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New data on the zoogeography and genital morphology of the lizards *Zonosaurus brygooi* Lang & Böhme 1990 and *Z. aeneus* (Grandidier 1872) from Madagascar (Reptilia Squamata Gerrhosauridae)

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In the course of recent field surveys, specimens of the lizard *Zonosaurus brygooi* Lang & Böhme 1990 were collected at two localities in northeastern Madagascar (Besariaka and Tsararano rainforests), which are situated about 50-70 km north of Nosy Mangabe, the northernmost population so far reliably known. The species was not found at Anjanaharibe and Marojejy massifs, nor in the corridor which connects these areas. One specimen collected at Andohahela in the South-East, about 750 km south of Betampona, the southernmost population so far known, is provisionally referred to *Z. brygooi*. It differs, however, by the presence of four supralabials anterior to the subocular, a character that may indicate its taxonomic distinctness. Together with two new locality records of *Z. aeneus* (Grandidier 1872), the new material enables us to discuss the distribution and zoogeography of the *Z. aeneus* group (*Z. aeneus, Z. brygooi, Z. rufipes* and *Z. subunicolor*), and to describe the genital morphology of *Z. brygooi* for the first time. Our data indicate a possible seasonal variation in the hemipenis ornamentation of the species.

KEY WORDS: Reptilia Gerrhosauridae, *Zonosaurus aeneus*, *Zonosaurus brygooi*, distribution, hemipenis description, seasonal hemipenis variation.

INTRODUCTION

Malagasy gerrhosaurids are moderately sized to large terrestrial lizards classified into two endemic genera, *Zonosaurus* Boulenger 1887 and *Tracheloptychus* Peters 1854 (Brygoo 1985). According to Lang (1991) they constitute a monophyletic group (subfamily Zonosaurinae) when compared to African genera (subfamily Gerrhosaurinae).

To date the genus *Zonosaurus* contains 13 species (Glaw & Vences 1994) which are mostly inhabitants of open landscapes. The rather adaptable *Z. madagascariensis* (Gray 1831) is usually a savannah inhabitant, although it may be found also in open spaces (e.g., deforested areas, or along streams) within true rainforests. Only three species, *Z. rufipes* (Boettger 1881), *Z. subunicolor* (Boettger 1881) and *Z. brygooi* Lang & Böhme 1990 are known to be more restricted to a rainforest habitat (Vences et al. 1997). Together with a fourth species living, as far as known, at rainforest edges, *Z. aeneus* (Grandidier 1872), these species share several characters, such as small size, three supralabials anterior to subocular, and two to three well defined mite pockets in the antehumeral fold, and are therefore likely to be a monophyletic group (Lang 1990). Vences et al. (1997) reviewed this group (defined as *Zonosaurus aeneus* group), formally resurrecting and redescribing *Z. subunicolor*, and providing new descriptions and definitions of *Z. aeneus* and *Z. brygooi*. However, several questions regarding the distribution of the four taxa still remain unsolved, especially the lack of confirmation of the presumed type locality of *Z. brygooi* (Nosy Be according to Lang & Böhme 1990) by our own surveys. Due to the recent herpetological fieldwork of F. Andreone and colleagues (see Randrianirina 1998), we were able to examine new material of *Z. brygooi* from three new localities in northeastern and southeastern Madagascar. Additionally, examination of specimens held in the Natural History Museum (London) yielded new localities of *Z. aeneus*.

The aim of the present paper is to discuss the distribution and zoogeography of the *Z. aeneus* group, especially of *Z. brygooi* and *Z. aeneus*, considering the new material. We also describe for the first time the genital morphology of a representative of the *Z. aeneus* group (*Z. brygooi*), and provide information on the ecology of the species.

MATERIALS AND METHODS

Museum acronyms used in the analysed material are BM (The Natural History Museum, London), MRSN (Museo Regionale di Scienze Naturali, Torino) and ZFMK (Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn). The terminology of the hemipenial characters follows Böhme (1988) and Ziegler & Böhme (1997). Scale counts and measurements were taken by Miguel Vences and Stefanie Visser. Abbreviations used in the text are SVL (snout vent length), TaL (tail length), HPL (hemipenis length). The following specimens were studied:

Zonosaurus aeneus: BM 96.10.9.5-9 [1] Ambohimanga, (most probably Ambohimanga Atsimo, 21°33'S 47°45'E), leg. C.I. Forsyth Major; BM 95.7.4.3, Ambohimitombo (= Ambohimitambo), Ambositra Fivondranana, Fianarantsoa, 20°43'S 47°23'E, 1200 m a.s.l., leg. C.I. Forsyth Major.

