



## Amphibians and reptiles of the Ankaratra Massif: reproductive diversity, biogeography and conservation of a montane fauna in Madagascar

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### ABSTRACT

The Ankaratra Massif in central Madagascar includes rainforest between ca. 1500 and 2000 m elevation and montane savannah and heathland between ca. 2000 and 2642 m elevation. It is populated by 15 species of amphibians and 12 species of reptiles, all of which were observed in our surveys between 1992-2001. Additionally, the Ankaratra material housed in several herpetological collections was revised. Examination of type material showed that *Scaphiophryne madagascariensis* is the name to be applied to the scaphiophryine microhylid frog occurring at Ankaratra; the previously used name *S. pustulosa* is a junior synonym, while populations from the Andringitra Massif so far considered as *S. madagascariensis* do not belong to this species. Reproductive behaviour and advertisement calls are described for *S. madagascariensis*. Two other frog species (*Boophis williamsi*, *Mantidactylus pauliani*) were observed for the first time for almost 30 years; their live coloration and morphology are described. The skink *Amphiglossus macrocerus* is shown to be live-bearing. Breeding in the austral summer could be demonstrated for most species, including the geckos *Lygodactylus mirabilis* and *Phebuma barbouri*

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which are known to lay eggs also in the cold winter months (July-September). The higher-level taxonomic composition of the Ankaratra herpetofauna recalls that of the rainforests of eastern Madagascar, and also the species show mainly eastern affinities. A number of groups (especially snakes) are under-represented and some (e.g., nocturnal geckos and dwarf chameleons) are totally lacking. Three high-elevation specialists (*B. williamsi*, *M. pauliani*, *L. mirabilis*) appear to be Ankaratra endemics (11% of the overall community). Pending further surveys and taxonomic revisions, more than one fifth of the herpetofauna (six species or more) may be endemic or semi-endemic to the region, which is not included in the network of Madagascar's protected areas. A monitoring program is therefore proposed to assess the conservation status of these poorly known taxa.

KEY WORDS: Amphibia - Reptilia - Madagascar - Biodiversity - Ankaratra Massif - Montane heathland - Rainforest - Conservation.

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### INTRODUCTION

Madagascar, the fourth largest island in the world, has a varied topography, with a central chain spanning from north to south and including peaks as high as 2876 m (Tsaratanana), 2133 m (Marojejy), 2642 m (Tsi-afajavona, Ankaratra Massif), 2658 m (Pic Boby, Andringitra Massif), and 1956 m (Anosy Massif) a.s.l. These high-elevation regions of Madagascar are populated by amphibian and reptile communities partly specialized to montane habitats. Several of these species are endemic to the massifs or to montane areas (Raxworthy & Nussbaum, 1996a; Vences & Glaw, 1999). While Andringitra, Anosy and Marojejy have been subject of extensive herpetofaunistic surveys in the past decade (Raxworthy & Nussbaum, 1996a, b; Andreone & Randriamantazo, 1997; Raxworthy *et al.*, 1998; Nussbaum *et al.*, 1999; Raselimanana, 1999; Raselimanana *et al.*, 2000), no recent comprehensive work is available on the amphibians

and reptiles of the easily accessible Ankaratra mountains south of Madagascar's capital Antananarivo. This may be due to two reasons. First, only small remains of primary (partly degraded) forest are found at Ankaratra, almost completely concentrated in the area managed by the Manjakatempo forestry station; second, due to the easy access to Manjakatempo and Ankaratra in general, many isolated works have been conducted on the herpetofauna of the region (Guibé, 1952; Pasteur, 1959, 1962; Andreone, 1993; Glaw & Vences, 1994), which leaves few 'spectacular' discoveries to be expected during intensive inventories.

The present paper reports the results of several surveys conducted during 1992, 1994, 2000 and 2001 in the Manjakatempo, Nosiarivo, and Tsiarafajavona areas. The distribution and biological information available on the amphibians and reptiles of Ankaratra is summarized, and their biogeographic relationships and conservation status are discussed.

