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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 paultani*) were observed for the first time for almost 30 years; their live coloration and morphology are described. The skink *Amphiglossus macrocercus* is shown to be live-bearing. Breeding in the austral summer could be demonstrated for most species, including the geckos *Lygodactylus mirabilis* and *Phelsuma barbouri* 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. paultani*, *L. mirabilis*) appear to be Ankaratra endemics (11% of the overall community). Pending further surveys and taxonomic revisions, more that 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 (Tsiafajavona, 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 & Randrianahazo, 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 Manjakatompo forestry station; second, due to the easy access to Manjakatompo 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 Manjakatompo, Nosiarivo, and Tsiafajavona 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), Zoölogisch 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 ± 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. Ninchери; SDM, S. De Michelis.

Study area

Geologically (Perrier de la Bâthie, 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: Tsiafajavona (2642 m), Tsiafakafo (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 Manjakatompo (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 Tsiafajavona, 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.* (1996), the forest in the area of the sacred royal Tankaratra tombs (Nosiarivo) is almost exclusively composed of a single tree species (*Weinmannia boyeriana*) 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 Manjakatompo 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).

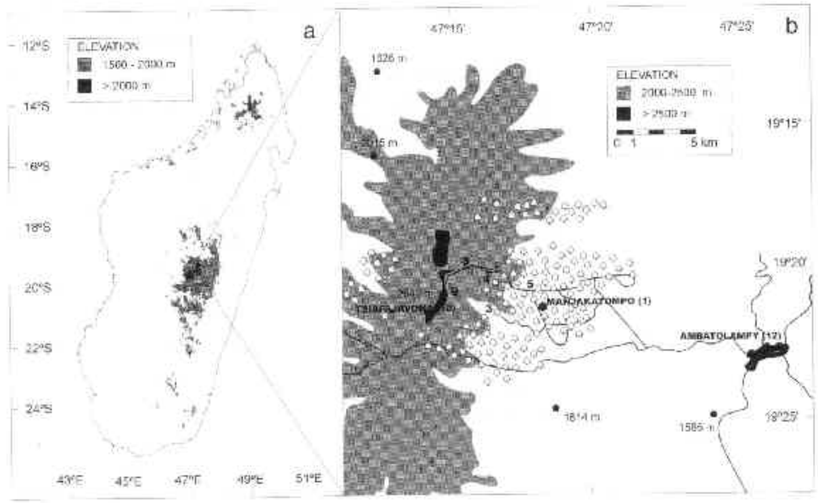

Fig. 1 - Map (**a**) of Madagascar, showing areas between 1500-2000 m and above 2000 m elevation and (**b**) of the Ankaratra region between Ambatolampy and the Tsiafajavona, showing areas of 2000-2500 m and above 2500 m, forested areas, and main roads. Numbers refer to several of the collection sites listed in Materials and Methods: 1, Manjakatompo; 3, Manjavona Valley; 4, Ambohimirandrana; 5, Nosiarivo; 8, Tsiafajavona road; 9, Tsiafajavona Plateau; 10, Tsiafajavona. 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.

Ankaratra localities reported in the following accounts are (see Fig. 1): 1, Manjakatompo (19°21' S, 47°18' E, ca. 1700 m); 2, Lac Froid; 3, Manjavona Valley (here considered as corresponding to "vallée Mahiavona" 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, Betay Forest; 8, Tsiafajavona road (used for different sites along a section of road that leads from the Ambohimirandrana area towards the Tsiafajavona summit); 9, Tsiafajavona Plateau (19°20' S, 47°14' E, 2380 m); 10, Tsiafajavona; 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