[1] (BM 96.10.9.7-9 are not individually labelled; one of these specimens, here attributed to BM 96.10.9.9, is a juvenile which we did not measure in detail).

Zonosaurus brygooi: MRSN R1642, Besariaka-Amponaomby forest, Campsite 1 (Ambinaninimiakamidina [2]), Andapa Fivondronana, Antsiranana (Diégo Suarez) Province, 14°50'45"S 49°35'40"E, 940 m a.s.l., leg. J.E. Randrianirina 28.IV.1996; MRSN R1643 (FN 5180), Besariaka-Amponaomby rainforest, Campsite 2 (Ambinanin'antsahamaloto), Andapa Fivondronana, Antsiranana (Diégo Suarez) Province, 14°49'39"S 49°35'44"E, 850 m a.s.l., leg. F. Andreone and J.E. Randrianirina 16.VI.1996; MRSN R1644 (FN 5278), Besariaka-Amponaomby rainforest, Campsite 2 (Ambinanin'antsahamaloto), Andapa Fivondronana, Antsiranana (Diégo Suarez) Province, 14°49'39"S 49°35'44"E, 850 m a.s.l., leg. F. Andreone and J.E. Randrianirina 26.VI.1996; MRSN R1645.1-2 (FN 6139-6140), Tsararano rainforest, Campsite 1 (Antsarahan'ny tsararano), Andapa Fivondronana, Antsiranana (Diégo Suarez) Province, 14°54'40"S 49°41'23"E, 700 m a.s.l., leg. J.E. Randrianirina 16.X.1996; MRSN R1646 (FN 6159), Tsararano rainforest, Campsite 1 (Antsarahan'ny tsararano), Andapa Fivondronana, Antsiranana (Diégo Suarez) Province, 14°54'40"S 49°41'23"E, 700 m a.s.l., leg. J.E. Randrianirina 17.X.1996; MRSN R1647.1-3 (FN 6248-6250), Tsararano rainforest, Campsite 1 (Antsarahan'ny tsararano), Andapa Fivondronana, Antsiranana (Diégo Suarez) Province, 14°54'40"S 49°41'23"E, 700 m a.s.l., leg. F. Andreone and J.E. Randrianirina 29.XI.1996; ZFMK 66656-66657, Ambatobe near Ambohitralanana, Antalaha Fivondronana, Antsiranana (Diégo Suarez) Province, 15°40'S 50°39'E, leg. K. Schmidt.

Zonosaurus cf. *brygooi*: MRSN R1144, forest between Isaka-Ivondro and Eminiminy, Andohahela Strict Nature Reserve, Tolagnaro (Fort Dauphin) Fivondronana, Toliara (Tuléar) Province, 24°45'30"S 46°51'15"E, leg. F. Andreone 14.XI.1994

Additionally, in Table 1 we include meristic data and measurements of some ZFMK specimens for which only incomplete data were given in Vences et al. (1997).

RESULTS AND DISCUSSION

Morphology

Meristic and morphometric data of the examined new material, as presented in Table 1, confirm the ranges and mean values given by Vences et al. (1997). All *Z. aeneus* examined (except ZFMK 62321 which shows an interesting aberration of colour pattern in the head region; see Glaw & Vences 1994: fig. 477) showed the diagnostic character of this species (supralabial posterior to subocular undivided). On the contrary, this scale was always divided in the new material of *Z. brygooi*.

Also colour patterns of the new material correspond to the diagnostic patterns as described by Vences et al. (1997). All *Z. aeneus* have continuous, distinct light dorsolateral stripes along the anterior half of the body, whereas *Z. brygooi* has distinct and sharply defined (not faded), discontinuous stripes which form a row of spots). Only in one juvenile specimen (MRSN 1644) are the stripes more continuous. No distinct dorsolateral stripes on the posterior back and anterior tail (typical for *Z. subunicolor*) nor longitudinal black throat stripes (typical for *Z. rufipes*) were recorded. The specimen BM 96.10.9.7 has a total length of 179.4 mm, being the largest known individual of *Z. aeneus*. All *Z. rufipes* specimens examined (including the juveniles < 40 mm SVL; see Table 1) show the black throat stripes typical for this species.