## MATERIALS AND METHODS

### Methods of analysis of preserved materials

The present data are based on the examination of specimens housed in the Natural History Museum (formerly British Museum of Natural History; BMNH), Muséum National d'Histoire Naturelle, Paris (MNHN), Museo Regionale di Scienze Naturali, Torino (MRSN and MRSN-FAZC), Université d'Antananarivo, Département de Biologie Animale (UADBA and RD), Zoologisches Forschungsinstitut und Museum A. Koenig, Bonn (ZFMK), Zoologisch Museum Amsterdam (ZMA), and Zoologische Staatssammlung, München (ZSM). UADBA specimens are given with preliminary numbers which correspond to the provisional field numbers assigned by F. Glaw and M. Vences (FG/MV) in 2000 and the ones assigned by M. Vences (MV) in 2001. For each species, a mention is made of the Ankaratra voucher specimens housed in these collections. When necessary for morphological, taxonomical or biogeographical discussions, also the specimens examined from other localities are listed as "further material".

Morphometric measurements were carried out by the senior Author with a calliper to the nearest tenth of a millimetre. SVL is used as abbreviation for snout-vent length. Bioacoustic analyses were made by F. G. with the sound analysing system MEDAV-Spektro 3.2. Bioacoustic and morphometric values are generally presented as range (mean  $\pm$  SD in parentheses).

Acronyms for the quoted collectors and authors are as follows: CPB, C. P. Blanc; DR, D. Rakotomalala; DRV, D. R. Vieites; DV, D. Vallan; FA, F. Andreone; FG, F. Glaw; JER, J. E. Randrianirina; MV, M. Vences; NR, N. Raminosoa; RN, R. Nincheri; SDM, S. De Michelis.

### Study area

Geologically (Perrier de la Bâtie, 1927; Besairie, 1954), the Ankaratra is an important and slightly curved barrier roughly extending in a north-south orientation (Fig. 1). Part of the central watershed that separates the rivers flowing towards the Mozambique channel from those flowing into the Indian Ocean, it is made up by different, partly overlapping volcanic zones which laterally extend about 30 km, contacting neighbouring volcanic centres. The northern part of the massif mostly corresponds to a younger, Pleistocene volcanic activity, with characteristic blackish, compact lavas. This area includes the highest peaks: Tsiarafajavona (2642 m), Tsiarafakao (2530 m), Ankavitra (2603 m), Ambohimainty (2595 m), and Ambohimirandrana (2412 m). The southern part, in contrast, originating from older (Pliocene) volcanic activity, is partly characterized by trachytic domes such as that of Famoizankova (2362 m).

The climate in this massif follows the general seasonal pattern typical for Madagascar, with a cold and dry season in the austral winter and a warm and wet one in the austral summer. According to meteorological data recorded at Manjakatempo (Donque, 1975), the mean temperatures range from 11.9° C (July) to 17.9° C (January); the extremes of the mean minimum and maximum temperatures per month were 5.5° C (July) and 24.7° C (November). However, at the high mountain areas of the Tsiarafajavona, low temperatures are also recorded in the austral summer (we recorded less than 10° C at night in February), and temperatures below 0° C are common in the austral winter. Mean annual precipitation is 2012 mm, with a recorded range of 1445–2662 mm. The highest amount of rainfall is in January (362 mm), while the minimum corresponds to June or July, with a mean total of about 200 mm in the whole period May–September.

The vegetation of the massif contains remnants of primary rainforest which are mainly located along the eastern slopes at elevations of 1700–2000 m (Fig. 2a). As discussed by Goodman *et al.*

