaller keels on each side. On the dorsal and vertebral scales there is a different number of small keels on both sides of the large keel; 4-5 keels laterally and 2-3 medially on the dorsal scales and 10 medially and 2-3 laterally on the vertebral scales.

Snout-vent length 86 mm, tail length 143 mm. Maximum head width 14.9 mm, maximum head depth 11.5 mm,

maximum body diameter about 18 mm, distance between insertion point of fore- and hindlimbs 38 mm. Forelimb length 25.5 mm, length of hindlimb 45 mm, length of third forelimb toe 6.7 mm, forelimb toe 3 and 4 of same length; length of fourth hindlimb toe 15.5 mm.

Mental in contact with postmentals and first supralabials on each side. Posterior edge of mental somewhat pointed. Postmentals largely contact each other. Post-postmentals not in contact with each other; left post-postmental entire, right post-postmental divided into two scales. One small scale interposed between post-postmentals; contacts both postmentals and post-postmentals.

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

Colour in preservative is dorsally and laterally uniform light brown to cream, without dark spots. Only in the axillary region some light spots (9-10 on each side), generally covering exactly one scale, are present. These are of bluish colour. Fore- and hindlimbs dorsally of same colouration as restant body. From the hindlimb insertion on, the dorsolateral scale row is somewhat lighter than the surrounding scales. This light stripe continues onto the first half of the tail. The first dorsal scale row bordering the light dorsolateral scales has a contrasting dark brown colour. On the tail the vertebral scales also become darker, resulting in an indistinct dark vertebral stripe. Ventral side uniformly whitish. Other specimens have a less uniform colouration.

Habits and distribution: According to our observations *Z. subunicolor* is clearly rarer than *Z. rufipes*. On Nosy Be the species was only found in rainforest, whereas the single specimen from Nosy Komba occurred along a path near secondary forest. *Z. subunicolor* differs ecologically from *Z. rufipes* by preferring sun-exposed and dry areas in the forest, not occurring near brooks (see Tab. 3).

When caught, individuals of *Z. subunicolor* showed a remarkable skin autotomy. Larger parts of the dorsal scales went off during the collection of specimens. We observed this phenomenon also in *Z. brygooi* from Nosy Mangabe and, to a lesser extent, in *Z. rufipes*. Malagasy geckos of the genus *Geckolepis* are famous for a similar, more extreme skin autotomy, which probably functions as anti-predator mechanism.

Z. subunicolor is presently only known from its type locality Nosy Be, and from the neighboured island Nosy Komba. However, in 1991, we photographed a *Zonosaurus* specimen on Nosy Mangabe (Fig. 5) which shows typical colouration patterns of *Z. subunicolor*. This specimen occurred near the top of the island, in a rather sunny patch of forest characterized by rather small trees. Unfortunately it was not collected, so its status remains dubious. Further fieldwork is necessary to clarify whether *Z. subunicolor* is restricted to the Sambirano region or also occurs in eastern Madagascar.