In life, the specimens of *Z. brygooi* captured at Besariaka and Tsararano were brownish on the back, with darker flanks, more contrasted in females. The throat and anterior breast were orange-reddish in the studied males, as well as the ventral side of the forelegs. In probable female specimens the throat was whitish-yellowish.

[2] The names of campsites were given by local people, and must be regarded as unofficial.

Table 1.

Morphometric and meristic data of the examined specimens of *Zonosaurus aeneus*, *Z. brygooi* and *Z. rufipes*. Abbreviations used: SVL (snout-vent length), TaL (tail length), FemPor (number of femoral pores), IP (interparietal scale: + present, – absent), Mid.Bod. (number of dorsal scale rows around midbody), Ch-Cl (number of scales between chin and cloaca), 4.Toe (number of lamellae under 4th toe). Lengths of regenerated or amputated tails are given in brackets. The locality of ZFMK 59798 was given as "near Tolagnaro" in VENCES et al. (1997). Its exact locality is a forest near Mandromodromotra, ca 20 km north of Tolagnaro, 24°06'S 46°58'E.

Collection No.	Locality	SVL+TaL (mm)	FemPor	IP	Mid.Bod.	Ch-Cl	4.Toe
Zonosaurus brygooi							
MRSN R1642	Besariaka, Camp 1	67+87	17/17		20	44	18/18
MRSN R1643	Besariaka, Camp 2	72+91	17/16	–	17	47	–
MRSN R1644	Besariaka, Camp 2	33+51	19/19	–	19	44	18/18
MRSN R1645.1	Tsararano, Camp 1	62+100	15/15		20	47	19/18
MRSN R1645.2	Tsararano, Camp 1	66+90	16/16	–	21	47	19/19
MRSN R1646	Tsararano, Camp 1	73+105	15/15	–	20	46	–
MRSN R1647.1	Tsararano, Camp 1	67+100	16/16	–	22	46	17/17
MRSN R1647.2	Tsararano, Camp 1	69+105	20/18	–	21	47	18/19
MRSN R1647.3	Tsararano, Camp 1	71+97	17/16	–	22	48	21/21
ZFMK 46795 (PT)	Nosy Be?	49+75	18/18	–	22	47	19/20
ZFMK 53152	Nosy Mangabe	78+121	16/16	–	24	45	18/18
ZFMK 66656	Ambatobe	67+120	17/16	–	22	46	20/20
ZFMK 66657	Ambatobe	69+(–)	17/16	–	24	47	21
Zonosaurus cf. *brygooi*							
MRSN R1144	Andohahela	85+(–)	17/16	–	22	45	17/18
Zonosaurus aeneus							
BM 96.10.9.5	Ambohimanga	76+(55)	14	–	21	–	18
BM 96.10.9.6	Ambohimanga	74+101	16	–	20	–	19
BM 96.10.9.7	Ambohimanga	69+110	14	–	20	–	16
BM 96.10.9.8	Ambohimanga	60+105	11	–	20	–	16
BM 95.7.4.3	Ambohimitombo	53+(–)	15	–	18		16
ZFMK 14365	Nosy Be?	57+94	13/14	–	19	52	19/19
ZFMK 59784	Andasibe	72+(–)	15/13	–	20	53	20/20
ZFMK 62321	Andasibe	71+90	13/12	–	21	51	20/20
ZFMK 21272	Fianarantsoa	67+80	15/15	–	20	50	21/21
ZFMK 59798	Mandromodromotra	50+89	16/16	–	20	54	19/19
Zonosaurus rufipes							
ZFMK 21270	Nosy Be	46+(57)	11/11	+	24	46	22/22
ZFMK 46796	Nosy Be	36+70	10/10	+	24	–	21/22
ZFMK 46797	Nosy Be	35+(35)	11/11	+	23	46	21/21
ZFMK 47295	Nosy Be	37+66	11/11	+	25	48	21/21
ZFMK 48239	Nosy Be	36+64	12/12	+	21	46	21/21
ZFMK 53978	Nosy Be	77+135	11/11	–	24	46	21/21
ZFMK 53979	Nosy Be	69+102	10/10	+	24	44	21/21
ZFMK 53980	Nosy Be	70+128	11/11	+	24	47	20/20
ZFMK 53982	Nosy Be	33+47	11/11	+	–	44	20/20

It was not possible to determine reliably the sex of specimens of *Z. subunicolor* as described by VENCES et al. (1997) due to a rather bad state of preservation of inner organs. However, one previously studied specimen of *Z. brygooi* (ZFMK 53152 from Nosy Mangabe) was an adult female containing two (probably immature) ovarian eggs as ascertained by dissection. The main difference between *Z. subunicolor* and *Z. brygooi* is the larger number of femoral pores in the latter; the fact that number of femoral pores of both male and female *Z. brygooi* is larger than in the known specimens of *Z. subunicolor* demonstrates that these differences are not due to sexual dimorphism.