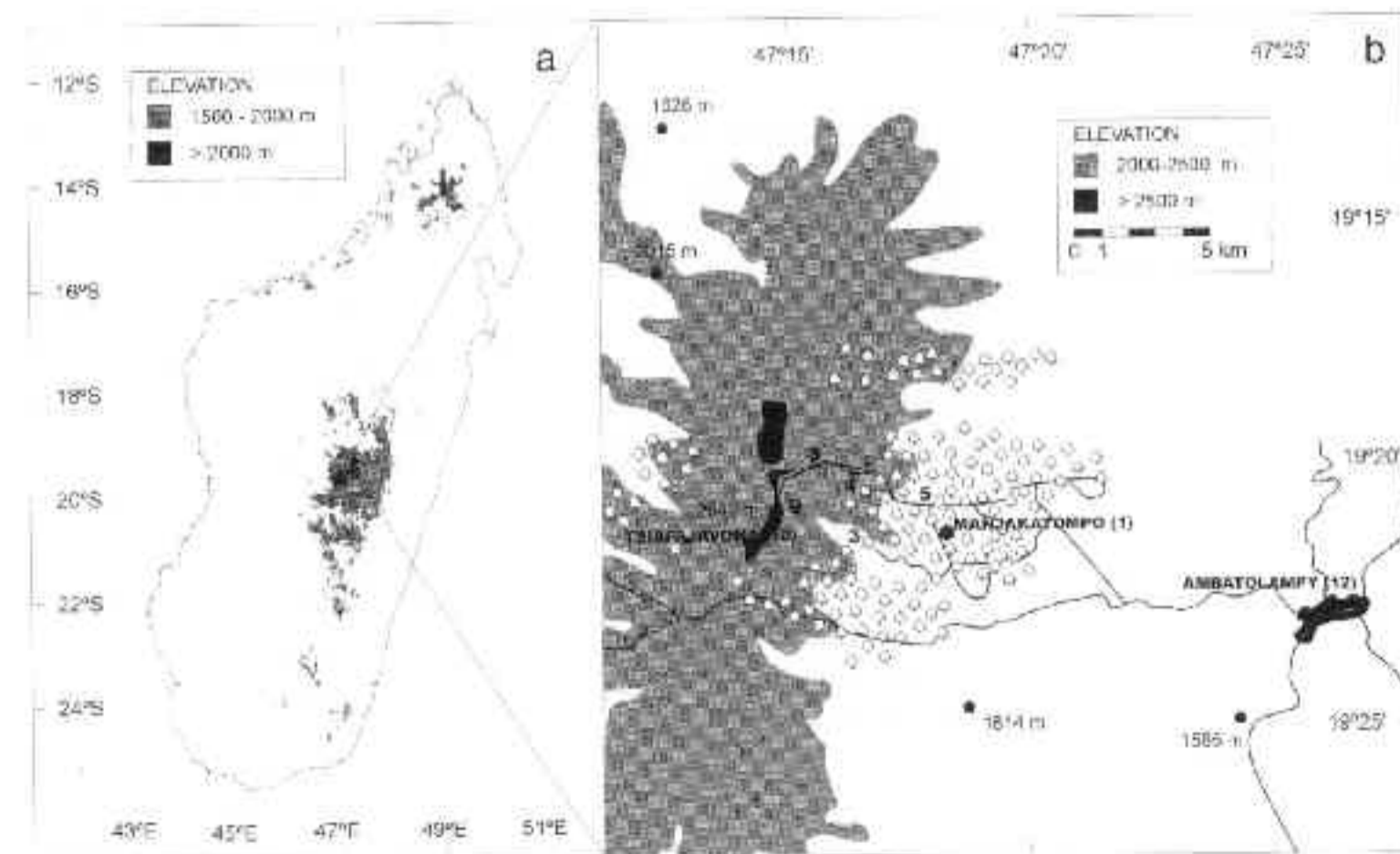


Fig. 1 - Map (a) of Madagascar, showing areas between 1500–2000 m and above 2000 m elevation and (b) of the Ankaratra region between Ambatolampy and the Tsiarafajavona, showing areas of 2000–2500 m and above 2500 m, forested areas, and main roads. Numbers refer to several of the collection sites listed in Materials and Methods: 1, Manjakatempo; 3, Manjavona Valley; 4, Ambohimirandrana; 5, Nosiarivo; 8, Tsiarafajavona road; 9, Tsiarafajavona Plateau; 10, Tsiarafajavona. The Ankaratra map is a simplified scheme based on the maps of the Malagasy geographical institute at a scale of 1:500,000; positioning of localities is only approximative. For detailed coordinates, see Materials and Methods.

(1996), the forest in the area of the sacred royal Tankarava tombs (Nosiarivo) is almost exclusively composed of a single tree species (*Weinmannia bojeriana*) and may be a historical plantation dating back to former centuries. The rainforest remnants (including the Nosiarivo Forest) are largely concentrated in the area of the Manjakatempo Forest station, which also contains large pine plantations. Roughly above 2000 m, the forests are replaced by an extensive grassland area, with plots of heathland (Fig. 2b) and remains of other vegetation types on steep slopes along brooks. This savannah landscape, with only rare occurrence of higher ericoid bushes, was already present in 1929 (Rand, 1936).