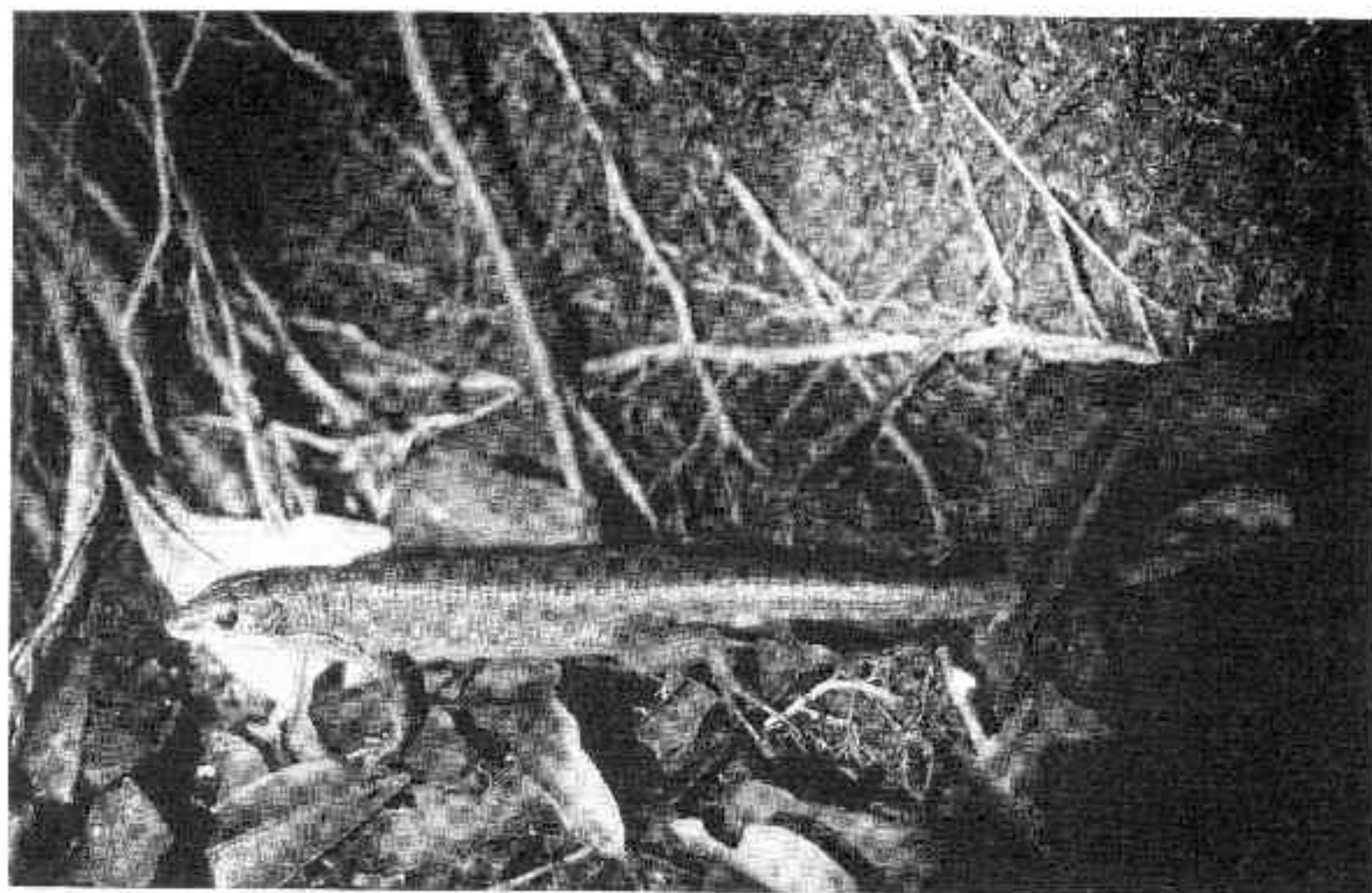


Fig. 5. *Zonosaurus* sp. from Nosy Mangabe. This specimen (not collected) shows colouration patterns typical for *Z. subunicolor*.

Discussion

The status of *Zonosaurus brygoi*

We found significant differences in several independent meristic characters between *Z. subunicolor* and *Z. brygoi*. Although the differences in colouration, number of femoral pores, and possibly even number of dorsal scale rows could theoretically be due to sexual dimorphism of a single species, such an origin is extremely improbable for the differences in number of lamellae under the fourth toe and in the presence or absence of an interparietal scale. These differences can at the present state only be understood as supporting a distinctness of the taxa.

Nevertheless, it must be considered that despite intensive surveys we were not able to confirm the presence of *Zonosaurus brygoi* on its type locality Nosy Be. Two alternative situations can be expected from future investigations:

a) *Z. brygoi* could be demonstrated to be absent from Nosy Be. In this case the type locality would be erroneous and due to a mistake of the collector. Nevertheless, the types of *Z. brygoi* correspond exactly with the east-coast populations, and thus *Z. brygoi* would be an allopatric sibling of *Z. subunicolor*. Many examples of amphibians and reptiles indicate that vicariant forms from the Sambirano region and eastern Madagascar generally are not due to gradual clines through Madagascar, but sharply separated taxa which often deserve specific status.

b) *Z. brygoi* could be rediscovered on Nosy Be. In this case the sympatric occurrence with *Z. subunicolor* would clearly demonstrate the validity of both species. The same argument would apply if *Z. subunicolor* would be discovered at Nosy Mangabe or other east coast localities.

Conservation

The Malagasy gerrhosaurids (genera *Zonosaurus* and *Tracheloptychus*) are rarely mentioned in the context of nature conservation. Individuals of the larger species are regularly exported to the pet markets of the USA and western Europe. Since trade with Malagasy gerrhosaurids is not regulated by CITES, no import statistics are available. Species as *Z. laticaudatus* and *Z. madagascariensis*, which are widely distributed in secondary habitats, are unlikely to be threatened by commercial collecting. Another situation is found in species with restricted distribution areas or specialized habitats such as *Z. haraldmeieri* and *Z. maximus*. The numbers of exported specimens of these taxa should be carefully examined, and, if necessary, maximum export quotas should be fixed.

