

Phylogeography, systematics and conservation status of boid snakes from Madagascar (*Sanzinia* and *Acrantophis*)

MIGUEL VENCES & FRANK GLAW

Abstract

To assess the phylogeography and genetic variation of Malagasy boas of the genera *Acrantophis* (*A. madagascariensis*, *A. dumerilii*) and *Sanzinia* (*S. madagascariensis*), we analysed sequences of the 16S rRNA gene in 12 *Sanzinia* and seven *Acrantophis* specimens. We found a surprisingly high differentiation between eastern and western/north-western populations of *Sanzinia*. This divergence was almost twice as high as between the two *Acrantophis* species. In spite of the absence of diagnostic morphological differences between eastern and western *Sanzinia*, the species status of these two ancient phylogeographic clades is probable, but can not be fully ascertained. We therefore describe the western *Sanzinia* populations as a new subspecies, based on a holotype specimen from Ankarafantsika forest, and diagnosed by its colour pattern (brown vs. mostly greenish in the nominate subspecies) and genetic differentiation. Unlike two widespread frog species that have a phylogeographically complementary east-west distribution, in *Sanzinia* the western subspecies reaches the Sambirano region (including Nosy Be) and probably Montagne des Français in northern Madagascar, while the rainforests of southern Madagascar (around Tolagnaro) are populated by the eastern subspecies. The Madagascar boas are widely distributed, relatively abundant and their occurrence is not restricted to pristine natural habitats. The current extent of local exploitation of these boas for food and leather apparently does not really threaten the species. However, the occurrence of the new subspecies seems to be more closely associated with the endangered dry forests of western Madagascar, and its status should therefore be carefully monitored.

Key words: Reptilia: Squamata: Boidae: *Acrantophis madagascariensis*, *Acrantophis dumerilii*, *Sanzinia madagascariensis*; new subspecies; Madagascar; biogeography; phylogeny.

1 Introduction

From a biogeographical point of view, boas are one of the most enigmatic reptile groups occurring on Madagascar (MERTENS 1972, BRYGOO 1982). Boine boas are distributed in South and Central America, the Pacific region, and Madagascar (KLUGE 1991, 1993). Madagascar is populated by tree boas (*Sanzinia*) and ground boas (*Acrantophis*). Both genera have been united with the Neotropical *Boa constrictor* in a single genus *Boa* by KLUGE (1991), but the molecular phylogeny suggested by VENCES et al. (2001) supports the validity of the genera *Acrantophis* and *Sanzinia*. Differences in morphology (e. g., enlarged versus not enlarged labials) and those in habits (mainly arboreal versus terrestrial roosting) corroborate this view.

Acrantophis is considered to contain two species, *A. madagascariensis* and *A. dumerilii*, whereas *Sanzinia* only contains *S. madagascariensis* (GUIBÉ 1949, 1958). Taking into account the attractiveness of these large animals, their importance for hobbyists and zoos (e.g., PROGSCHA & LEHMANN 1970, FOEKEMA 1975, BRANCH & ERASMUS 1976, WENGLER 1996), and their potential to control rats and mice, it is surprising that very few basic natural history data from the field have become available so far. The distributional data of Malagasy boas as summarized by GLAW & VENCES (1994) were still based largely on the account of GUIBÉ (1958). MEIER (1980) had noted conspicuous colour differences between *Sanzinia* populations from eastern and north-western Madagascar, but no thorough analysis of distribution, taxonomy or phylogeography of these snakes has so far been carried out. The inclusion of Malagasy boas on the

appendix I of CITES is a result of the concern about their potential vulnerability by the pet trade (e.g., ANONYMOUS 1991). Basic information on their natural history, distribution and differentiation is necessary to assess the actual risk and the priorities for their conservation.

In this paper, we summarize distributional data for Malagasy boas, and study the external morphology and colouration of *Sanzinia* populations from all over the island. We also provide mitochondrial DNA sequence data for 12 *Sanzinia* and seven *Acrantophis* specimens that demonstrate a surprisingly high differentiation between *Sanzinia* populations from eastern and western Madagascar, and lead us to describe the western populations as a new subspecies.

2 Materials and methods

Voucher specimens were killed by injection of an anesthetic, fixed by injection of 5 % formalin and preserved in 70 % ethanol. Of the preserved specimens, tissue samples were taken from the musculature. Other specimens were anesthetized in the tail region by repeated application of local anesthetic (ice spray), and subsequently a minute sample of skin and attached muscle removed and the wound disinfected with pure ethanol. Specimens were kept for 1-2 days before being released to assure a preliminary healing of the wound. Before releasing specimens, a number of morphometric and meristic measurements were taken and colouration was recorded by photographs. For a list of metric and meristic characters taken, see caption to Tables 2-3.

Preserved specimens were examined from the collection of the Museum national d'Histoire naturelle, Paris (MNHN), which was one source of previous distributional data (GUIBÉ 1949, 1958). Further museum acronyms used herein are ZFMK (Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn) and ZSM (Zoologische Staatssammlung München).

Tissue samples were preserved in pure ethanol. DNA was obtained using salt extraction protocols and a fragment of the mitochondrial 16S rRNA gene was amplified using primers and protocols given in VENCES et al. (2001).

Sequences were aligned using Sequence Navigator software (Applied Biosystems). Few indels were observed (see VENCES et al. 2001), and an unambiguous alignment was therefore possible. Phylogenetic analysis was carried out using PAUP* 4b10 (SWOFFORD 2002), after selecting the preferred model of nucleotide substitution using Modeltest version 3.06 (POSADA & CRANDALL 1998). We calculated Maximum Likelihood trees using heuristic searches with the tree-bisection reconnection algorithm, and Maximum Parsimony trees using the same algorithm, and coding gaps alternatively as fifth state. Bootstrapping was performed to test the robustness of the tree topology; 100 replicates were carried out under Maximum Likelihood and 2000 replicates under Maximum Parsimony. Sequences were deposited in Genbank (accession numbers AY336060-AY336074). Accession numbers of previously obtained sequences are AF215276 (AD1) and AF215272 (SM1).

3 Results and discussion

3.1 Molecular phylogeography of Malagasy boas

The phylogenetic analysis of 16S rRNA gene sequences (484 nucleotides) from 12 *Sanzinia* and seven *Acrantophis* specimens (Fig. 1) distinguished three major clades: One clade containing all *Acrantophis*, one clade containing all *Sanzinia* from western

and north-western localities, and one clade containing all *Sanzinia* from eastern localities. Within *Acrantophis*, the observed divergence largely corresponded to specimens from the distribution areas of *A. dumerilii* (south-west) and *A. madagascariensis* (west and north-west; Figs. 1-2). However, the examined specimen from Berenty in the extreme south of Madagascar had a unique haplotype that clustered with the north-western specimens rather than with the *A. dumerilii* from the Toliara region.

The genetic divergence between the eastern and western *Sanzinia* clades was very high (Table 1). Between-clade differences were 15-18 substitutions (3.0-3.6 % uncorrected pairwise divergence), while within-clade variation was 0-4 substitutions (0-0.4 %) in the eastern and 0-7 (0-1.4 %) substitutions in the western clade (see Tab. 1 for values after application of the Jukes-Cantor correction). Indeed, rooting the cladogram in Figure 1 with any Neotropical boa as outgroup did not result in monophyly of *Sanzinia*, but placed the eastern *Sanzinia* as sister group of *Acrantophis*. This placement is almost certainly an artefact but it emphasizes the strong divergence between the eastern and western clades of *Sanzinia*. This divergence is even distinctly higher than between the two *Acrantophis* species. Excluding the Berenty haplotype, *A. dumerilii* (Toliara) differed from *A. madagascariensis* by only 8-10 substitutions (1.0-1.8 %).

3.2 Variation in coloration and morphology of *Sanzinia*

Meristic and morphometric data of the *Sanzinia* specimens examined are presented in Tables 2 and 3. Some other characters were invariable. All specimens had an undivided anal scale, and the subcaudals were undivided except for SM6 from Nahampoana in which they were partly divided. As obvious from the data, there is no clearly diagnostic difference between the eastern and western populations of *Sanzinia*. There is a slight tendency of western specimens to have a lower number of supralabials and infralabials, and possibly also of perioculars. The difference in infralabial number resulted to be statistically significant (Mann-Whitney U-test, $P < 0.01$), but the rather low number of specimens examined renders this statistical comparison rather unreliable as we cannot exclude a geographic pattern independent from subspecies assignation or a sexual dimorphism. In any case these tendencies do not constitute diagnostic differences because the values of both subspecies do overlap.