Ankaratra localities reported in the following accounts are (see Fig. 1): 1, Manjakatempo (19°21' S, 47°18' E, ca. 1700 m); 2, Lac

Froid; 3, Manjavona Valley (here considered as corresponding to "vallée Mahavona" in the MNHN catalogue and "Mihavona" in Blommers-Schlösser & Blanc (1991): 19°21' S, 47°16' E, ca. 1800 m); 4, Ambohimirandrana (19°20' S, 47°16' E, ca. 2000 m); 5, Nosiarivo (19°20' S, 47°17' E, ca. 2000 m); 6, Marizana swamp (listed as "marais Marizana" in the MNHN catalogue); 7, Hctay Forest; 8, Tsiarafajavona road (used for different sites along a section of road that leads from the Ambohimirandrana area towards the Tsiarafajavona summit); 9, Tsiarafajavona Plateau (19°20' S, 47°14' E, 2380 m); 10, Tsiarafajavona; 11, Analamilona (19°20' S, 47°18' E, 1800 m). Although not strictly part of the Ankaratra massif, records from 12, Ambatolampy (19°22' S, 47°26' E, 1600 m), are also considered. As Ankaratra slopes are often rather steep, and

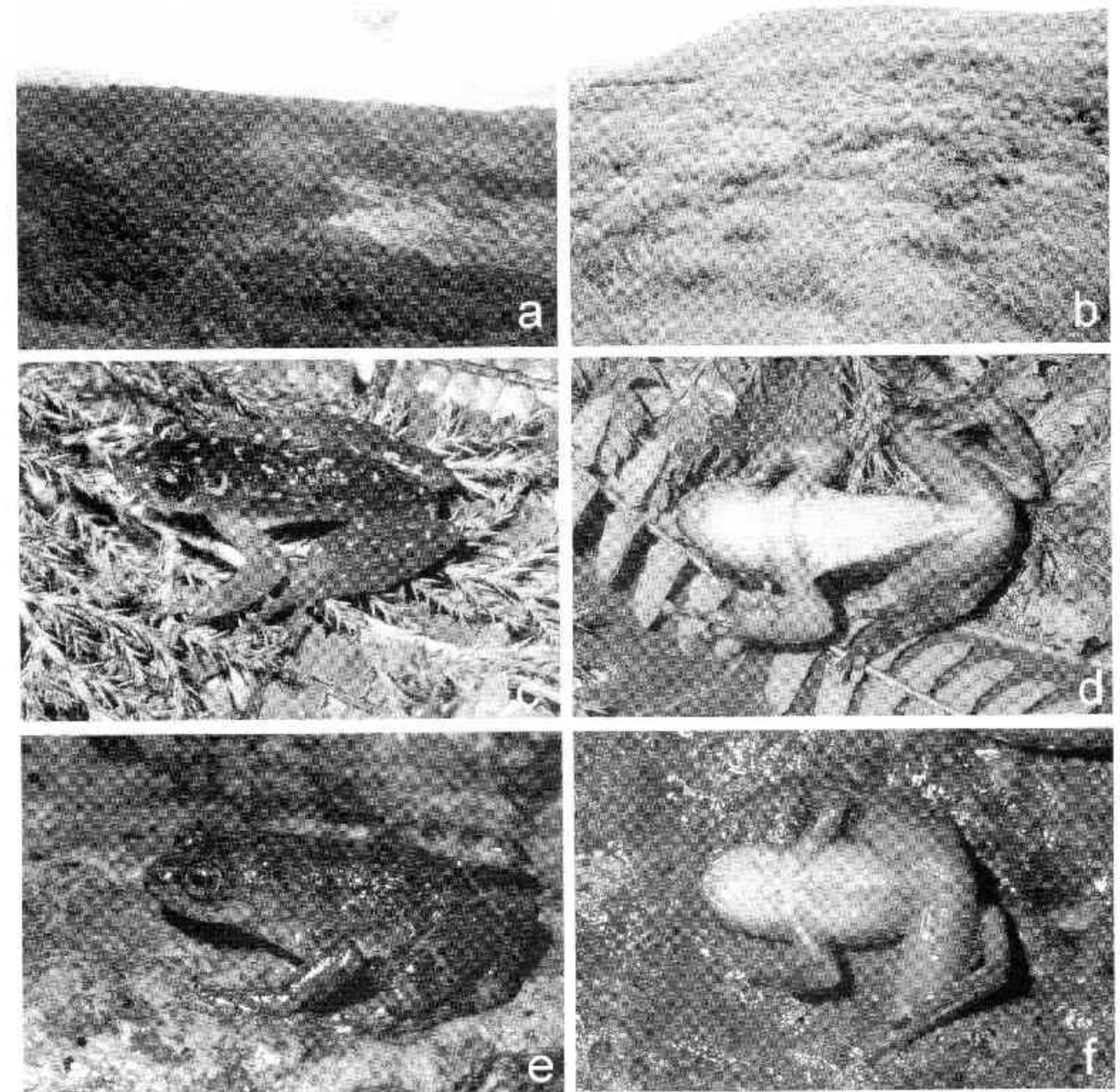


Fig. 2 - Ankaratra landscapes, and rediscovered endemic montane frogs: a, Nosiarivo Forest; b, savannah with ericoid vegetation alongside the Tsiarafajavona road; c, d, dorsolateral and ventral view of *Boophis williamsi* from Ambohimirandrana (male, ZSM 734/2001); e, f, dorsolateral and ventral views of *Mantidactylus pauliani* from Ambohimirandrana (ZSM 756/2001).