One specimen (MRSN R1144) from the Andohahela low altitude rainforest is of doubtful specific attribution and was preliminarily named *Z.* cf. *madagascariensis* (ANDREONE & RANDRIAMAHAZO 1997). It is an adult male as shown by its well developed yellowish testes (testes size: left 6.5 × 5.5 mm; right 8.1 × 5.1 mm). We here assign it to *Z. brygooi* due to its similar meristic values (see Table 1) and colouration (distinct and sharply defined, discontinuous dorsolateral stripes on the anterior dorsum; otherwise rather uniform brownish dorsal surface). In life, it showed a bright orange-reddish throat colouration, similar to the specimens of *Z. brygooi* from NE Madagascar. Its prefrontals are separated; there are two supralabials posterior to the subocular, and three distinct mite pockets in the antehumeral folds (with a large number of small mites inside). However, the presence of four supralabials anterior to the subocular distinguishes the specimen from all other known *Z. brygooi* specimens. It is known that some variability in this character exists: in *Z. madagascariensis*, a species usually with four supralabials anterior to the subocular, BRYGOO (1985) found one specimen with only three on both sides of the head out of 80 examined individuals. On the other hand, the southeastern lowland forest is inhabited by several reptile species differing at the species level from their siblings found in the central-eastern lowlands. Examples include the colubrid snakes *Pseudoxyrhopus heterurus* (central east) and *P. sokosoko* (southeast), as well as *Stenophis gaimardi* (central east) and *S. carleti* from the southeast (DOMERGUE 1994, RAXWORTHY & NUSSBAUM 1994b). In this context, the aberrant head scalation of MRSN R1144, together with its southeastern locality (about 750 km south of its hitherto known distribution area) must be considered as possible indication of taxonomic distinctness. Two other specimens were observed in the same locality (ANDREONE & RANDRIAMAHAZO 1997) but unfortunately were not captured. More material is necessary for definite conclusions on the status of this population.

Genital morphology

The description of the hemipenis of *Z. brygooi* as follows is based on an analysis of the genital organs of MRSN R1647.2, an adult male specimen (Fig. 1; SVL 69 mm, TaL 105 mm, HPL ca 10 mm; size of the yellowish testes: left 4.9 × 3.5 mm, right 4.9 × 3.3 mm). Hemipenis rather stout, getting broader from the slim pedicel towards truncus and apex. Apex with a slight bilobed appearance. Pedicel smooth, without ornaments. Apex and upper truncus covered with plicae (petala sensu SAVAGE 1997). Sulcus spermaticus bordered by distinct lips and underlaid with dense binding tissue. Sulcus has a basal, exteriorly directed curve and continues almost straightly to the apex. Terminally it is directed laterally to both faintly expressed lobes and ends between the plica ornamentation. The terminally diverging part of the sulcus appears darker than the surrounding tissue. Except for the

sulcus and the plica ornamentation, the hemipenes appear rather hyaline. At least basally, the retractor muscle can be seen through the thin skin. There are 12-14 rows of plicae which horizontally surround the top of the organ, nearly reaching the sulcus. The plica ornamentation is divided by five vertical furrows into six more or less distinct compartments. These plica compartments show a slightly tubercular surface and a tendency to express a median vertical comb-structure. On

Fig. 1. Hemipenis of *Zonosaurus brygooi* (MRSN R1647.2): (a) schematic overall view of right organ in situ, (b) detailed view of left organ (left sulcal view, right asulcal view).

the asulcal side, slightly below the plica compartments, the truncus bears a median, transverse fold, building a pouch-like structure. This hemipenial pouch is, according to BÖHME (1988), a synapomorphic character of the genera *Gerrhosaurus*, *Trachelopiychus* and *Zonosaurus*. In the hemipenis of *Z. brygooi*, the pouch is divided by a median tissue band which is separately connected to the truncus.