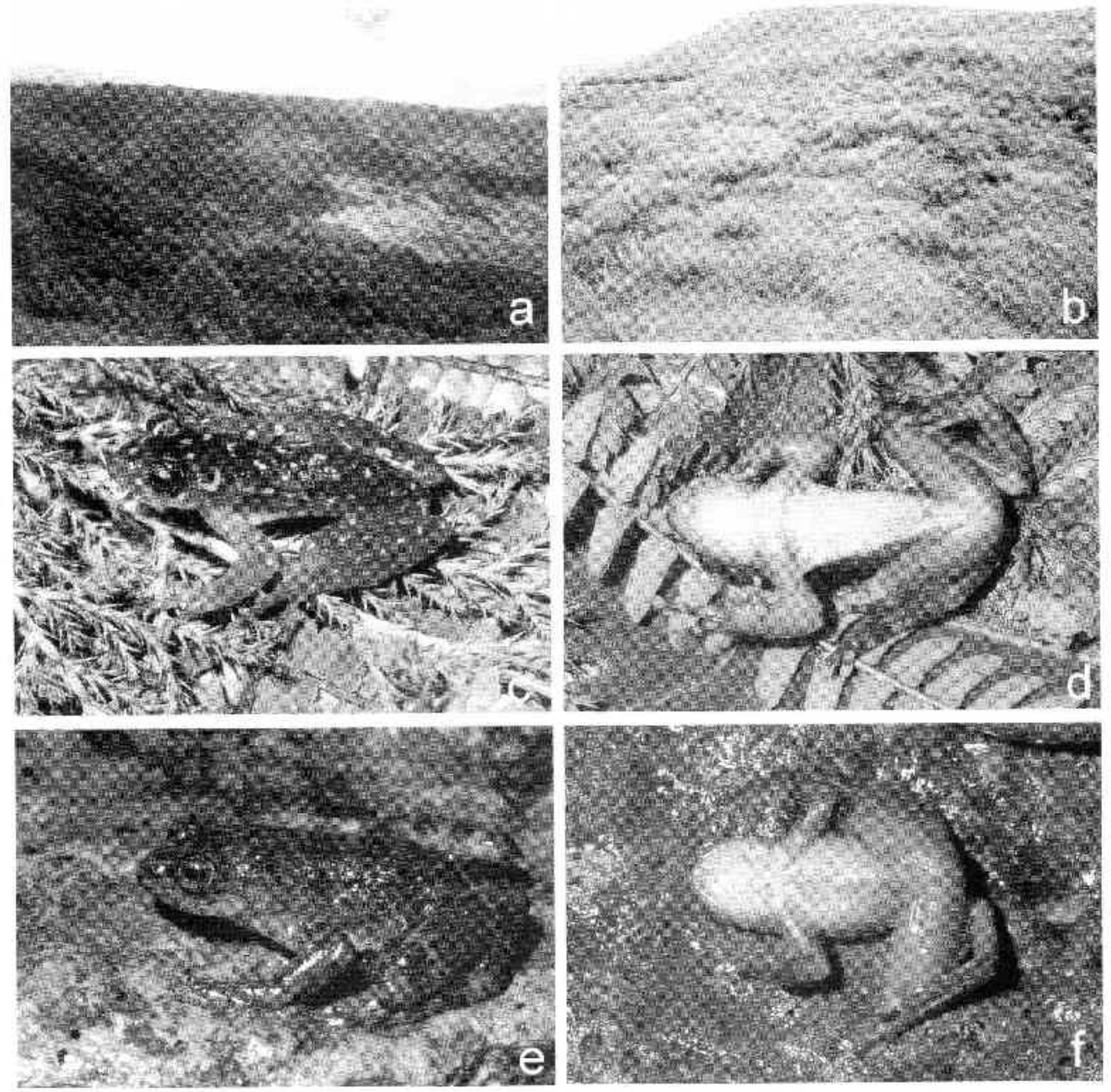

Fig. 2 - Ankaratra landscapes, and rediscovered endemic montane frogs: **a**, Nosiarivo Forest; **b**, savannah with ericoid vegetation alongside the Tsiafajavona road; **c**, **d**, dorsolateral and ventral view of *Boophis williamsi* from Ambohimirandrana (male, ZSM 734/2001); **e**, **f**, dorsolateral 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, Manjakatompo); MNHN 1973.1102, 1973.1106-1107 (5-14.I.1972, Ambohimirandrana); MRSN A73.1-10 (FA, DV, 1.I.1993, Manjakatompo; holotype and paratypes); UADBA 2000.456-2000.457 (MV, NR, 2.III.2000, Manjakatompo); ZFMK 59846-59847 (FG, MV, 8.I.1994, Manjakatompo); ZSM 367/2000 (FG, MV, 11.II. 2000, Manjakatompo).

Boophis ankaratra was originally described from Manjakatompo. Andreone (1993) had only Manjakatompo 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 Itremo (46°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) quored *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 Manjakatompo 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 Manjakatompo 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, Manjakatompo); ZSM 391/2000 and UADBA 2000.455 (MV, NR, 2.III.2000, Manjakatompo); 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 Manjakatompo, 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 Manjakatompo 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 ± 19 ms, n = 10), duration of intervals between notes of one series being 493-676 ms (589 ± 63 ms, n = 9). Notes consisted of 9-14 (12 ± 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, Ambatohimirandrana); MNHN 1973.1047-1048 (10.I.1972, Manjakatompo);

Fig. 3 - Aspects of reproductive biology in the Ankaratra herpetofauna: **a**, fighting males of *Heterixalus betsileo*, Manjakatompo; **b**, calling male of *Scaphiophryne madagascariensis*, Manjakatompo; **c**, eggs of *S. madagascariensis*, Manjakatompo; **d**, tadpole of *S. madagascariensis*, Manjakatompo; **e**, tadpole of *Boophis ankaratra*, Nosiarivo; **f**, tadpole of *B. williamsi*, Ambohimirandrana (ZSM 802/2001); **g**, clutch of *Plethodontohyla tuberata* in jelly nest under a stone, Nosiarivo; **h**, clutch of *Lygodactylus 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 Manjakatompo); 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, Itremo); 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, Ambatomenaloha, Itremo); MNHN 1973.1065-1071 (8-14.I.1973, Ampandrianombilapa?, Itremo); ZSM 461/2000 (MV, Col des Tapias, III.2000); ZSM 722/2001 and UADBA 2001.484-485 (MV, DRV, DR, 10.III.2001, Itremo).