no detailed information on the collecting circumstances of most MNHN specimens is available, the coordinates and especially elevations of the localities can only be approximate. As an example, specimens from Nosiarivo may well have been collected at localities between 2000 and 1800 m around this site. It is also uncertain where MNHN frog specimens from Ambohimirandrana were collected, as we did not locate any brook directly on this mountain; our data (ZSM and UADBA specimens) refer to a brook flowing down the Tsiafajavona and separating its foothills from the Ambohimirandrana slopes. Most or all Ankaratra amphibian specimens catalogued between 1972 and 1974 in the MNHN refer to collections made by C. P. Blanc. As the catalogue, however, does not give precise information for most specimens, the collector only is reported in cases where it is explicitly stated in the catalogue entry or in publications.

#### TAXONOMIC ACCOUNTS

Class AMPHIBIA  
Order ANURA  
Family Mantellidae

#### *Boophis ankaratra* Andreone, 1993

MRSN-FAZC 7930, 7946, 7953 (FA, JER, SDM, 11.I.1999, Manjakatomp); MNHN 1973.1102, 1973.1106-1107 (5-14.I.1972, Ambohimirandrana); MRSN A73.1-10 (FA, DV, 11.1993, Manjakatomp; holotype and paratypes); UADBA 2000.456-2000.457 (MV, NR, 2.III.2000, Manjakatomp); ZFMK 59846-59847 (FG, MV, 8.I.1994, Manjakatomp); ZSM 367/2000 (FG, MV, 11.II. 2000, Manjakatomp).

*Boophis ankaratra* was originally described from Manjakatomp. Andreone (1993) had only Manjakatomp material available for the description of the new species. Glaw & Vences (1994) recorded the species from a forest near Ambalamarina in the Andringitra Massif (vouchers ZFMK 59826-59827). We recently found the species also near Mandraka (18°55' S, 47°56' E, ca. 1100 m elevation; ZSM 400/2000, UADBA 2000.415), at Ireimo (16°34' E, 20°36' S, 1650 m elevation, ZSM 735/2001, UADBA 2001.481-482) and on the "Col des Tapias" (240th km of National Road 7; 20°14' S, 47°05' E, 1425 m elevation; ZSM 399/2000). Calling specimens were always heard at night along brooks (maximum distance from water ca. 20 m). Calls from all localities were similar to each other; detailed call data will be published elsewhere.

Blommers-Schlösser & Blanc (1991) quoted *B. mandraka* from Ankaratra. Andreone (1993) already stated that this record probably refers to *B. ankaratra* and was in need of confirmation. In the Paris museum, three adult male specimens (MNHN 1973.1102, 1106 and 1107) from Ambohimirandrana are catalogued as *B. mandraka*. Almost certainly, the record of Blommers-Schlösser & Blanc (1991) was based on these specimens, which, however, correspond to *B. ankaratra* by morphology. Their rather large size (SVL, 27.1-28.1 mm vs 21-26 mm in *B. mandraka*; see Blommers-Schlösser 1979b) as well as their iris coloration which is still perfectly recognizable (reddish-brown inner and beige outer iris area; no reticulations) exclude that these specimens belong to *B.*

*mandraka*. We therefore assign them to *B. ankaratra*, and propose to consider the Ankaratra locality for *B. mandraka* as erroneous. Tadpoles assignable to *B. ankaratra*, as described by Glaw & Vences (1994), were regularly collected in forest brooks (Fig. 3e).

Guibé (1952) recorded *Rhacophorus luteus longicrus* from Manjakatomp without mentioning any voucher specimens. The description given by him most probably refers to *B. ankaratra* (a small species of green colour in life, living on trees along brooks). However, his statement that the species also lives on rocks and jumps into the water when disturbed may also apply to *B. microtympanum*. In their distribution maps, Blommers-Schlösser & Blanc (1991) gave Manjakatomp as the locality of *B. luteus*. This species is very easy to recognize by its calls, which we never heard in Ankaratra. Therefore, the record of *B. luteus* may actually refer to *B. ankaratra*.