Additionally, everted hemipenes of two other adult male specimens of *Z. brygooi* were available for comparison. The hemipenes of MRSN R1647.1 (SVL 67 mm, TaL 100 mm, HPL ca 7-8 mm; testes size: left 4.9 × 3.6 mm, right 5.0 × 3.2 mm) correspond well to those of MRSN R1647.2. On the contrary, the everted right hemipenis of MRSN R1643 (SVL 72 mm, TaL 91 mm, HPL about 8 mm; size of testes: left 6.3 × 4.3 mm, right 6.1 × 4.0 mm) is of a remarkably hyaline appearance and poorly structured. The tendency of a terminally bilobed overall structure is easily seen, but the sulcus spermaticus is only slightly emphasised and plicae are faintly expressed and only terminally recognisable. The specimen was collected at Besariaka-Amponaomby during the cold season (June), whereas MRSN R1647.1 and R1647.2 were captured at Tsararano during the hot rainy season (November). Generally, in Malagasy reptiles breeding takes place during the rainy season (GLAW & VENCES 1996). The differences in hemipenial ornamentation may therefore be due to seasonal factors. The testes of MRSN R1643 were large (even slightly larger than those of MRSN 1647.1-2), suggesting that this specimen may also have been collected in breeding condition; however, nothing is known of gonadic cycles in *Zonosaurus*. According to BÖHME (1988), seasonal variation of squamate outer genital structures are only known for members of the families Lacertidae, Chamaeleonidae and perhaps Iguanidae. A possible indication of such a phenomenon in teid lizards is provided by ZIEGLER & BÖHME (1997) but still has to be verified in further material.

Ecology

Although several specimens of *Z. brygooi* from Tsararano were observed during the day, all specimens examined were captured in pitfall traps (see RAXWORTHY et al. 1998 for detailed pitfall description) buried along a stream, in a quite open area exposed to the sun. Other pitfall lines were built up in the same locality but yielded no additional specimens, indicating that at Tsararano *Z. brygooi* lives mainly along streams in open areas. At the same site many *Z. madagascariensis* were also observed, but generally in even more exposed areas. They were never seen next to the drift fence nor captured in the pitfalls. This corresponds with the observations of VENCES et al. (1997) on Nosy Mangabe, and suggests that in rainforests sympatric *Z. brygooi* and *Z. madagascariensis* do not share the same microhabitat. *Z. brygooi* specimens were active during the daylight, mainly in the late morning and early afternoon, especially during dryer periods when sun exposition was more continuous. Other syntopic species captured in great number in pitfall traps were *Amphiglossus moroundavae* and *A. melanopleura*. At Besariaka the habitat appeared more disturbed than at Tsararano, due to the human deforestation activity. Many cleared areas were visible within the forest. Here, *Z. brygooi* was found along the stream Betsivakiana during the hottest hours of the day, but it must be taken into account that this survey was carried out during the cold (dry) season.

The specimen MRSN R1144 from Andohahela low altitude rainforest was observed in November within the forest, after a prolongated period of drought. The three observed specimens at this locality were active in late morning-midday.

Distribution and zoogeography

Published localities of the species of the *Z. aeneus* group have been largely discussed in VENCES et al. (1997). Localities given in the following list are based on VENCES et al. (1997) unless otherwise stated. Locality numbers correspond to those in Fig. 2. *Z. aeneus*: (1) Antorotorofotsy, (2) Mandraka, (3) Andasibe, (4) Moramanga, (5) Anosibe, (6) Ambohimitombo (BM voucher specimen), (7) Ambohimanga