The basic colouration of *Sanzinia* is a dorsal and lateral ground colour from grey to brown or green, and a relatively regularly spaced series of dark lateral markings (Figs. 3-6). Within these dark markings, small light markings may be present, and the dark markings may further have a light border. The ventral surface also shows no consistent pattern; it is usually light coloured and can present few (MNHN 1906.94) or many (MNHN 8932, MNHN 1970.384-385, 1970.387) dark spots and markings, or be uniformly coloured (MNHN A225). Table 4 summarizes the variation of dorsal pattern in those *Sanzinia* individuals from which photos of colouration in life were available. It is evident that there is remarkable variability, and only a single character seems useful to distinguish more or less reliably between western and eastern populations: the basic adult colouration of the former is brown whereas that of the latter usually (but not always) has greenish tones. Besides the specimens listed in Table 4 (which informs about live colouration exclusively), this was also obvious in the preserved vouchers MNHN 8932, MNHN 1907.93, and MNHN 1970.384, while the vouchers from western Madagascar (1906.94, 1950.196, MNHN 1978.96-97) all had a basically brown colour. The syntype specimen MNHN 43 had a partly faded

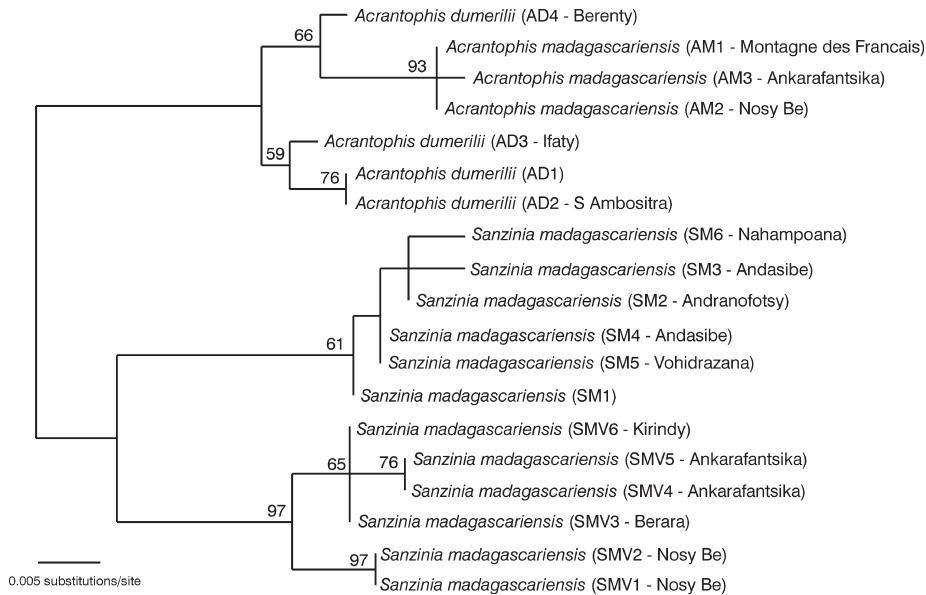


Fig. 1. Unrooted Maximum Likelihood phylogram based on 484 nucleotides from the 16S rRNA gene, showing the phylogeny of the available *Acrantophis* and *Sanzinia* samples. Numbers are bootstrap values in percent from a Maximum Likelihood analysis (100 replicates). The tree was calculated using a TrN+G substitution model selected by Modeltest. Maximum Parsimony analyses yielded largely compatible results, except for the position of the *Sanzinia* specimen from Nahampoana which was arranged at the basis of the eastern *Sanzinia* clade.

Maximum-Likelihood-Phylogramm der verfügbaren *Sanzinia* und *Acrantophis* Sequenzen, basierend auf der Analyse von 484 Nukleotiden des mitochondrialen 16S rRNA-Gens. Die Zahlen stellen Bootstrap-Werte (Maximum Likelihood; 100 Replikate) in Prozent dar. Der Baum wurde unter einem TrN+G Substitutionsmodell berechnet, welches mit Modeltest ausgewählt wurde. Parsimonie-Analysen erbrachten weitgehend kompatible Kladogramme, mit Ausnahme des *Sanzinia*-Exemplars aus Nahampoana, welches an die Basis der östlichen *Sanzinia*-Linie gestellt wurde.

colour; ventrally there were some dark markings, and most ocellae were extended to the ventral scales.

Several other factors render a colour-based determination of the two *Sanzinia* forms difficult: (1) juvenile colouration in *Sanzinia* is more contrasting than in adults, and the colouration tends to be more brownish; (2) the ontogenetic colour change of adult specimens is unknown (the age of specimens could be responsible for certain differences, e. g. the light borders of the dark spots); (3) the size (and therefore the age) and the sex of most animals on the photos is unknown; (4) the colour photos were taken from different photographers and were made with different exposures, perhaps leading to artificial colours in some cases; (5) at least one additional colour morph of unknown origin exists (ground colour yellowish, called "mandarine" among hobbyists).

An important consideration is the insufficient information on sexual dimorphism. First, the external distinction between male and female specimens is largely uncertain. We assume that male specimens have a distinct cloacal spur as usual in boas, but we

	SM1	SM2	SM3	SM4	SM5	SM6	SMV1	SMV2	SMV3	SMV4	SMV5	SMV6	AD1	AD2	AD3	AD4	AM1	AM2	AM3
SM1 <i>Sanzinia m. madagascariensis</i>	–	2	1	4	1	4	16	16	15	15	15	15	17	17	17	17	20	20	21
SM2 <i>Sanzinia m. madagascariensis</i> (Andranofotsy)	0.4	–	1	2	1	2	18	18	17	17	17	17	17	17	17	17	20	20	21
SM3 <i>Sanzinia m. madagascariensis</i> (Andasibe)	0.2	0.2	–	3	0	3	17	17	16	16	16	16	16	16	16	17	19	19	20
SM4 <i>Sanzinia m. madagascariensis</i> (Andasibe)	0.9	0.4	0.6	–	3	4	18	18	17	17	17	17	17	18	18	19	21	21	22
SM5 <i>Sanzinia m. madagascariensis</i> (Vohidrazana)	0.2	0.2	0.0	0.7	–	3	17	17	16	16	16	16	16	15	15	16	17	18	19
SM6 <i>Sanzinia m. madagascariensis</i> (Nahampoana)	0.9	0.4	0.6	0.8	0.6	–	18	18	17	17	17	17	17	15	15	16	18	18	19
SMV1 <i>Sanzinia m. volontany</i> (Nosy Be)	3.5	3.7	3.5	3.7	3.9	3.7	–	0	5	7	7	7	5	20	20	19	17	17	18
SMV2 <i>Sanzinia m. volontany</i> (Nosy Be)	3.5	3.7	3.5	3.7	3.8	3.7	0.0	–	5	7	7	5	20	20	19	18	17	17	18
SMV3 <i>Sanzinia m. volontany</i> (Berara)	3.3	3.5	3.3	3.5	3.6	3.5	1.0	1.0	–	2	2	0	19	19	18	19	18	18	19
SMV4 <i>Sanzinia m. volontany</i> (Ankarafantsika)	3.3	3.5	3.3	3.5	3.6	3.5	1.4	1.4	0.4	–	0	2	19	19	18	19	18	18	19
SMV5 <i>Sanzinia m. volontany</i> (Ankarafantsika)	3.4	3.6	3.4	3.6	3.6	3.5	1.5	1.5	0.4	0.0	–	2	19	19	18	19	18	18	19
SMV6 <i>Sanzinia m. volontany</i> (Kirindy)	3.3	3.5	3.3	3.5	3.6	3.5	1.0	1.0	0.0	0.4	0.4	–	19	19	18	19	18	18	19
AD1 <i>Acrantophis dumerilii</i>	3.8	3.8	3.5	4.0	3.6	3.3	4.4	4.4	4.2	4.2	4.3	4.2	–	0	3	6	9	9	10
AD2 <i>Acrantophis dumerilii</i> (S Ambositra)	3.8	3.5	3.3	3.7	3.3	3.1	4.2	4.1	3.9	3.9	4.0	3.9	0.0	–	3	6	9	9	10
AD3 <i>Acrantophis dumerilii</i> (Ifaty)	4.0	3.8	3.6	4.0	3.7	3.3	4.0	4.0	3.8	3.8	3.9	3.8	0.7	0.6	–	5	8	8	9
AD4 <i>Acrantophis dumerilii</i> (Berenty)	4.2	3.5	3.8	3.8	3.9	3.1	3.7	3.7	4.0	4.0	4.1	4.0	1.3	1.2	1.0	–	5	5	6
AM1 <i>Acrantophis madagascariensis</i> (M. des Français)	4.5	4.2	4.0	4.4	4.1	3.8	3.5	3.5	3.8	3.8	3.9	3.8	2.0	1.9	1.7	1.0	–	0	1
AM2 <i>Acrantophis madagascariensis</i> (Nosy Be)	4.4	4.1	4.0	4.3	4.0	3.7	3.5	3.5	3.7	3.7	3.8	3.7	2.0	1.8	1.6	1.0	0.0	–	1
AM3 <i>Acrantophis madagascariensis</i> (Ankarafantsika)	4.7	4.5	4.2	4.7	4.4	4.0	3.8	3.8	4.1	4.0	4.1	4.1	2.2	2.1	1.9	1.3	0.2	0.2	–

Tab. 1. Genetic distances between mitochondrial sequences of a fragment of the 16S rRNA gene (484 nucleotides) of Malagasy boas. Total pairwise substitutions are shown above the diagonal, percentages after Jukes-Cantor correction for multiple substitutions are shown below the diagonal. The bold numbers are comparisons between *Sanzinia m. madagascariensis* and *S. m. volontany* or between *Acrantophis madagascariensis* and *A. dumerilii* and show that the differentiation among the two *Sanzinia* forms is on average the double of that between the two *Acrantophis* species. Sample numbers are the same as used in Fig. 1.

Genetische Distanzen zwischen mitochondrialen DNA-Sequenzen eines Fragments des 16S rRNA-Gens (484 Nukleotide) bei madagassischen Boas. Die Tabelle zeigt die absolute Anzahl Substitutionen (oben rechts) und die Sequenzunterschiede in Prozent (Jukes-Cantor-Distanzen; unten links). Die fett gedruckten Werte sind Vergleiche zwischen *Sanzinia m. madagascariensis* und *S. m. volontany*, beziehungsweise zwischen *Acrantophis madagascariensis* und *A. dumerilii* und zeigen, dass die Divergenz zwischen den beiden *Sanzinia*-Formen im Mittel doppelt so groß ist wie zwischen den beiden *Acrantophis*-Arten. Die Nummern der Sequenzen stimmt mit denen in Fig. 1 überein.