#### *Boophis goudoti* Tschudi, 1838

MRSN-FAZC 7939-7940 (FA, JER, SDM, 8.I.1999, Manjakatomp); ZSM 391/2000 and UADBA 2000.455 (MV, NR, 2.III.2000, Manjakatomp); ZSM 741/2001-742/2001, UADBA 2001.428-429 (MV, DRV, 8.III.2001, Tsiafajavona Plateau).

*Boophis goudoti* is a rather ubiquitous species in the central highlands of Madagascar. In Manjakatomp, we found specimens at night on the ground and about 1 m high on the vegetation in degraded forest. The large tadpoles were found in ponds and swamps. The presence of *B. goudoti* on the Tsiafajavona Plateau is the first confirmed record of the species above 2000 m, demonstrating that it is able to penetrate into real montane habitats.

Calls recorded in March 1992 at Manjakatomp and most probably belonging to *B. goudoti* consisted of unharmonious notes (duration = 152-203 ms,  $n = 4$ ), repeated after intervals of 606-915 ms ( $n = 4$ ). Dominant frequency was 600-800 Hz. These calls corresponded well to recordings of R. Blommers-Schlösser (who made them available to us for re-analysis) which probably refer to specimens from Tsinjoarivo. Notes were arranged more or less regularly in a series. Note duration was 300-351 ms ( $323 \pm 19$  ms,  $n = 10$ ), duration of intervals between notes of one series being 493-676 ms ( $589 \pm 63$  ms,  $n = 9$ ). Notes consisted of 9-14 ( $12 \pm 1$ ,  $n = 10$ ) pulses. Pulse rate increased continuously towards the end of each note, sometimes leading to a pulse group at the end of a note. Frequency ranged between 0 and 2000 Hz, exceptionally up to 3000 Hz; dominant frequency was below 1000 Hz.

#### *Boophis microtympanum* (Boettger, 1881)

MNHN 1973.1041-1046 and 1973.1051-1055 (5-7.I.1972, Ambohimirandrana); MNHN 1973.1047-1048 (10.I.1972, Manjakatomp);



Fig. 3 - Aspects of reproductive biology in the Ankaratra herpetofauna: a, fighting males of *Heterixalus betsileo*, Manjakatomp; b, calling male of *Scaphiophryne madagascariensis*, Manjakatomp; c, eggs of *S. madagascariensis*, Manjakatomp; d, tadpole of *S. madagascariensis*, Manjakatomp; e, tadpole of *Boophis ankaratra*, Nosiarivo; f, tadpole of *B. williamsi*, Ambohimirandrana (ZSM 802/2001); g, clutch of *Plethodontohyla tuberculata* in jelly nest under a stone, Nosiarivo; h, clutch of *Tygodactylus mirabilis*, Tsiafajavona Plateau.

MNHN 1973.1049-1050 (12.I.1972, Tsiafajavona); MNHN 1973.1056-1057 (12.I.1972, Betay Forest); UADBA 2000.430 (MV, NR, 3.III.2000, Tsiafajavona Plateau); ZFMK 53654-53663, 56161-56162 (FG, J. Müller, 14.III.1992, Ankaratra, obtained from a local collector near Manjakatampo); ZSM 366/2000 (FG, MV, 12.II.2000, Nosiarivo-Tsiafajavona); ZSM 365/2000 and UADBA 2000.114 (FG, MV, 12.II.2000, Tsiafajavona Plateau); ZSM 725/2001 and 726/2001, and UADBA 2001.407, UADBA 2001.410-411 (MV, DRV, 8.III.2001, Tsiafajavona Plateau).

Further material MNHN 1962.857 (J. Millot, 1949, Ireimo); MNHN 1972.649-650 (18.I.1971, Namoly Plateau, Andringitra); MNHN 1972.651 (20.I.1971, Ambalamarovandana, Andringitra); MNHN 1973.1058-1064 (8-17.I.1973, Ambatomenaoloa, Ireimo); MNHN 1973.1065-1071 (8-14.I.1973, Ampandianombilapa, Ireimo); ZSM 461/2000 (MV, Col des Tapias, III.2000); ZSM 722/2001 and UADBA 2001.484-485 (MV, DRV, DR, 10.III.2001, Ireimo).