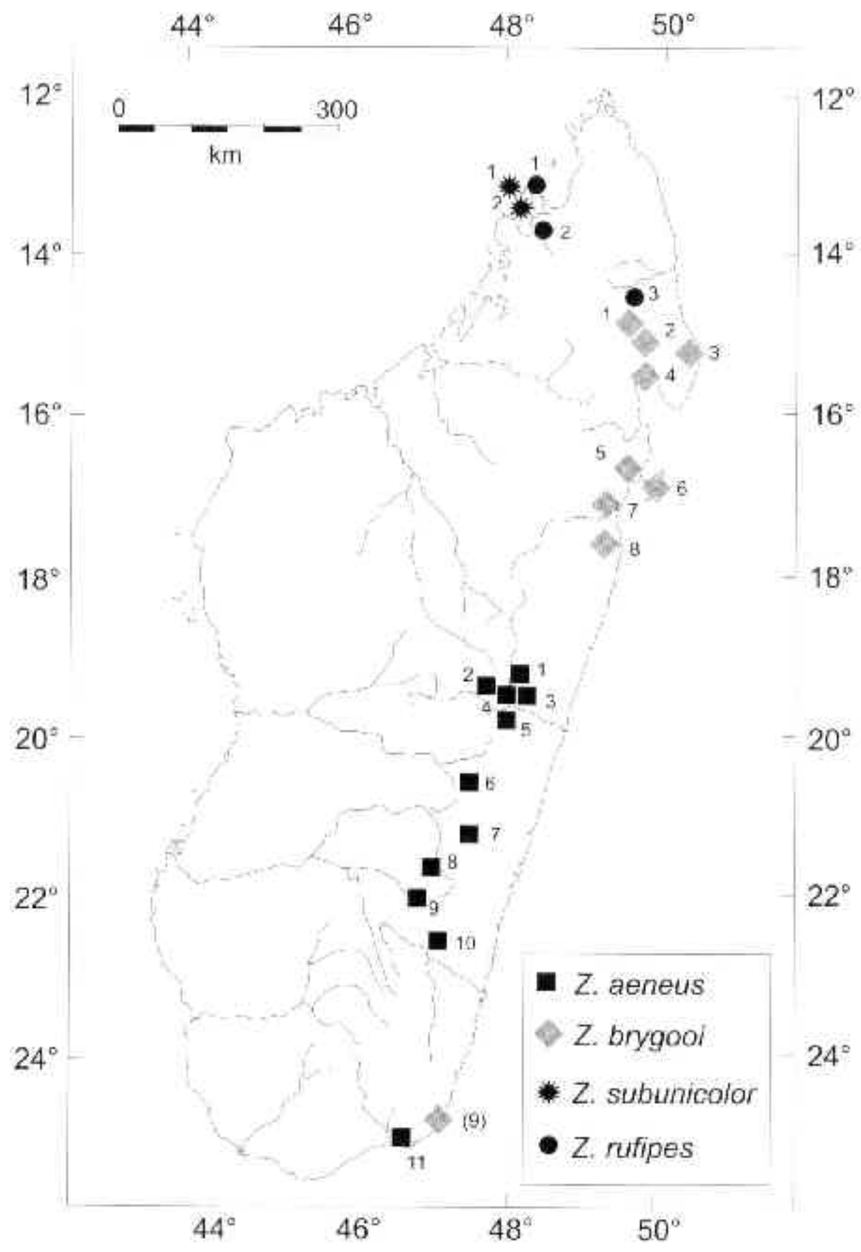

Fig. 2. — Distribution map of the species of the *Z. aeneus* group. Locality numbers correspond to those in the text. Localities considered as erroneous or in need of confirmation are not included.

(BM voucher specimens), (8) Fianarantsoa, (9) Ikongo, (10) Ivohibe, (11) Mandromodromotra (near Tolagnaro). *Z. brygooi*: (1) Tsararano (MRSN voucher specimens), (2) Besariaka-Amponaomby (MRSN voucher specimen), (3) Ambatobe (ZFMK voucher specimens), (4) Nosy Mangabe, (5) Manompana, (6) Nosy Boraha, (7) Fenoarivo, (8) Betampona, (9) Andohahela (MRSN voucher specimen; Z. cf. *brygooi*). *Z. rufipes*: (1) Nosy Be, (2) Benavony, (3) Marojejy. *Z. subunicolor*: (1) Nosy Be, (2) Nosy Komba.

Localities considered as erroneous, or as in need of confirmation, in VENCES et al. (1997) are the following. *Z. aeneus*: type locality Malaimbandy, and Nosy Be, both in need of confirmation. *Z. rufipes*: Imerina, probably erroneous. *Z. subunicolor*: Nosy Mangabe (specimen pictured in VENCES et al. 1997: fig. 5), in need of confirmation. *Z. brygooi*: type locality Nosy Be, in need of confirmation. The presence of the species at Tsararano and Besariaka-Amponaomby sites, however, makes its occurrence at Nosy Be less unlikely since it reduces the gap between the known localities. The specific identity of one juvenile MNHN voucher specimen from Antsingy (western Madagascar; preliminarily attributed to *Z. brygooi* by VENCES et al. 1997) is still to be verified. Localities which could not be traced were Sakana and Manjabe forest (both *Z. brygooi*).