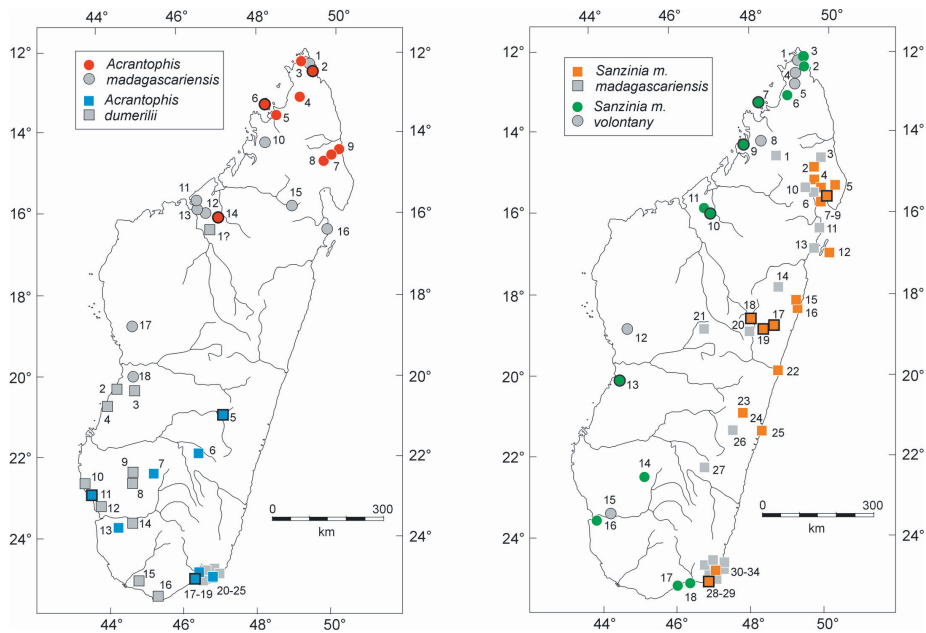


Fig. 2. Distribution maps of *Sanzinia* and *Acrantophis*. The coloured symbols represent localities from which a preserved specimen or photograph was examined by us. Grey symbols refer to localities taken from the literature or from photos that did not allow for a reliable specific/subspecific identification; assignment is especially doubtful for localities 1-4 of *Acrantophis dumerilii*. Furthermore, localities 1 and 30-34 of *Sanzinia m. madagascariensis* and localities 1-6 of *S. m. voluntary* need confirmation of subspecific assignment. Symbols with a strong black outline mark localities from which a DNA sequence was included in the analysis. Numbering corresponds to the locality record list in the appendix.

Verbreitungskarten von *Sanzinia* und *Acrantophis*. Die farbigen Symbole zeigen Fundorte, von denen konservierte Exemplare oder Fotos im Rahmen der vorliegenden Arbeit untersucht wurden. Die grauen Symbole stehen für nicht überprüfte Literaturangaben oder Fotobelege, die sich nicht zuverlässig zuordnen liessen. Dies trifft insbesondere auf die Fundorte 1-4 von *Acrantophis dumerilii* zu. Zudem muss die Unterart-Zuweisung der Fundorte 1 und 30-34 von *S. m. madagascariensis* und 1-6 von *Sanzinia m. voluntary* genetisch überprüft werden. Symbole mit deutlicher schwarzer Umrandung zeigen die Fundorte, von denen molekulargenetische Ergebnisse vorliegen. Die Nummerierung der Fundorte entspricht der Auflistung im Anhang.

do not know how dimorphic this character is in the Malagasy species. According to our data, in western populations, all *Sanzinia* specimens show a brownish colour, without greenish tones except a particular bluish-greenish-grey in subadult specimens from Ankarafantsika and Kirindy. This is also true for males as exemplified by the brownish ZSM 804/2001 from Ankarafantsika. In contrast, eastern specimens are usually olive-greenish, but sometimes brown specimens are found as well (Fig. 3f). These brown eastern specimens, however, usually seem to be rather large and stout specimens. It could be hypothesized that they are females, but the brown specimen SM4 from Andasibe had recognizable, though small, cloacal spurs. Observations of hobbyist breeders (available via the internet) indicate that the colour of females gets



Fig. 3. Colour and pattern in living *Sanzinia* specimens from eastern and north-eastern Madagascar, assignable to *S. m. madagascariensis* / Lebendfärbung und -zeichnung von *Sanzinia*-Exemplaren aus Ost- und Nordostmadagaskar, die sich der Nominatform zuordnen lassen. (a) Andapa, 1997 (K. SCHMIDT); (b) Nahampoana, December 2001 (genetic sample SM6); (c) Andohahela (F. ANDREONE, November 1994); (d) Ambohimamarivo, December 2001; (e) Vohidrazana, male, February 2001 (ZSM 803/2001; genetic sample SM5); (f) Andasibe, December 2001 (genetic sample SM4).

darker after successful mating. The correlations between sex and colour in eastern *Sanzinia*, and between sex and size of cloacal spurs, merit further studies.

3.3 Taxonomic conclusions

Despite the lack of consistent morphological differences between the eastern and western *Sanzinia* populations, we believe that the deep divergences observed between their mitochondrial haplotypes merit recognition as indicators of taxonomic distinctness. The degree of divergence observed between eastern and western *Sanzinia*

Catalogue Number	Locality	Sex	SPUR	SVL	TAL	HL	HW	ENS	EED	NND	ROSTH	ROSTWup	ROSTWlow
<i>S. m. madagascariensis</i>													
MNHN 43	Madagascar	SA		472	46	23	15	6.2	9.4	3.0	3.7	3.5	3.3
MNHN 1970.385	Besane	SA	(yes)	474	53	25	16	6.5	8.5	3.7	3.4	3.5	3.3
SM2	Andranofotsy	F?	no	1095	135	42	28	12.4	—	—	6.7	5.5	—
MNHN 1970.384	Ivoloina	A	(yes)	835	131	46	31	12.2	17.5	7.2	7.2	6.5	6.2
MNHN 1974.1105	Toamasina	SA	yes	434	46	24	17	6.5	9.0	4.0	3.3	3.4	3.2
ZSM 803/2001	Vohidrazana	M	yes	1190	118	42	31	11.8	17.0	6.6	6.9	6.6	6.1
SM4	Andasibe	M?	(yes)	1320	120	48	36	13.4	—	—	—	—	—
SM7 – not sequenced	Ambohimananarivo	F?	no	1240	130	43	32	13.5	—	—	—	—	—
MNHN A.225	Moramanga	SA	(yes)	402	49	22	14	6.0	8.5	4.0	3.2	3.3	3.0
MNHN 1975.134	Miarinarivo	SA	no	498	52	26	16	6.0	8.8	4.4	3.6	3.5	3.5
MNHN 1970.387	Ambatolampy	SA	(yes)	410	50	23	16	6.4	8.5	2.9	?	?	?
MNHN 1970.386	Ambatolampy	SA	no	452	54	23	14	6.4	7.1	3.9	3.4	3.2	2.9
MNHN 1992.5312	Mahanoro	M?	yes	1620	180	52	33	14.6	22.2	8.3	9.9	8.6	6.6
MNHN 1978.95	Ifanadiana	SA	(yes)	527	55	26	19	6.7	9.7	4.2	3.7	3.5	3.5
MNHN 1950.429	Ambohimanga	SA	no	401	45	22	15	5.7	8.7	3.8	3.3	3.3	2.5
MNHN 1907.94	Mandotra	SA	(yes)	425	48	24	15	6.4	8.3	4.1	3.7	3.4	3.3
MNHN 1907.93	Mandotra	SA	yes	792	79	35	25	9.9	13.4	6.0	5.1	4.9	4.1
SM6	Nahampoana	M?	yes	975	115	39	28	12.5	—	—	6.5	6.0	—
<i>S. m. volontany</i>													
SMV2	Nosy Be	M?	yes	1245	(42)	46	32	13.6	—	—	7.0	6.4	—
MNHN 1978.96	Ampijoroa	SA	(yes)	424	50	23	14	6.0	8.4	4.2	3.7	3.4	3.0
MNHN 1978.97	Ampijoroa	SA	(yes)	461	51	23	15	6.0	7.6	3.5	3.3	3.2	2.0
MNHN 8932	Bevazaha	M?	yes	1135	135	44	26	12.1	16.4	6.5	?	?	?
ZSM 804/2001	Ankarafantsika	M	yes	1420	158	52	32	14.1	19.0	8.2	8.2	7.0	5.4
MNHN 1906.94	Bas Fiherenana	SA	yes	579	59	25	18	7.4	10.6	4.5	4.3	3.6	3.5
MNHN 1950.196	Ambovombe	?	yes	1150	120	42	27	11.8	17.1	6.9	6.9	6.5	5.0

haplotypes is larger than that observed between the frog species *Boophis tephraeomystax* (east) and *B. doulioti* (west) (VENCES & GLAW 2002). We suspect that the divergence between eastern and western *Sanzinia* populations might reflect separation at the species level.

A related question is the status of the two species of *Acrantophis*. According to our data, the haplotypes of *A. dumerilii* and *A. madagascariensis* show only a relatively low divergence to each other, while a comparatively large differentiation is observed within either species. This pattern would rather suggest that only a single species with distinctly differentiated local populations or subspecies exists. Although we did not find any published data, several – though very unprecise – mentions of hybridization among the two *Acrantophis* species could be traced via the internet in November 2002. However, considering the relatively important differentiation between *A. dumerilii* and *A. madagascariensis* in head scalation (Fig. 7; see also GUIBÉ 1949, 1958) and the partly unclarified distribution of the two taxa, a conclusive statement on this issue is not possible at present.

According to our data, the genetic divergence between eastern and western *Sanzinia* almost doubles that between the two species of *Acrantophis*. If the species status of the two *Acrantophis* were unequivocal and distinct morphological divergence were present in *Sanzinia*, this could be seen as strong argument to distinguish the two *Sanzinia* forms at the species level. However, as discussed above, these two requirements are not fulfilled. Additionally, the persistence of ancient haplotypes in a population is not automatically indicative of taxonomic distinctness. Extremely divergent mitochondrial haplotypes persist in conspecific land snail populations (THOMAZ et al. 1996). Among and within probably conspecific populations of Malagasy snakes (*Madagascarophis*) and lizards (*Mabuya*) we have also observed the existence of moderately divergent haplotypes (Z. NAGY, P. MAUSFELD and M. VENCES, unpublished). The sample sizes of *Sanzinia* populations taken by us are insufficient

left page: Tab. 2. Morphometric measurements (in mm) of *Sanzinia* specimens examined. Abbreviations used: M, male; F, female; SA, subadult; SPUR, presence of cloacal spur (indistinct or small if in parentheses); SVL, snout-vent length; TAL, tail length; HL, head length; HW, head width; ENS, distance between anterior eye corner and posterior corner of nostril; EED, minimum distance between superior margins of eyes; NND, minimum distance between superior margins of nostrils; ROSTH, height of rostral scale; ROSTWup, width of rostral scale at its upper edge; ROSTWlow, width of rostral scale at its lower edge. Specimens are housed in the collections of the Muséum national d'Histoire naturelle in Paris (MNHN) or the Zoologische Staatssammlung München (ZSM). Other specimens were measured in the field and posteriorly released; they are identified by the sample numbers for genetic analysis (same as in Fig. 1 and Tab. 1).