A species of high elevation open areas, such as montane heathlands and savannah. We found single specimens on the Tsiafajavona road close to Ambohimirandana (just above the treeline), but records also exist from Manjakatampo (a site largely covered by forest). Along the Tsiafajavona road as well as at Anamilona, we found specimens during night and day on the ground in grassland areas, far from the brooks used for reproduction.

On the Tsiafajavona Plateau, the species was rather common along small brooks running through grassland. We found specimens during the day sitting on the ground and in the grass. When disturbed, they jumped into the water and dived. Tadpoles of different sizes with the characters typical for this species (see Blommers-Schlösser, 1979b) were very common in these brooks. According to Blommers-Schlösser & Blanc (1991), the species is also known from Ireimo, Ankafana, Ambalamarovandana, and Namoly (the latter two localities situated in the Andringitra massif). Type locality is the "Imerina" Region. We did not find vouchers for the Ankafana locality, but collected a specimen on the "Col des Tapias" (240th km of National Road 7; 20°14'17" S, 47°05'59" E, 1425 m elevation; ZSM 461/2000). Together with the Ireimo locality this confirms that the species is distributed at suitable localities between the high-elevation areas of Ankaratra and Andringitra.

The Ankaratra sample available in the MNHN consists mainly of males, while the Ireimo sample consists mainly of females. SVL was 27.8-32.5 mm ( $29.7 \pm 1.4$  mm,  $n = 12$ ) for males and 32.8-34.5 mm ( $33.7 \pm 1.2$  mm,  $n = 2$ ) for females in the Ankaratra samples, while it was respectively 24.7 mm ( $n = 1$ ) and 31.7-37.10 mm ( $33.9 \pm 1.7$  mm,  $n = 12$ ) in the Ireimo sample. Overall mean male/female size ratio was 87%.

Calls from Ankaratra specimens (obtained from a local collector without precise locality) were recorded in 1992 in captivity. Frogs called submerged under water. Two note types could be distinguished (Fig. 4a). Notes of type 1 were unharmonious and had a duration of 39-65 ms ( $51 \pm 9$  ms,  $n = 6$ ). Intensity was highest at the beginning of each note and decreased towards its end. Notes of type 2 were short clicks of a duration of 21-31 ms ( $24 \pm 4$  ms,  $n = 7$ ). Intensity was normally slightly

higher than in notes of type 1. Duration of intervals between notes altogether ranged from 170-919 ms ( $361 \pm 217$  ms,  $n = 12$ ), duration of intervals between one note of type 1 and one note of type 2 was 170-242 ms ( $206 \pm 32$  ms,  $n = 5$ ). Frequency of both notes was between 600-6700 Hz, the dominant frequency was between 600-2700 Hz. Notes of both types were generally but not exclusively emitted in an alternating order. As an example, one call had the note order '2-2-1-2-1-1-2-1-2-1-2'. On 8.III.2001, we heard similar calls on the Tsiafajavona Plateau at water and air temperatures around 10° C. All calling males were below the water surface, at depths of 10-30 cm, on the bottom, in small groups of 2-6 individuals in brook sections of 1-2 m.

### *Boophis williamsi* (Guibé, 1974)

MNHN 1973.1091 (holotype) and 1973.1092-1099 (paratypes (CPB, 4.I.1972, Ambohimirandana); ZSM 734/2001 (MV, DRV, 20.III.2001, Ambohimirandana); ZSM 802/2001 (tadpoles; MV, DRV, 20.III.2001, Ambohimirandana).

This is one of the least known anuran species from Madagascar. The original description was based on nine specimens of unknown sexual maturity. Blommers-Schlösser (1979b) further described tadpoles and recently metamorphosed specimens which may belong to this species. Re-examination of the type series corroborated the validity of *B. williamsi* and its distinctness from *B. laurenti* (from Andringitra) and the sympatric *B. microtympanum*. Several if not all type specimens are females, as was especially obvious in the holotype by gonad inspection. The most obvious distinctive character of *B. williamsi* is the colour pattern. *Boophis microtympanum* has brown vermiculation on a greenish (exceptionally light brown) back, and each dark brown marking is more or less distinctly bordered by light (whitish) colour, giving the impression of a very sharply delimited pattern. The whitish borders of the markings and spots are lacking in *B. williamsi*, which in preservative shows brown spots or markings (of variable size), partly poorly delimited, on a light brown back. The markings generally form a clearly vermiculated pattern in *B. microtympanum*, but less so in *B. williamsi*. Further morphological differences between the species are (1) the more distinct and broader tips of fingers and toes in *B. williamsi*, (2) a more distinctly expressed supratympanic fold in *B. williamsi* (3) a generally more coarse granulation on the venter in *B. williamsi*. Measurement of all available specimens are included in Table 1.