As far as we know, the small species of the *Z. aeneus* group are presently not regularly exported. The rather low attractiveness of these species indicate that a threat from exportations is not likely. More important is the fact that all species of this group are more restricted to primary rainforest habitat than other *Zonosaurus*. Since Malagasy forests are increasingly destroyed by slash and burn agriculture ('tavy'), the survival of forest fauna is only assured in forested nature reserves within their distribution area. Up to now, the only reserve in which *Z. aeneus* is known to occur is the Special Reserve Analamazaotra (near Andasibe), but it may also occur in other preserved areas such as the Mantady National Park. *Z. brygoi* is known from the Strict Nature Reserve Betampona and the Special Reserve Nosy Mangabe; it can also be expected in other low-altitude east coast reserves (Mananara, Ambatovaky, Man-

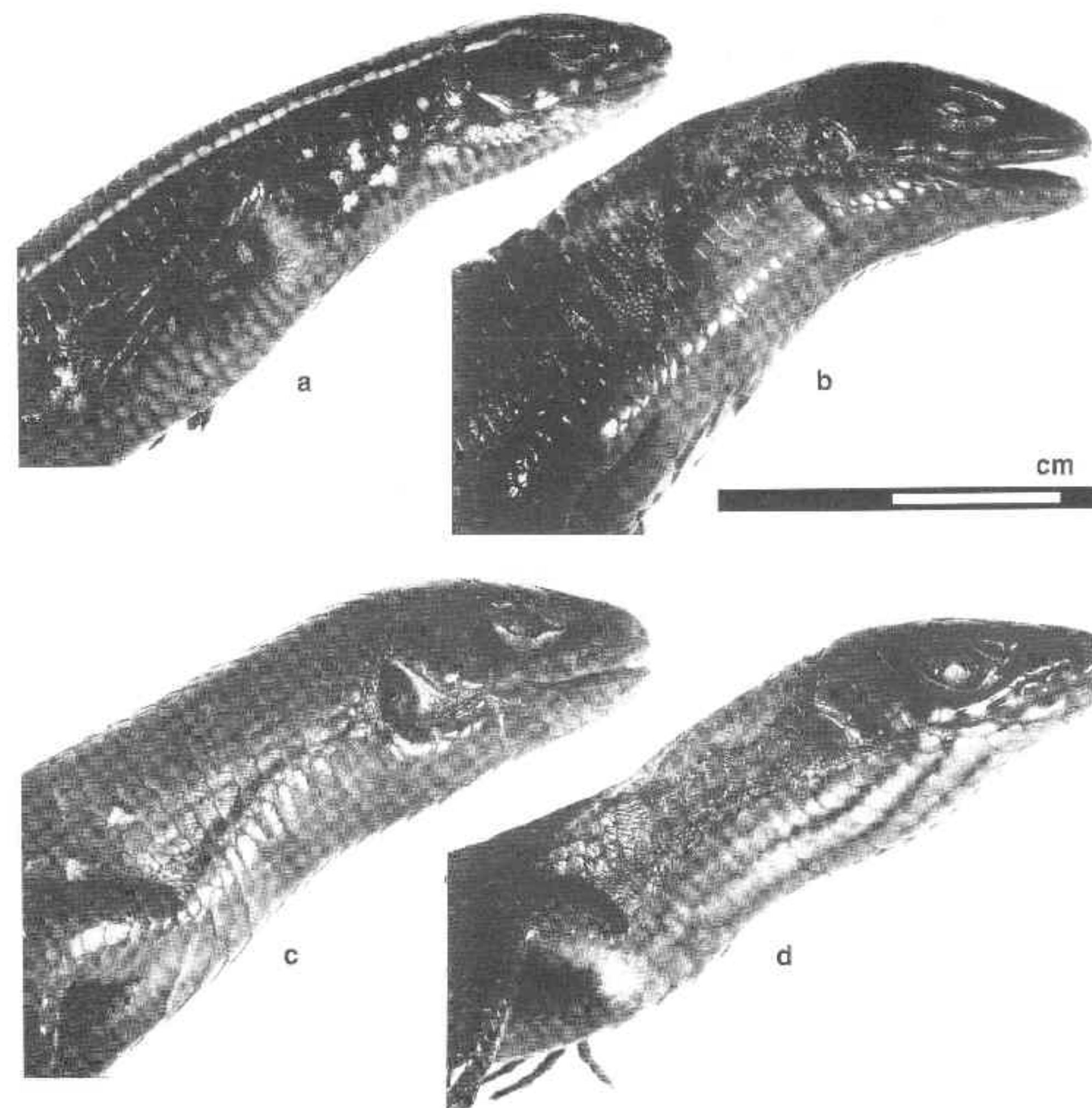


Fig. 6. Lateral view of head of the species of the *Zonosaurus aeneus* group. — a) *Z. aeneus* (ZFMK 59784); b) *Z. brygoi* (ZFMK 53152); c) *Z. subunicolor* (ZFMK 53984); d) *Z. rufipes* (ZFMK 53980).

gerivola), and its occurrence in the Strict Nature Reserve Lokobe (Nosy Be) needs confirmation. *Z. rufipes* is known from the Strict Nature Reserves Marojejy and Lokobe (Nosy Be), *Z. subunicolor* only from Lokobe. This latter reserve is therefore a rather important refuge for rainforest *Zonosaurus*; this status of Lokobe is further supported by the occurrence of *Z. boettgeri*, which seems to be a quite rare species, and by the possible occurrence of *Z. aeneus*.