Morphometrische Messungen (in mm) der untersuchten *Sanzinia*-Exemplare. Verwendete Abkürzungen: M, Männchen; F, Weibchen; SA, subadultes Tier; SPUR, Vorhandensein von After-Sporen (undeutlich oder klein wenn in Klammern); SVL, Kopf-Rumpf-Länge; TAL, Schwanzlänge; HL, Kopflänge; HW, Kopfbreite; ENS, Abstand zwischen Augenrand und Nasenloch; EED, Abstand zwischen dorsalen Augenrändern; NND, Abstand zwischen den Nasenlöchern; ROSTH, Höhe der Rostralschuppe; ROSTWup, Breite der Rostralschuppe am oberen Rand; ROSTWlow, Breite der Rostralschuppe am unteren Rand. Konservierte Exemplare stammen aus dem Muséum national d'Histoire naturelle, Paris (MNHN) oder der Zoologischen Staatssammlung München (ZSM). Weitere Tiere wurden im Freiland vermessen und wieder freigelassen; sie sind durch ihre Probennummern identifiziert, die mit denen der genetischen Analysen übereinstimmen (vgl. Fig. 1 und Tab. 1).



Fig. 4. Colour and pattern in living *Sanzinia* specimens from north-western, western and south-western Madagascar, assignable to *S. madagascariensis voluntany* / Lebendfärbung und -zeichnung von *Sanzinia*-Exemplaren aus Nordwest-, West- und Südwestmadagaskar, die sich *S. m. voluntany* zuordnen lassen. (a) Berara, February 2000 (genetic sample SMV3); (b) male holotype specimen, Ankarafantsika, 1 March 2001 (ZSM 804/2001, genetic sample SMV4); (c) Isalo, near Relais de la Reine (B. LOVE); (d) Berenty (E. GUTHMANN); (e) Nosy Be, December 2001 (genetic sample SMV2); (f) Kirindy, November 2000 (B. LOVE).



Fig. 5. Head portrait of a specimen of *Sanzinia m. madagascariensis* from south-eastern Madagascar / Kopfportrait eines Exemplars von *Sanzinia m. madagascariensis* aus Südostmadagaskar (Nahampoana 1992).



Fig. 6. Head portrait of the male holotype of *Sanzinia madagascariensis volontany* from Ankarafantsika in western Madagascar / Kopfportrait des Holotypus von *Sanzinia m. volontany* aus Ankarafantsika in Westmadagaskar (ZSM 804/2001, 1 March 2001).

Catalogue Number	Locality	V	SC	D	SUPL	SUPLF	SUPLE	INFL	INFLF	PEROC	INTOC	LOR	OCEL
<i>S. m. madagascariensis</i>													
MNHN 43	Madagascar	207	ca. 38	43	15-15	13-12	8,9	15-16	14-14	11-11	10	3-3	ca. 35
MNHN 1970.385	Besane	222	44	49	15-15	13-13	9,10	15-15	14-14	10-10	12		41
SM2	Andranofotsy	220	42	49	13	—	—	14	—	11	10	3	38
MNHN 1970.384	Ivoloina	213	38	45	13-14	12-12	8,9	15-15	14-14	8-9	11	2-2	38
MNHN 1974.1105	Toamasina	218	41	51	15-15	14-14	no contact	16-17	15-16	16-15	—	4-3	35
ZSM 803/2001	Vohidrazana	215	38	43	14-14	13-12	9,10-8,9	13-14	12-13	12-13	7	3-3	35
MNHN A.225	Moramanga	210	44	41	14-14	13-13	8,9	14-14	13-13	12-10	9	2-2	—
SM4	Andasibe	216	42	45	14	—	—	15	—	11	15	3	37
SM7 – not sequenced	Ambohimananarivo	218	35	43	14	—	—	15	—	10	10	2	35
MNHN 1975.134	Miarinarivo	211	42	47	13-13	12-12	9,10-8,9	14-15	13-14	11-12	10	2-2	36
MNHN 1970.387	Ambatolampy	?	40	43	14-?	13-?	9,10	15	14	11	11	3	39
MNHN 1970.386	Ambatolampy	199	41	41	14-13	11-12	8,9	14-15	13-14	10-10	?	2-3	39
MNHN 1992.5312	Mahanoro	214	42	41	14-14	13-13	9-9,10	15-15	14-13	12-12	9	4	38
MNHN 1978.95	Ifanadiana	214	40	43	13-14	12-12	8,9-7,8,9	15-15	14-14	11-11	9	3-3	34
MNHN 1950.429	Ambohimanga	215	ca. 38	41	14-14	13-13	8,9	16-15	14-13	9-9	9	2-2	—
MNHN 1907.94	Mandotra	232	45	49	14-15	13-13	9,10	15-15	14-14	10-8	12	2-3	ca. 41
MNHN 1907.93	Mandotra	226	39	47	15-15	13-14	9,10	16-16	15-15	11-11	10	3-3	32
SM6	Nahampoana	212	36	45	15	—	—	15	—	12	10	4	32
Mean		215.4	40.3	44.8	14.1	12.7	—	15.0*	13.9*	10.9	10.3	2.7	36.6
± standard deviation		±7.4	±2.8	±3.2	±0.7	±0.7	—	±0.8	±0.8	±1.7	±1.8	±0.7	±2.8
<i>S. m. volontany</i>													
SMV2	Nosy Be	230	(10)	50	14	—	9,10	15	—	9	10	2	(35)
MNHN 1978.96	Ampijoroa	215	42	43	13-13	12-12	8,9	13-13	12-12	8-8	9	2-2	37
MNHN 1978.97	Ampijoroa	216	46	47	13-15	12-13	8,9-8,9,10	14-14	13-12	8-7	10	3-3	36
ZSM 804/2001	Ankarafantsika	217	45	45	14-14	12-12	8,9	14-14	12-13	11-13	11	2-2	32-34
MNHN 8932	Bevazaha	203	41	41	14-?	13-?	8,9	14-13	13-12	10	10	?	ca. 33
MNHN 1906.94	Bas Fiherenana	208	36	39	12-14	11-13	7,8-8,9	13	12	10-10	10	3-3	ca. 31
MNHN 1950.196	Ambovombe	220	40	39	14-14	13-13	8,9	14-14	12-12	12-10	12	3-3	34
Mean		215.6	41.7	43.4	13.7	12.4	—	13.8*	12.3*	9.7	10.3	2.5	34.1
± standard deviation		±8.6	±3.6	±4.2	±0.8	±0.7	—	±0.6	±0.5	±1.8	±1.0	±0.5	±2.0

to significantly exclude that “eastern” haplotypes are also present in western populations and vice-versa. Ultimately, only studies of introgression of nuclear markers in contact or hybrid zones will clarify whether the eastern and western *Sanzinia* are reproductively isolated, and thus fulfilling the requirements for being recognized as separate species under a biological species concept. Microsatellite primers (MATSON et al. 2001) that have been developed for *Sanzinia* and *Acrantophis* will be very useful in this respect. Among snake breeders, *Sanzinia* are said to be sometimes difficult to breed and one reason for this could be genetic incompatibility between snakes from eastern and western Madagascar.

We nevertheless feel the urge to reflect the divergence between western and eastern *Sanzinia* populations (as already noted by MEIER 1980) by classification. We therefore propose to divide the eastern and western populations into two separate subspecies.

Sanzinia madagascariensis madagascariensis (DUMÉRIL & BIBRON, 1844)

Type material: MNHN 43, Madagascar (ROUSSEAU, syntype); MNHN 7329, Madagascar (SGANZIN [= SANZIN?], syntype). These two specimens are marked in the MNHN catalogue as types of *Sanzinia madagascariensis*. MNHN 7329 is a stuffed and mounted specimen in which scale counts and measurements are somewhat difficult; it seems to have 15 infralabials. MNHN 43 is a subadult specimen preserved in ethanol, and its morphometric and meristic data are given in Table 2 and 3. More research is necessary to assess whether both these specimens actually can be considered as types, and whether there might be other type specimens in other collections (see McDIARMID et al. 1999; BAUER et al. 2002). For this reason we here refrain from designating a lectotype.

left page: Tab. 3. Meristic and pattern data of *Sanzinia* specimens examined (same as in Tab. 2). Abbreviations used: V, number of ventral scales; SC, number of subcaudal scales; D, number of dorsal scale rows; SUPL, number of supralabial scales; SUPLF, number of supralabial scales bearing a distinct vertical furrow; SUPLE, supralabials (counted from the snout tip) which are in contact with the eye; INFL, number of infralabial scales; INFLF, number of infralabial scales bearing a distinct vertical furrow; PEROC, number of periocular scales; INTOC, minimum count of scales between the superior margins of the eyes; LOR, number of loreal scales; OCEL, number of ocellae (lateral dark markings, usually, with smaller white markings in their center). If two values are given separated by a dash, they refer to the left and right side of the head, respectively. Asterisks mark the mean values of those characters (INFL and INFLF) in which the two forms were significantly different (Mann-Whitney U-test; $P < 0.01$ after Bonferroni correction over 11 pairwise comparisons).