In March 2001, a single adult male specimen of *B. williamsi* was collected at Ambohimirandana (ZSM 734/2001; Fig. 2c, d). The specimen was sitting at night ca. 1 m high on leaves in the vegetation along a fast flowing brook, close to a small cascade. At this spot, few native trees are scattered along the brook, but the vegetation is largely made up by exposed ferns, ericacees and other shrubs. Considering the importance of

TABLE 1 - Morphological measurements of selected amphibian specimens relevant for the present study.

Species and catalogue number	Status	Sex	Locality	SVL	HW	HL	TD	ED	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TT
<i>Scaphiophrynus madagascariensis</i>																	
MNHN 1947.2.7.41	HT	F	East Betsileo	55.6	18.3	14.3	-	5.6	2.6	2.8	3.5	27.4	15.5	58.8	32.8	25.2	0
MNHN 1945.25*	HT*	F	Madagascar	45.0	17.2	12.4	(1.6)	4.4	2.2	2.8	2.9	26.1	13.2	56.5	29.8	20.3	0
<i>Boophis williamsi</i>																	
MNHN 1973.1091	HT	F	Ankaratra	41.3	12.7	13.5		3.7	2.7	3.8	4.7	27.2	13.6	72.9	35.0	22.4	3
MNHN 1973.1093	PT	F	Ankaratra	40.0	13.1	13.0	1.6	3.9	2.4	4.1	4.5	25.2	13.1	67.4	32.5	22.2	4
MNHN 1973.1094	PT	SA	Ankaratra	36.3	10.8	11.3	-	3.7	2.6	3.2	4.3	23.7	13.4	63.4	32.4	21.8	1
MNHN 1973.1095	PT	SA	Ankaratra	33.5	10.0	11.0	1.6	3.4	2.2	2.9	4.5	23.5	12.0	56.0	27.4	18.0	4
MNHN 1973.1099	PT	SA	Ankaratra	33.5	9.7	11.0	(1.5)	3.4	2.1	3.0	4.0	23.1	11.3	56.8	27.9	18.2	5
MNHN 1973.1092	PT	SA	Ankaratra	32.0	10.5	10.3	-	3.3	2.2	2.8	3.7	22.2	11.6	57.6	28.2	18.6	6
MNHN 1973.1097	PT	SA	Ankaratra	35.0	10.7	11.0	(1.6)	3.2	2.4	3.1	3.8	22.7	11.7	62.9	29.2	19.2	4
MNHN 1973.1096	PT	SA	Ankaratra	31.9	10.3	10.2	1.1	3.1	2.3	2.7	3.8	22.0	11.7	55.2	27.8	18.3	5
MNHN 1973.1098	PT	SA	Ankaratra	33.9	10.0	10.8	-	3.4	2.4	2.8	4.5	22.5	11.7	55.9	27.1	18.0	4
ZSM 734/2001	-	M	Ankaratra	37.1	10.4	11.7	1.7	3.7	2.1	3.3	3.7	23.3	12.2	57.5	29.4	19.7	2
<i>Mantidactylus pauliani</i>																	
ZSM 756/2001	-	SA	Ankaratra	26.1	8.4	9.4	1.8	3.1	1.1	1.5	2.2	16.5	7.6	44.8	21.5	14.4	4

Treated taxa: 4, holotypes of *Scaphiophrynus madagascariensis* and its junior synonym *Pseudobombus pastuosus*, marked with an asterisk (\*); b, types of *Boophis williamsi*; c, ZSM specimens of *B. williamsi* and *Mantidactylus pauliani*. Used abbreviations: HT, holotype; PT, paratype; F, female; M, male; SA, subadult; SVL, snout-vent length; HW, head width; HL, head length; TD, horizontal tympanum diameter (in parentheses when tympanum is not well visible); ED, horizontal eye diameter; END, eye-nostril distance; NSD, nostril-snout tip distance; NND, nostril-nostril distance; FORL, forelimb length; HAL, hand length; HIL, hindlimb length; FOTL, fore length including tarsus; FOL, foot length; TT, position where fibiarticular articulation reaches when the hindlimb is adpressed along the body (0, not reaching forelimbs; 1, tympanum; 2, posterior eye corner; 3, eye centre; 4, anterior eye corner; 5, between eye and nostril; 6, nostril).