Appendix

During our studies on the *Zonosaurus aeneus* group we made two additional observations, referring to other members of the genus, which we mention in the following.

A. *Zonosaurus karsteni* is known from several scattered localities in dry western Madagascar. Two localities exist for eastern Madagascar. These are Fianarantsoa (SMF 13991)

and Mandraka (MHNP 8887). After examination of SMT 13991 we conclude that the specimen is clearly misidentified; in fact it belongs to *Zonosaurus ornatus*, a species common at mid-altitude localities (and known from Trianantsoa; see BRYGOO 1985a). The specimen MHNP 8887, on the contrary, is clearly a *Z. karsteni*. It belongs to a series of three *Zonosaurus* specimens with the locality information „La Mandraka“. The other two specimens are *Z. trilineatus* (MHNP 8878) and *Z. laticaudatus* (MHNP 8879). These taxa are restricted to western (*Z. laticaudatus*) and southern (*Z. trilineatus*) Madagascar, and Mandraka was not considered as locality of these two species by BRYGOO (1985a). Moreover, of the whole series of Malagasy reptiles numbered as MHNP 8877-8937, only very few specimens were collected in eastern Madagascar. We therefore conclude that the specimen MHNP 8887 has been mislabelled, and that *Z. karsteni* is absent from eastern Madagascar.

B. Near Tolagnaro in south-eastern Madagascar we observed how temporal and spatial niches were segregated between *Zonosaurus laticaudatus*, a large species that inhabits dry regions as well as secondary habitats in humid areas (e.g. around Ambanja, north-western Madagascar), and the iguanid *Oplurus quadrimaculatus* (see MÜLLER 1993). Both species used partly the same resources (e.g. fruits and flowers of the same bush), but their daily activity periods were different. The territorial *Oplurus* left their refuges shortly after sunrise (around 6.30 h am), secured their territories by head-bobbing, and began with foraging. *Oplurus* foraging generally was finished when the first *Zonosaurus laticaudatus* appeared (first observation: 7.30 h am, generally 8.30–9.00 h am). Main activity period of the *Zonosaurus* was around 10 h am; at this time most *Oplurus* were basking on the surrounding rocks.

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museums available for this study. JÖRN KÖHLER and FRANCO ANDREONE made some of the photographs. MARIUS BURGER contributed a locality record of *Z. aeneus* (near Tolagnaro). We thank the Malagasy authorities for the permissions to enter nature reserves and collect specimens; part of the fieldwork of FRANK GLAW was made possible by a cooperation accord between the Zoological Institute of the University of Antananarivo, Madagascar, and the ZFMK, and was financially supported by the Heinrich Hertz-Stiftung of the Ministerium für Wissenschaft und Forschung NRW and the Deutscher Akademischer Austauschdienst.

Zusammenfassung

Eine taxonomische Revision der *Zonosaurus*-Arten mit drei Supralabialia vor dem Suboculare (bisher *Z. aeneus*, *Z. rufipes*, *Z. brygoi*; hier als *Z. aeneus*-Artengruppe bezeichnet) zeigte die Validität des Taxons *Gerrhosaurus rufipes* var. *subunicolor* BOETTGER 1881, das in der vorliegenden Arbeit als *Zonosaurus subunicolor* revalidiert wird. Diese Art kommt sympatrisch mit *Z. rufipes* vor und ist durch Zeichnungsmerkmale wie durch Habitatpräferenzen charakterisiert. *Z. subunicolor* unterscheidet sich von *Z. brygoi* durch die geringere Anzahl Femoralporen, die höhere Zahl von Schuppenreihen um die Körpermitte, die größere Anzahl von Lamellen unter der vierten Zehe und die Existenz eines (kleinen) Interparietale.

Z. aeneus und *Z. brygoi* können durch die Zeichnung und die Ausprägung des ersten Supralabiale hinter dem Suboculare unterschieden werden. Es ist bei *Z. aeneus* ungeteilt und bei *Z. brygoi* geteilt. Während *Z. aeneus* deutliche und bis zur Körpermitte durchgehende helle Dorsolateralstreifen besitzt, bestehen diese bei *Z. brygoi* aus einer unterbrochenen Reihe heller Flecken oder fehlen. *Z. aeneus* ist in mittleren Höhenlagen Ost-Madagaskars verbreitet, während *Z. brygoi* tiefliegende Gebiete an der Ostküste besiedelt. Das Vorkommen von *Z. brygoi* an seiner Typuslokalität, Nosy Be in Nordwest-Madagaskar, konnte durch unsere Felduntersuchungen nicht bestätigt werden.

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