Beschuppungs- und Färbungsmerkmale der untersuchten *Sanzinia*-Exemplare. Verwendete Abkürzungen: V, Anzahl Ventralia; SC, Anzahl Reihen Dorsalia in der Körpermitte; SUPL, Anzahl Supralabialia; SUPLF, Anzahl Supralabialia mit deutlicher vertikaler Furchung; SUPLE, Supralabialia in Kontakt mit dem Auge; INFL, Anzahl Infralabialia; INFLF, Anzahl Infralabialia mit deutlicher vertikaler Furchung; PEROC, Anzahl von Schuppen rund um das Auge; INTOC, minimale Schuppenanzahl zwischen beiden Augen; LOR, Anzahl Lorealschuppen; OCEL, Anzahl von Ocellen (seitliche dunkle Flecken, meist mit kleineren weissen Flecken in ihrer Mitte) auf Körper und Schwanz. Zwei mit einem Bindestrich verbundene Werte wurden auf der linken und rechten Seite des Kopfes gezählt. Die Mittelwerte für INFL und INFLF, in denen signifikante Unterschiede zwischen den beiden Formen gefunden wurden, sind mit einem Stern markiert (Mann-Whitney U-tests; $P < 0.01$ nach Bonferroni-Korrektur für 11 paarweise Vergleiche).

Identity: Because at least one syntype of *Sanzinia madagascariensis* (MNHN 43; without precise locality) has a relatively high infralabial and supralabial count as more typical for eastern populations, we consider these as the nominate subspecies *S. m. madagascariensis*. An origin of the type specimens from eastern Madagascar is also probable since the species is more common and much more easily collected in this region.

Sanzinia madagascariensis voluntary n. ssp.

Holotype: ZSM 804/2001, adult male from Ampijoroa (Ankarafantsika Reserve), collected by M. VENCES, D. R. VIEITES, G. GARCÍA, V. H. RAHERISOA and A. RASOAMAMONJINIRINA on 1 March 2001 (Figs. 5b and 7).

Paratypes: MNHN 1978.96 and 1978.97, two subadult specimens from Ampijoroa, collected by C. DOMERGUE on 20 January 1965.

Further material: We assign four further specimens (MNHN 8932, 1906.94, 1950.196, 1966-977 see appendix) to this subspecies but do not include this material in the type series because we prefer to restrict it to a single locality (Ampijoroa) in which we verified distinct haplotypes and colouration in life for two specimens collected by ourselves.

Diagnosis: *Sanzinia madagascariensis voluntary* differs from *S. m. madagascariensis* by a predominantly brownish adult colouration (predominantly greenish in *S. m. m.*) and a high genetic differentiation in the 16S rRNA gene (Tab. 1) which is nearly twice as high as between *Acrantophis madagascariensis* and *A. dumerilii*. Morphologically, there is a tendency of the new subspecies to have a lower number of infralabials, and possibly of supralabials and perioculars (see Tab. 3), but none of these characters can be used as a reliably diagnostic difference.

Description of the holotype: Specimen in good state of preservation, fixed in formalin and stored in 70 % ethanol; hemipenis everted; lateral cut present; tissue sample for DNA studies removed. Total length 143 cm, counts and measurements are given in Tables 2 and 3. Head narrow, distinctly longer than wide; rostral more or less pentagonal, slightly higher than wide; one pair of internasals; anal scale undivided. The colouration in life is shown in Figures 4b and 6. The ground colour is light brown, with 32-34 dark brown markings of irregular shape on each side of the body (round, drop-like or triangular) which partly extend ventrally to contact the ventrals. In the posterior part of the body, the brown markings partly fuse in the vertebral region with each other, whereas they are generally not in contact in the anterior body part. Dorsally, the brown markings are bordered by a yellowish band which becomes broader and more distinct towards the vertebral region. In each dark marking, there is a yellowish marking of irregular shape (triangular, round or elongated). The head is dorsally brown and largely unspotted (Fig. 6) and ventrally whitish and unspotted. The ventral side of the body is whitish with numerous brownish spots which partly form irregular and interrupted dark bands. The subcaudal scales are largely brown. The colouration in preservative (after about 20 months) appears virtually identical to that in life, perhaps slightly faded. The light borders and the light markings in the brown markings have become partly whitish.

Variation: Based on the data of the seven specimens as given in Table 3, *S. m. voluntary* is characterized by the following meristic values: 203-230 ventrals; 36-46 subcaudals; 39-50 dorsals; 12-15 supralabial scales (11-13 of them with distinct vertical furrow), any supralabial between the 7th and 10th can have contact with the

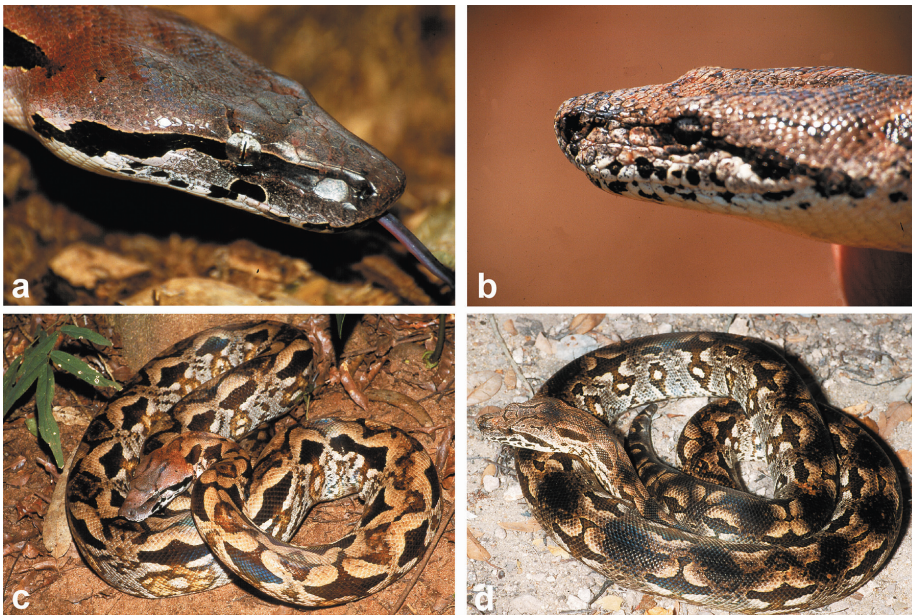


Fig. 7. Head scalation, colour and pattern in living specimens of *Acrantophis* / Kopfbeschuppung, Lebendfärbung und -zeichnung der beiden *Acrantophis*. (a) *A. madagascariensis*, Montagne des Français (genetic sample AM1), 2000 (K. SCHMIDT); (b) *A. dumerilii*, road between Toliara and Ranohira, 1997, note the small head scales / auffällig sind die kleinen Kopfschuppen; (c) *A. madagascariensis*, Ankarafantsika (ZSM 805/2001), 1 March 2001 (genetic sample AM3); (d) *A. dumerilii*, Ifaty, 2000 (genetic sample AD3).

eye; 13-15 infralabials (12-13 of them with distinct vertical furrow); 7-13 periocular scales; 9-12 interocular scales (as defined in Tab. 3); 2-3 loreal scales. Variation in colouration and patterns is shown in Figures 5 and 7 and described in Table 4.

Distribution (Fig. 2 and Appendix): The new subspecies is largely restricted to the dry western regions of Madagascar, from the private Berenty reserve in the southeast to Montagne des Français in the far north, but reaches rainforest in the Sambirano region (including Nosy Be).

Natural history: The general habits are apparently very similar to that of the nominate subspecies in that adults generally seem to spend the day in trees some meters above the ground whereas they become partly terrestrial at night (e. g. BLOXAM et al. 1996). On 9 March 2000, in the afternoon, we discovered an adult specimen on a tree in remnant rain forest on Nosy Be, about 5 m above the ground. In the karstic dry forest of Montagne des Français, after heavy rains several days earlier, we observed a juvenile on 14 March 2000 at night on a small tree, about 3 m above the ground and an adult specimen (at 264 m alt.) on 21 March 2000, also in a tree at night. At Windsor castle, a mating couple was observed by M. GRUBENMANN on the ground.

Etymology: The Malagasy word “volontany” means brown and refers to the predominant ground colour of the subspecies. It is used as invariable noun in apposition.

SSP	Locality	Source	Colour	DM	DM form	DM v.ext.	DM fused	LM	LB
SMM	Andapa	KS1997	olive green	brown-black	irregular	yes!	partly	beige	–
SMM	Andapa	FG1995	greenish	grey-black	rhomboid	(yes)	partly	white	white
SMM	Antanambao-Ampokafo	PB	brown	dark brown	drop-like	yes	partly	(beige)	–
SMM	Masala, littoral forest	PB	grey	brown-black	irregular	yes	partly	white	white
SMM	Andranofotsy	KS1995	green-grey	dark brown	irregular	?	?	beige	beige
SMM	Maroantsetra	GV1991	green-brown	black?	irregular	yes	?	white	(white)
SMM	Nosy Boraha	GV1991	brownish	black	oblong	partly	no?	(light brown)	–
SMM	Andasibe	MV2001	greenish-brown	grey-black	irregular	?	partly	beige	beige
SMM	Andasibe	GV1991	olive green	grey-black	irregular	?	no?	(–)	(–)
SMM	Ambohimananarivo	KS1995	greenish brown	dunkelbraun	drop-like	yes	?	white	white
SMM	Vohidrazana	MV2001	greenish	grey-black	irregular	yes	yes	white	white!
SMM	Andohahela	FA1994	greenish	green-grey	drop-like	yes	?	white	(whitish)
SMM	Nahampoana	GM1992	green	grey-black	rhomboid	partly	partly	white	white
SMM	Nahampoana	MV2001	olive green	green-brown	irregular	?	?	whitish	whitish
SMM	Andasibe juv.	GV1991	green	brown	irregular	yes	partly	(greenish)	(whitish)
SMM	Andasibe	GV1991	reddish brown	black	?	yes	?	yellowish	–
SMV?	Montagne des Français	MG	light brown	dark brown	irregular	partly	partly	light grey	–
SMV?	Montagne des Français	KS2000	brownish	grey-black	?	?	?	whitish	(–)
SMV	Nosy Be	MV2001	light brown	brown-black	irregular	yes	partly	(light brown)	–
SMV	Berara	MV2000	brown	black	oblong	?	no?	light brown	–
SMV	Ankarafantsika	MV2001	brown	dark brown	irregular	partly	partly	yellowish	yellowish
SMV	Ankarafantsika	GG	reddish brown	brown	?	?	partly	beige	beige
SMV	Isalo, Relais de la Reine	BL	grey-brown	black	drop-like	partly	partly	white	white!
SMV?	Berenty	EG	grey	dark brown	oblong	partly	partly	white	white
SMV	Kirindy, juv?	BL	dark brown	black	?	?	no?	beige	beige!
SMV	Ankarafantsika, juv?	MV2001	green-grey	black	irregular	partly	partly	yellow	yellow
SMV	Nosy Be, juv.	GM1992	reddish brown	black	rhomboid-ovoid	partly	partly	white	white
SMV?	M. des Français juv.	FG2000	brown	black	rhomboid	yes	partly	white	white