The distribution map (Fig. 2), which only contains the localities not considered as in need of confirmation or erroneous, shows that distribution patterns in the *Z. aeneus* group are largely in accordance with the zoogeographic zonation of Madagascar as outlined by ANGEL (1942) and modified by GLAW & VENCES (1994) and RAXWORTHY & NUSSBAUM (1995). *Z. subunicolor* is so far only reliably known from the Sambirano Region (= North-Western Region sensu RAXWORTHY & NUSSBAUM 1995). *Z. rufipes* occurs in the North-Western and North-Eastern Regions. *Z. brygooi* reliably occurs in the North-Eastern, Eastern, and possibly South-Eastern Regions, whereas *Z. aeneus* occurs in the Eastern and South-Eastern Regions. In the Eastern Region, *Zonosaurus brygooi* is so far mainly known from coastal low-altitude localities (contrasting with the north-eastern localities Tsararano and Besariaka-Amponaomby, at 600-850 m and 800-900 m respectively), whereas *Z. aeneus* is mainly known from mid-altitude localities. In the region around Tolagnaro and Andohahela, where *Z. aeneus* was found in lowlands, several amphibian and reptile species otherwise possibly restricted to mid-altitudes are known to nearly reach sea level along the forested coastal mountain chains and hills (e.g., *Boophis luteus*, *B. albipunctatus*, *B. boehmei*; GLAW & VENCES 1994, ANDREONE & RANDRIAMAHAZO 1997).

Until now, no populations of the *Z. aeneus* group are known from the Northern Region of Madagascar, and several intensive surveys (ANDREONE 1991, RAXWORTHY & NUSSBAUM 1994a; pers. obs.) seem to indicate that the group is absent at least from the Montagne d'Ambre National Park. Interesting areas to prospect are the mid-altitude areas of the northern part of the Eastern Region. Here, *Z. aeneus* populations reaching north of the hitherto known distribution borders can be expected. Surveys at low altitude sites south of Betampona and north of Andohahela may help clarifying the status of Z. cf. *brygooi* from Andohahela.

Zonosaurus brygooi was not found during field surveys on the Anjanaharibe chain. *Z. madagascariensis* was the only species of this genus collected both on the eastern and on the western slope (RAXWORTHY et al. 1998). *Z. brygooi* seems also to be absent from the Marojejy Massif and the Ambolokopatrika corridor which lies midway between Marojejy and Anjanaharibe (surveys carried out by F. Andreone and J.E. Randrinirina in May-June and November-December 1997). Its occurrence was confirmed only at Besariaka-Amponaomby and Tsararano rainforests. These

two rainforests, in some way, play the role of corridors towards the Masoala peninsula and Nosy Mangabe island, up to now the northernmost site of *Z. brygooi*. At Marojejy *Z. rufipes* occurs, and perhaps this is the southernmost location of the species. The reason for these distributional patterns must be carefully analysed. If *Z. brygooi* is really absent from Anjanaharibe and Marojejy it can be argued that these massifs, as well as the Ambolokopatrika and Betaolana ridges, may act as a barrier for the diffusion of *Z. brygooi* northwards, as well as for the movement of *Z. rufipes* southwards.

Of the four known species of the *Z. aeneus* group, three occur in the zoogeographic regions of northern Madagascar, and two (*Z. rufipes* and *Z. subunicolor*) seem to be endemic to these regions. According to LANG (1990), phylogenetically basal species of *Zonosaurus* mostly occur in southern and western Madagascar. In the case of the *Z. aeneus* group, it may be hypothesised that speciation largely occurred in northern Madagascar, as it is probable for several other amphibian and reptile groups with highest species diversity in this area, e.g. the cophyline anurans, and the dwarf chameleons of genus *Brookesia* (see RAXWORTHY & NUSSBAUM 1995). Also the green *Boophis* of the *luteus* group show a remarkable pattern of endemism in the northern regions (ANDREONE 1996).

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REFERENCES

ANDREONE F. 1991. Reptile field records from Malagasy rainforests. *Bollettino del Museo Regionale di Scienze Naturali, Torino* 9 (2): 437-460.

ANDREONE F. 1996. Another new green treefrog, *Boophis anjanaharibeensis* n. sp. (Ranidae: Rhacophorinae), from northeastern Madagascar. *Aqua, Journal of Ichthyology and Aquatic Biology* 2: 25-32.

ANDREONE F. & RANDRIAMAHAZO H. 1997. Ecological and taxonomic observations on the amphibians and reptiles of the Andohahela low altitude rainforest, S. Madagascar. *Revue Française d'Aquariologie et d'Herpetologie* 24 (3-4): 95-128.