3.4 Distribution of *Sanzinia* and *Acrantophis*

Posterior to the distributional information given by GLAW & VENCES (1994), a large number of faunal inventories in Madagascar yielded records of the three boid species. Often these followed KLUGE (1991) and recorded the two *Acrantophis* species as *Boa dumerilii* and *B. madagascariensis*, and *Sanzinia madagascariensis* as *Boa manditra*. Merging the published data with our own observations and with the unpublished data kindly communicated (usually as colour photos) by other colleagues has led to an updated picture as presented in Figure 2. The major novelty is the discovery of numerous localities of *Sanzinia* in the xeric areas of western and south-western Madagascar. Despite the presence of voucher specimens in the Paris museum (see appendix) these had not been considered by GUIBÉ (1949, 1958) who apparently based his locality data mainly on previously published literature rather than MNHN material. Combining the data on mitochondrial DNA haplotypes and colouration, the whole western coast from Montagne des Français in the north to Berenty in the south seems to be populated by the western subspecies *S. m. voluntary*, whereas the eastern coast from Nahampoana in the south to the Marojejy massif in the northeast is populated by the nominate subspecies. In *Acrantophis*, a relatively broad overlap of occurrence of *A. madagascariensis* and *A. dumerilii* seems to exist between Mahajanga and Morondava (like in the iguanid species pair *O. cuvieri* and *O. cyclurus*), but no genetic samples, high-resolution pictures or voucher specimens from this area were available to us for a confirmation or rejection of this hypothesis. The northernmost record of *A. dumerilii* (from Andranolava in northwestern Madagascar) was based on a single specimen of about 1.5 m length that was kept in a house, apparently to control rats (see KAUDERN 1922). No reason for its determination as *A. dumerilii* was provided, although KAUDERN has also found several *A. madagascariensis* and therefore may have

left page: Tab. 4. Colouration of *Sanzinia m. madagascariensis* and *S. m. voluntary* individuals, after available colour slides. A long dash indicates that the corresponding pattern was absent; if the dash is in parentheses, it indicates that the state could not be fully verified (in cases of unsharp or partial photos). Other characters in parentheses indicate that the corresponding state (spot, colour border) was faintly expressed. Colour is the basic dorsal and lateral colour. Other pattern abbreviations: DM, dark lateral markings; DM form, form of dark lateral markings; DM v.ext., ventral extension of dark lateral markings; DM fused, fusion of dark lateral markings with each other in the vertebral area; LM, light markings within the lateral dark markings; LB, light border of lateral dark markings.

Färbung von *Sanzinia m. madagascariensis* und *S. m. voluntary* nach verfügbaren Farbfotos. Ein langer Bindestrich weist darauf hin, dass das entsprechende Merkmal nicht vorhanden war; ein Strich in Klammern bedeutet, dass das Merkmal nicht zuverlässig überprüft werden konnte (unscharfe oder unvollständige Aufnahmen). Merkmalszustände in Klammern weisen darauf hin, dass das entsprechende Merkmal (Flecken, Umgrenzung der Flecken) schwach ausgeprägt war. "Colour" ist die dorsale und laterale Grundfärbung. Die übrigen Merkmale sind wie folgt abgekürzt: DM, dunkle Flankenflecken; DM form, Form der dunklen Lateralflecken; DM v.ext., ventrale Ausdehnung der dunklen Flankenflecken; DM fused, Verschmelzung der dunklen Lateralflecken auf dem Rücken; LM, helle Flecken innerhalb der dunklen Flankenflecken; LB, helle Umgrenzung der dunklen Flankenflecken.

Photographers are abbreviated as follows / Autoren der Fotos werden wie folgt abgekürzt: BL, B. LOVE; EG, E. GUTHMANN; FA, F. ANDREONE; FG, F. GLAW; GG, G. GARCÍA; GM, F. GLAW and J. MÜLLER; GV, F. GLAW and M. VENCES; KS, K. SCHMIDT; MG, M. GRUBENMANN; MV, M. VENCES; PB, P. VAN BEEST.

been able to distinguish between both species. However, it cannot be excluded that the specimen from Andranolava was either misidentified or of allochthonous origin. New records are therefore necessary to confirm the existence of *A. dumerilii* in northwestern Madagascar. Judging from the available photographs, *A. madagascariensis* seems to occur southwards at least up to the Kirindy forest near Morondava, but the identity of this population is still to be confirmed by thorough morphological or genetic examination. Summarizing, the available data provide no unambiguous evidence for any sympatric occurrence of both *Acrantophis* taxa which would strongly confirm their status as distinct species rather than subspecies.

A list of localities of Malagasy boas currently known to us is given in Appendix 1.

Regarding altitudinal distribution, all four taxa occur at low elevations near sea level, and reach different elevational limits. *Acrantophis* seem to be largely lowland inhabitants. The highest record of *A. madagascariensis* is from Andapa (576 m). *A. dumerilii* has been recorded up to ca. 1000-1300 m asl (south of Ambositra). *Sanzinia m. voluntany* has so far only been recorded up to at least 770 m asl (Isalo; altitude referring to Ranohira at the base of this massif). The identity of *Sanzinia* specimens from the upper Sambirano (1200 m) is unclear. They possibly refer to *Sanzinia m. madagascariensis* which probably also occurs at 1350 m (Anjanaharibe-Sud). This subspecies is very common around 900 m altitude in the Andasibe region in central eastern Madagascar but appears to be less frequent at higher altitudes. For instance, no *Sanzinia* were recorded from the Andringitra and Ankaratra Massifs (RAXWORTHY & NUSSBAUM 1996, VENCES et al. 2002), and no records exist at altitudes higher than 780 m from the Marojejy and Andohahela Massifs (RASELIMANANA et al. 2000, NUSSBAUM et al. 1999).

The distribution patterns of Malagasy boas are biogeographically interesting because they add data to the identification of transition zones between typically eastern and western faunal elements in Madagascar. In the widespread complex of *Boophis tephraeomystax* (east) and *B. doulioti* (west), north-western Madagascar including Nosy Be seems to be populated by the eastern species while the western species occurs at least from Ankarafantsika on southwards and reaches the rainforest areas around Tolagnaro in the south (VENCES & GLAW 2002). This seems to be rather in accordance with another frog species, *Mantella betsileo*, in which eastern and north-western populations are genetically very similar to each other while the populations in western and south-western Madagascar are strongly divergent (SCHAEFER et al. 2002). Also *Acrantophis* shows a similar pattern: *A. madagascariensis* occurring in the east (Tampolo, Andrakata and Andapa) and north-west, while *A. dumerilii* is distributed in the west and south-west reaching rainforests around Tolagnaro. In contrast, in *Sanzinia*, the north-west seems to be populated by the western subspecies *S. m. voluntany* and the southern rainforests (e. g., Nahampoana and Andohahela) by the eastern (nominate) subspecies. The area around Tolagnaro, where humid rainforests border on very xeric areas, seems to be a region of secondary contact between populations of the two subspecies, and therefore a suitable area to comparatively study their ecological requirements and phenomena of hybridization and genetic introgression.

3.5 Conservation

Giant snakes have received particular attention by international trade regulation, because of their attractiveness both for the pet market and for the leather industry. In at least one case, smuggled boas from Madagascar were discovered by custom officers and returned to their original habitat (ANONYMOUS 1991). Both *Sanzinia* and *Acranto-*

phis are included in CITES appendix I, and their export from Madagascar and their import to other countries is therefore strictly regulated. The two genera have been used to test the validity of individual recognition by photographic documentation of head pattern (BONNY 2000, BENDER 2001, BENDER & HENLE 2001) to control the identity of captive specimens. The three Malagasy boa species are classified as vulnerable according to IUCN criteria (HILTON-TAYLOR 2000). RAXWORTHY & NUSSBAUM (2000) assume a historical bias towards turtles and boas in this list, and state that all three of the Malagasy boas are frequently found in heavily degraded habitats and cultivated areas, even including close proximity to villages where they are probably feeding on commensal rats. According to these authors, the loss of primary forest will not lead to extinction of boa species, although their population changes are not known. HENKEL & SCHMIDT (1995) state that *Sanzinia* is the most common snake in several regions of Madagascar which agrees with our observations for the eastern region.

Furthermore, it is evident from Figure 2 that all four taxa of Madagascar boas have a rather large distribution range and are known from numerous localities including many nature reserves, confirming doubts on the reasons for their inclusion in CITES appendix I. Madagascar boas are often found close to villages where they feed on rats and mice (specimen ZSM 803/2001 from Vohidrazana contained one adult *Rattus rattus*; S. M. GOODMAN pers. comm.). Hence, they very probably are important to control these species, and local people in western Madagascar have in the past even kept these snakes close to or in their homes for this purpose (KAUDERN 1922). In contrast, in other regions of Madagascar people are very afraid of boas, although we have only seldom observed snakes that had been killed by people except roadkills by traffic. In some cases, Chinese people in Madagascar collect boas for consumption as food; K. SCHMIDT (personal communication) made such observations in the Andapa region, where also the skins of the consumed snakes were used for leather. RAXWORTHY & NUSSBAUM (2000) also report on the collection of boas in the Marovoay area to supply a domestic leather trade. However, as long as the international trade of *Sanzinia* and *Acrantophis* is banned or strictly regulated, it is very unlikely that consumption by humans will constitute a serious danger for any population of Malagasy boas.

A partially different situation emerges if habitat destruction in western Madagascar and our data on the high genetic differentiation of western Malagasy *Sanzinia* populations are taken into account. Although *S. m. voluntary* also occurs close to villages (e. g., specimens at Ampijoroa were collected close to the village's dump area), it seems to be less common and is certainly much less often encountered than the nominal subspecies in the east (e. g., BLOXAM et al. 1996), as is also indicated by the lack of exact records from the whole of western Madagascar in previous accounts (GUIBÉ 1958). All specimens with detailed collecting data were found close to or in dry forest areas (except for those from rainforest on Nosy Be). However, Madagascar's western seasonal forest and south-western "spiny" shrub are among the most endangered vegetation types on the island (e. g., GANZHORN 1992). Therefore, the fate of *S. m. voluntary* may be strongly linked to the conservation of these last primary xeric habitats in Madagascar, and this emblematic giant snake may even become one of the flagship species to advocate the need for improved protection of these ecosystems.

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Phylogeographie, Systematik und Gefährdung der Boas aus Madagaskar (*Sanzinia* und *Acrantophis*)

Einleitung

Boas gehören zu den biogeografisch faszinierendsten Reptiliengruppen Madagaskars. Echte Boas (die Unterfamilie Boinae innerhalb der Boidae) sind in Süd- und Mittelamerika, der Pazifikregion und in Madagaskar verbreitet, während sie in Afrika und Asien nicht vorkommen und die Riesenschlangen dort im wesentlichen von Pythons vertreten werden. Die madagassischen Boas werden in drei Arten in zwei Gattungen eingeteilt: Die zum Teil baumlebende *Sanzinia madagascariensis* und die fast ausschließlich terrestrischen *Acrantophis madagascariensis* und *A. dumerilii*. Vorschläge, alle diese Arten zusammen mit der mittel- und südamerikanischen *Boa constrictor* in der Gattung *Boa* zu vereinen (KLUGE 1991) stehen mit molekulargenetischen Daten in Konflikt und sind nicht allgemein anerkannt worden (VENCES et al. 2001). In den vergangenen zehn Jahren sind viele neue *Sanzinia*- und *Acrantophis*-Lokalitäten bekannt geworden. Dabei sticht besonders hervor, dass *Sanzinia* erstmals von einigen Fundorten im trockenen Westen Madagaskars nachgewiesen wurde. Darüber hinaus sind die madagassischen Riesenschlangen jedoch kaum untersucht worden. In der vorliegenden Arbeit berichten wir über die genetische, morphologische und farbliche Differenzierung der westmadagassischen *Sanzinia*, die wir als neue Unterart beschreiben. Daneben fassen wir die verfügbaren Kenntnisse zur Verbreitung der madagassischen Riesenschlangen zusammen.

Material und Methoden

Unsere Verbreitungsdaten basieren auf einer Zusammenfassung von Literaturangaben, Fotos, persönlichen Mitteilungen und eigenen Beobachtungen. Um morphologische und meristische Daten zu erheben, untersuchten wir konservierte *Sanzinia*-Exemplare aus verschiedenen Museen, darunter das Muséum National d'Histoire Naturelle in Paris (MNHN) und die Zoologische Staatssammlung München (ZSM). Weiterhin wurden auch Tiere im Freiland vermessen und nach Entnahme einer Gewebeprobe wieder freigelassen. Die in Ethanol konservierten Gewebeproben wurden zur Extraktion von DNA genutzt. Ein Fragment des mitochondrialen 16S rRNA Gens wurde mittels PCR unter Einsatz von Standard-Primern amplifiziert und im Anschluss sequenziert.

Ergebnisse und Diskussion

Die molekulargenetischen Ergebnisse sind in Tab. 1 und Fig. 1 zusammengefasst. Sie ergeben ein sehr überraschendes Bild. Innerhalb von *Sanzinia* lassen sich zwei deutlich getrennte Linien unterscheiden, von denen die eine die Exemplare aus dem Westen Madagaskars enthält, die andere die Tiere aus dem Regenwald Ostmadagaskars. Die genetischen Unterschiede zwischen diesen beiden Linien (3-3.6 % im betrachteten DNA Fragment) sind sogar deutlich größer als zwischen den beiden *Acrantophis*-Arten (1-1.8 %).

Die morphologischen Untersuchungen erbrachten jedoch kein eindeutiges Bild. Die vermessenen Parameter (vgl. Tab. 2) zeigten keine deutlichen Unterschiede zwischen den *Sanzinia*-Populationen aus Ost- und Westmadagaskar. Allein die Anzahl von Supralabialia und Infralabialia

unterschied sich, wobei letzterer Parameter statistische Signifikanz aufwies ($P < 0.01$). Die Werte sämtlicher Parameter überlappten sich jedoch zwischen den beiden Gruppen, so dass keines der Merkmale als diagnostisch gelten kann. Auch die in Tab. 3 zusammengefasste Analyse der Färbung und Zeichnung erbrachte keine konsistenten Unterschiede, mit Ausnahme der Grundfärbung: Diese ist bei Tieren aus Westmadagaskar immer bräunlich, während Tiere aus dem Osten meist (aber nicht immer) olivgrüne Töne zeigen. Unsere Analyse wurde dadurch erschwert, dass eine zuverlässige Geschlechtsbestimmung vieler Exemplare (insbesondere der nur fotografierten und wieder freigelassenen) nicht möglich war. Die Ausprägung eines Kloakalspornes könnte geschlechtsdimorph sein, aber zu dieser Frage sind weitere Daten notwendig.

Angesichts des Fehlens von zuverlässigen morphologischen Unterschieden und der relativ geringen Stichprobengröße der molekularen Daten, die ein „haplotype sharing“ und einen regelmäßigen Genfluss zwischen den beiden *Sanzinia*-Linien nicht ausschließen lassen, halten wir eine Klassifizierung der beiden Linien als zwei Unterarten für die zur Zeit am ehesten angebrachte taxonomische Schlussfolgerung.

Ein untersuchter Syntypus von *Sanzinia madagascariensis* (das Exemplar MNHN 43) weist eine relativ hohe Anzahl von Infralabialia auf und ist damit eher der östlichen Form zuzurechnen. Auch aufgrund der größeren Häufigkeit der östlichen Tiere und des historischen Sammelschwerpunkts in Ostmadagaskar ist es am wahrscheinlichsten, dass das Typusmaterial von *Sanzinia madagascariensis* aus Ostmadagaskar stammt. Aus diesem Grund beschreiben wir die westmadagassische *Sanzinia*-Form anhand eines Holotypus aus Ampijoroa (ZSM 804/2001) als neue Unterart *Sanzinia madagascariensis volontary* („volontary“ ist das madagassische Wort für „braun“).

In den Verbreitungskarten (Fig. 2) haben wir die verfügbaren Funde so weit wie möglich den einzelnen Taxa zugeordnet. Dabei sind sowohl die genetischen Daten in die Bestimmung eingeflossen als auch die Färbung derjenigen Nachweise, von denen Farabbildungen oder Belegexemplare untersucht werden konnten. Die Unterart *Sanzinia madagascariensis volontary* scheint vom äußersten Norden bei Montagne des Français bis in den Süden bei Berenty entlang der gesamten Westküste von Madagaskar verbreitet zu sein. In den südlichen Regenwäldern bei Tolagnaro wird sie dagegen von der Nominatform ersetzt.

Dies steht im Kontrast zu einigen Froscharten, die ebenfalls eine komplementäre Ost-West Verbreitung aufweisen: Im Artenkomplex *Boophis tephraeomystax* und *B. doulioti* dringt die Westart (*B. doulioti*) bis in die Regenwälder bei Tolagnaro vor, während die Ostart (*B. tephraeomystax*) auch den Norden und Nordwesten (bis Ambanja) besiedelt. Letzteres trifft auch auf *Mantella betsileo* zu, bei der die Populationen aus dem Nordwesten um Ambanja und Nosy Be genetisch denen der Ostküste sehr ähnlich sind, während in Westmadagaskar andere Varianten leben. Auch die Verbreitungsmuster der beiden *Sanzinia*- und *Acrantophis*-Formen korrelieren nicht: Während bei *Sanzinia* eine westliche und eine östliche Form auftritt, findet sich bei *Acrantophis* eine nördliche und eine südliche Form. Diese Unterschiede weisen darauf hin, dass die Artbildungsprozesse in beiden Gattungen nicht parallel und nicht gleichzeitig abgelaufen sind, was auch aus der unterschiedlich großen genetischen Divergenz beider Formenpaare deutlich wird.

Die Madagaskar-Boas sind weit verbreitet und relativ häufig und ihr Vorkommen ist nicht auf primäre Lebensräume beschränkt. Das Ausmaß ihrer lokalen Nutzung als Nahrung und für Leder scheint derzeit nicht bedrohlich zu sein. Allerdings könnte die neue Unterart teilweise an die primären Trockenwälder Westmadagaskars gebunden sein. Ihr potenzieller Gefährdungsstatus sollte daher aufmerksam untersucht werden.

Schlagwörter: Reptilia: Squamata: Boidae: *Acrantophis madagascariensis*, *Acrantophis dumerilii*, *Sanzinia madagascariensis*, neue Unterart; Madagaskar; Biogeografie; Phylogenie.