ANGEL F. 1942. Les lézards de Madagascar. *Mémoires de l'Academie Malgache* 36: 1-193.

BÖHME W. 1988. Zur Genitalmorphologie der Sauria: funktionelle und stammesgeschichtliche Aspekte. *Bonner Zoologische Monographien* 27: 1-176.

BRYGOO E.R. 1985. Les Gerrhosaurinae de Madagascar (Sauria Cordylidae). *Mémoires du Muséum National d'Histoire Naturelle (A, Zoologie)* 134: 1-65.

DOMERGUE C.A. 1994. Serpents de Madagascar: Note liminaire sur des espèces nouvelles du genre *Stenophis* Boulenger, 1896 (Colubridae-Boiginae). *Archives de l'Institut Pasteur de Madagascar* 61: 121-122.

GLAW F. & VENCES M. 1994. A fieldguide to the amphibians and reptiles of Madagascar. Second edition, including mammals and freshwater fish. *Köln: Vences & Glaw Verlag*, 480 pp.

GLAW F. & VENCES M. 1996. Bemerkungen zur Fortpflanzung des Waldskinks *Amphiglossus melanopleura* (Sauria: Scincidae) aus Madagaskar, mit einer Übersicht über die Fortpflanzungsperioden madagassischer Reptilien. *Salamandra* 32 (3): 211-216.

LANG M. 1990. Phylogenetic analysis of the genus group *Tracheloptychus-Zonosaurus* (Reptilia: Gerrhosauridae) with a hypothesis of biogeographical unit relationships in Madagascar. pp. 261-274. In: Peters G. & Hutterer R., Edits. Vertebrates in the Tropics. *Bonn: Museum Alexander Koenig*, 424 pp.

LANG M. 1991. Generic relationships within the Cordyliformes (Reptilia: Squamata). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique (Biologie)* 61: 121-188.

LANG M. & BOHME W. 1990. A new species of the *Zonosaurus rufipes*-complex (Reptilia: Squamata: Gerrhosauridae), from Northern Madagascar. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique (Biologie)* 59: 163-168.

RANDRIANIRINA J.E. 1998. Contribution à l'étude écologique et biogéographique des amphibiens de la region nord-est de Madagascar (R.S. 4 d'Anjanaharibe-Sud, corridor de Besariaka et forêt de Tsararano). *Mémoire de Diplome d'Études Approfondies, University of Antananarivo* (unpublished).

RAXWORTHY C.J., ANDREONE F., NUSSBAUM R.A., RABIBISOA N. & RANDRIAMAHAZO H. 1998. Amphibians and reptiles of the Anjanaharibe-Sud Massif, Madagascar: elevational distribution and regional endemicity, pp. 79-92. In: Goodman S.M., Edit. A floral and faunal inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: with reference to elevational variation. *Fieldiana: Zoology (New Series)* 90: VII – 246.

RAXWORTHY C.J. & NUSSBAUM R.A. 1994a. A rainforest survey of amphibians, reptiles and small mammals at Montagne d'Ambre, Madagascar. *Biological Conservation* 69: 65-73.

RAXWORTHY C.J. & NUSSBAUM R.A. 1994b. A review of the Madagascan snake genera *Pseudoxyrhopus, Pararhadinaea*, and *Heterolisodon* (Squamata: Colubridae). *Miscellaneous Publications, Museum of Zoology, University of Michigan, Ann Arbor* 182: IV + 37.

RAXWORTHY C.J. & NUSSBAUM R.A. 1995. Systematics, speciation and biogeography of the dwarf chameleons (*Brookesia*; Reptilia, Squamata, Chamaeleontidae) of northern Madagascar. *Journal of Zoology, London* 235: 525-558.

SAVAGE J.M. 1997. On terminology for the description of the hemipenes of squamate reptiles. *Herpetological Journal* 7: 23-25.

VENCES M., MÜLLER-JUNG J., GLAW F. & BÖHME W. 1997. Review of the *Zonosaurus aeneus* species group, with resurrection of *Zonosaurus subunicolor* (Boettger 1881) (Reptilia: Squamata: Gerrhosauridae). *Senckenbergiana Biologica* 76 (1/2): 47-59.

ZIEGLER T. & BÖHME W. 1997. Genitalstrukturen und Paarungsbiologie bei squamaten Reptilien, speziell den Platynota, mit Bemerkungen zur Systematik. *Mertensiella* 8: 1-210.