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Appendix:

List of localities and voucher specimens of Malagasy boas (numbers corresponding to those in Fig. 2; asterisks marking those localities from which a DNA sequence is available).

Sanzinia madagascariensis. – **A.** Within distribution area of eastern haplotypes (nominate subspecies): (1) Besane valley, high Sambirano, 1200 m (MNHN 1970.385); (2) Andapa (14°37'S, 49°37'E, 576 m, own observations 1995; photo of K. SCHMIDT in 1997, Fig. 3a); (3) Marojejy, 350-780 m (GLAW & VENCES 1994, RASELIMANANA et al. 2000); (4) Anjanaharibe-Sud, 800-1350 m (RAXWORTHY et al. 1998; photo in ANDREONE 1997); (5) between Antanambao and Ampokafo, Masoala (photos of P. VAN BEEST); (6) Anandrivola (RAXWORTHY 1988); (7) Maroantsetra (GLAW & VENCES 1994); (8*) Andranofotsy (own observation in 2001); (9) Nosy Mangabe (RAXWORTHY 1988; ANDREONE 1991); (10) Col Pierre Radama, 1000 m (MERTENS 1933); (11) Tampolo (RASELIMANANA et al. 1998); (12) Nosy Boraha (GLAW & VENCES 1994); (13) Fandarazana (KAUDERN 1922, GUIBÉ 1958); (14) Zahamena (RAXWORTHY 1988); (15) Toamasina [=Tamatave] (MNHN 1966.977; GUIBÉ 1958); (16) Tampina (MERTENS 1933, GUIBÉ 1958); (17*) Vohidrazana (ZSM 803/2001; D.R. VIEITES and M. VENCES, 17 February 2001, Fig. 3e); (18*) Ambohimananarivo (own observation in 2002, Fig. 3d); (19*) Andasibe (RAXWORTHY 1988;

ANDREONE 1991; own observations, Fig. 3f; MNHN 1961.656); (20) Moramanga (MEIER 1980); (21) Miarinarivo (MNHN 1975.134), westernmost locality, identification uncertain, based on general colour; (22) Mahanoro (MNHN 1992.5312, BOUR and VANDERHAEGE, 1976); (23) Ambohimanga du Sud (MNHN 1950.429; MILLOT); (24) Ifanadiana (MNHN 1978.95; THEREZIEN, 30 January 1964); (25) Mandotra, Mananjary province (MNHN 1907.94; GUIBÉ 1958); (26) Ankafana (GUIBÉ 1958); (27) Ivohibe corridor, 900 m (RASELIMANANA 1999); (28) Andohahela, 780 m (ANDREONE & RANDRIAMHAZO 1997, Fig. 3c; NUSSBAUM et al. 1999); (29*) Nahampoana (GLAW & VENCES 1994, Fig. 3b, Fig. 5); (30) Malahelo (RAMANAMANJATO et al. 2002); (31) Mandena (RAMANAMANJATO et al. 2002); (32) Ste Luce (RAMANAMANJATO et al. 2002); (33) Manantantely (RAMANAMANJATO et al. 2002); (34) Eminiminy, ca. 400 m (MERTENS 1933). Further material of unprecise or unlocated origin assigned to the eastern form but not included in the map: MNHN 3288, Madagascar (L. ROUSSEAU); MNHN 1970.384, forêt de Ivovana (ARNOULT); MNHN 1989.2833, Perinet? (Ch. A. DOMERGUE); MNHN 1970.386-87, Ambatolampy (several villages with this name exist in Madagascar).

B. Within distribution area of western haplotypes and/or brown dorsal colour (subspecies *volontary*): (1) Antsiranana (BRANCH & ERASMUS 1976); (2) Montagne des Français (GUIBÉ 1958, own observations in 2000); (3) Windsor castle (observation of M. GRUBENMANN); (4) Montagne d'Ambre, 650-950 m (RAXWORTHY & NUSSBAUM 1994); (5) Ankarana (BLOXAM & BARLOW 1987); (6) Ambilobe (MEIER 1980); (7*) Nosy Be (ZSM 184/1912; MNHN 1966-977; GUIBÉ 1958; own observations in 2000 and 2001, Fig. 4e); (8) Manongarivo (RAKOTOMALALA 2002); (9*) Berara forest, Sahamalaza peninsula (ANDREONE et al. 2001, Fig. 4a); (10*) Ampijoroa, Ankarafantsika (ZSM, holotype, Fig. 4b, Fig. 6); MNHN (paratypes); photo of M. GRUBENMANN; own observations in 2001); (11) Bevazaha (MNHN 8932) (12) Tsingy de Bemaraha (records quoted by EMANUELI & JESU 1995); (13*) Kirindy (BLOXAM et al. 1996; photo of B. LOVE, Fig. 4f); (14) Isalo (photo of B. LOVE, Fig. 4c); (15) Andranohinaly, 23°16'S, 43°58'E, 301 m (BOETTGER, 1913, probably identical with "Androhinaly" of GUIBÉ 1958); (16) Bas Fiherenana, Toliara province (MNHN 1906.94; GUIBÉ 1958); (17) Ambovombe (MNHN 1950.196); (18) Berenty (photo of E. GUTHMANN, Fig. 4d).

Acrantophis madagascariensis. – (1) Antsiranana (BRANCH & ERASMUS 1976); (2*) Montagne des Français (12°19'17"S, 49°20'13"E, 174 m, own observations in 2000, Fig. 7a); (3) Nosy Hara (photo of B. LOVE); (4) Ankarana (photos of M. GRUBENMANN and B. LOVE); (5) Ambanja (own observations in 2000); (6*) Nosy Be (GUIBÉ 1958; own observations in 2000 and 2001); (7) Andrakata (14°37'S, 49°43'E, 454 m, GLAW & VENCES 1994); (8) Andapa (14°37'S, 49°37'E, 576 m, photo of K. SCHMIDT); (9) Nosiarina, 14°13'S, 50°02'E, 113 m, near Sambava (SCHMIDT & GLAW 1997); (10) Manongarivo (RAKOTOMALALA 2002); (11) Mahajanga (BOETTGER 1913, GUIBÉ 1958); (12) Ste Marie de Marovoay (KAUDERN 1922, GUIBÉ 1958); (13) Kandani, Süd-Bemba-tokabai [probably = Kandran, south of baie de Bombetoka, 16°03'S, 46°21'E, 41 m] (BOETTGER 1913); (14*) Ampijoroa, Ankarafantsika (own observation in 2001, Fig. 7c); (15) Mandritsara (MNHN 1989.2809); (16) Tampolo (RASELIMANANA et al. 1998); (17) Tsingy de Bemaraha (records quoted in EMANUELI & JESU 1995); (18) Kirindy (BLOXAM et al. 1996; photos of B. LOVE and K. SCHMIDT). Records not included in the map: Amboasary, lower Mandrare, Prov. Fort Dauphin (MERTENS 1933), this record is dubious and needs verification.

Acrantophis dumerilii. – (1) Andranolava? (KAUDERN 1922, GUIBÉ 1958, this record needs confirmation); (2) Morondava (GUIBÉ 1958); (3) Mahabo (MNHN 1899.384, GUIBÉ 1958); (4) Belo (GUIBÉ 1958); (5*) National road VII, ca. 40 km south of Ambositra (DNA voucher AD2); (6) on the road between Ambalavao and Ihosy (photo of P. VAN BEEST); (7) Isalo (photos of B. LOVE and M. GRUBENMANN); (8) Zombitse (RAXWORTHY et al. 1994); (9) Vohibasia (GOODMAN et al. 1997); (10) Mikea forest, 22°40'S, 43°25'E (SEDDON et al. 2000); (11*) Ifaty (own observation in 2000, deposited in UADBA, Fig. 7d); (12) Toliara (BOETTGER 1913, GUIBÉ 1958); (13) between Andranovory and Betioky (photo of P. VAN BEEST); (14) Réserve Speciale de Beza Mahafaly, 23°30'S, 44°40'E, (SEDDON et al. 2000); (15) Zampongotra (MNHN 1989.2824) and ouest Zampongotra (MNHN 1989.2822); (16) Réserve Speciale de Cap St. Marie, 25°03'S, 49°09'E (SEDDON et al. 2000); (17) Kaleta Reserve near Amboasary (photos of B. LOVE and M. BURGER);

(18) between Tolagnaro and Amboasary (GLAW & VENCES 1994); (19*) Berenty (own observation in 2001); (20) Amboasary (MERTENS, 1933, GUIBÉ 1958); (21) Malahelo (RAMANAMANJATO et al. 2002); (22) Petriky (RAMANAMANJATO et al. 2002); (23) Mandena (RAMANAMANJATO et al. 2002); (24) Ste Luce (RAMANAMANJATO et al. 2002); (25) Andohahela, 120 m (NUSSBAUM et al. 1999; RAMANAMANJATO et al. 2002).

The record from La Réunion island (GUIBÉ 1958, BLANC 1971) is apparently only based on the (early collected) specimen MNHN 8161 from Saint Denis, the capital of this island. This record is here considered as erroneous, since the existence of *Acrantophis* on La Réunion was apparently never confirmed (it is not mentioned in recent natural history books on the island, e. g. in PROBST 1997) and such a giant species is extremely unlikely to be overlooked. Probably, the specimen was shipped from La Réunion to Paris and this may have led to the confusion about its origin (a similar problem is known from early collected Madagascan frog specimens of *Rhombophryne testudo* and *Mantella baroni* and is also likely for the La Réunion record of the snake *Liophidium vaillanti*).

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Authors: MIGUEL VENCES, Institute for Biodiversity and Ecosystem Dynamics, Zoological Museum, University of Amsterdam, P.O. Box 94766, NL-1090 GT Amsterdam, The Netherlands, E-Mail: vences@science.nl; FRANK GLAW, Zoologische Staatssammlung, Münchhausenstraße 21, D-81247 München, Germany, E-Mail: Frank.Glaw@zsm.mwn.de.