A species of high elevation open areas, such as montane heathlands and savannah. We found single specimens on the Tsiafajavona road close to Ambohimirandrana (just above the treeline), but records also exist from Manjakatompo (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 Itremo, 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 Itremo 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 Itremo sample consists mainly of females. SVL was 27.8-32.5 mm (29.7 ± 1.4 mm, n = 12) for males and 32.8-34.5 mm (33.7 ± 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 ± 1.7 mm, n = 12) in the Itremo 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 ± 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 ± 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 ± 217 ms, n = 12), duration of intervals between one note of type 1 and one note of type 2 was 170-242 ms (206 ± 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 "2-2-1-2-1-1-2-1-2-1-2-1-2-1". 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, Ambohimirandrana); ZSM 734/2001 (MV, DRV 20.III.2001, Ambohimirandrana); ZSM 802/2001 (tadpoles: MV DRV, 20.III.2001, Ambohimirandrana).

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*. Measurements of all available specimens are included in Table I.

In March 2001, a single adult male specimen of *B. williamsi* was collected at Ambohimirandrana (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, ericaceaes and other shrubs. Considering the importance of

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

Species and catalogue number	Status	Sex	Locality	SVL	HW	HL	ED	UED	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TT
Scaphiophryne madagascariensis																
BMNH 1947.2.7.41	HT	F	East Betsileo	55.6	18.3	14.3	-	2.6	2.8	3.5	27.4	15.5	58.8	32.8	23.2	0
MNHN 1915.25*	HT*	F	Madagascar	45.0	17.2	12.4	(1.6)	2.2	2.8	2.9	26.1	13.2	56.5	29.8	20.3	0
Boophis williamsi																
MNHN 1973.1091	HT	F	Ankaratra	31.3	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	30.0	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	(1.3)	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	32.1	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
Mantidactylus pauliani																
ZSM 756/2001	-	SA	Ankaratra	26.1	8.4	9.4	1.8	3.1	1.4	1.5	2.2	16.5	7.6	44.8	21.5	14.4	4

Treated taxa: =, holotypes of *Scaphiophryne madagascariensis* and its junior synonym *Pseudohemisus pustulosus*, 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, foot length including tarsus; FOL, foot length; TT, position where tibiotarsal articulation reaches when the hindlimb is adpressed along the body (0, not reaching forelimbs; 1, between eye and nostril; 6, nostril).

this first record of the species since the 1970s, we here give a detailed description of the specimen, including the first data on life coloration. The head was much broader than the body. The general impression was that of a rather elongated body. The dorsal skin was smooth with the exception of the posterior part of the back which was distinctly and coarsely granular (with distinct knob-like elevated granules of 0.5-1 mm diameter), a character not known in any other montane *Boophis* species. There were distinct light nuptial pads on the inner finger. The dorsal coloration in life was brown with translucent shade. Small orange markings were scattered on the dorsal surface. The ventral surface was dirty whitish. The iris was light brown, with a bluish-grey iris periphery. Large tadpoles which agreed with Blommers-Schlösser's (1979b) description of *B. williamsi* larvae were found under boulders in fast-flowing parts of the same brook section (Fig. 3D).

Mantidactylus (Blommersia) domerguei
(Guibé, 1974)

MRSN-FAZC 7928 (FA, JER, SDM, 10.I.1999, Manjakatompo); ZFMK 59852 (FG, MV, 8.I.1994, Manjakatompo); ZSM 370/2000 (FG, MV, 12.II.2000, Manjakatompo).

Further material: MNHN 1972.190 (holotype) and MNHN 1972.191 1972.232 (paratypes) (CPB, 20.I.1971, Ambalamarovandana, Andringitra); MNHN 1975.957-1975.958 (without locality).

A small species which lives in swamp areas and calls from the low vegetation, or from the ground, hidden in dense vegetation. At many places in Manjakatompo, the species occurs syntopically with *M. kely*. The holotype and several paratypes are in mediocre state of preservation caused by an apparently very intensive fixation. Colour pattern of the holotype is hardly recognizable, but most paratypes still show the pattern typical for *domerguei*. Most specimens are rather small; among the largest are MNHN 1972.196 (SVL = 19.4 mm) and MNHN 1972.197 (SVL = 20.3 mm).

Calls of *M. domerguei* were heard in January 1994 and February and March 2000, during the day and at least up to 21:30 h in the night. At least in February-March 2000, *M. domerguei* called mainly at night, while *M. kely* was mainly calling during the day; only at dusk were both species occasionally heard in mixed choruses.

The call of *M. domerguei* from Manjakatompo and from the Andringitra Massif has been briefly described by Glaw & Vences (1994). We here provide a more detailed description. The calls were recorded on 8.I.1994 at Manjakatompo with 18° C air temperature. They were rather complex (Fig. 4b). Three note types could be distinguished: notes of type 1 were distinctly pulsed (pulse repetition rate ca. 190/s) and had a duration of 184-491 ms (307 ± 102 ms, n = 19); each of these notes was emitted during one expiration, and the vocal sac did not remain partly inflated between notes. Notes of type 2 were single pulses (clicks) of a duration of 6-10 ms (8

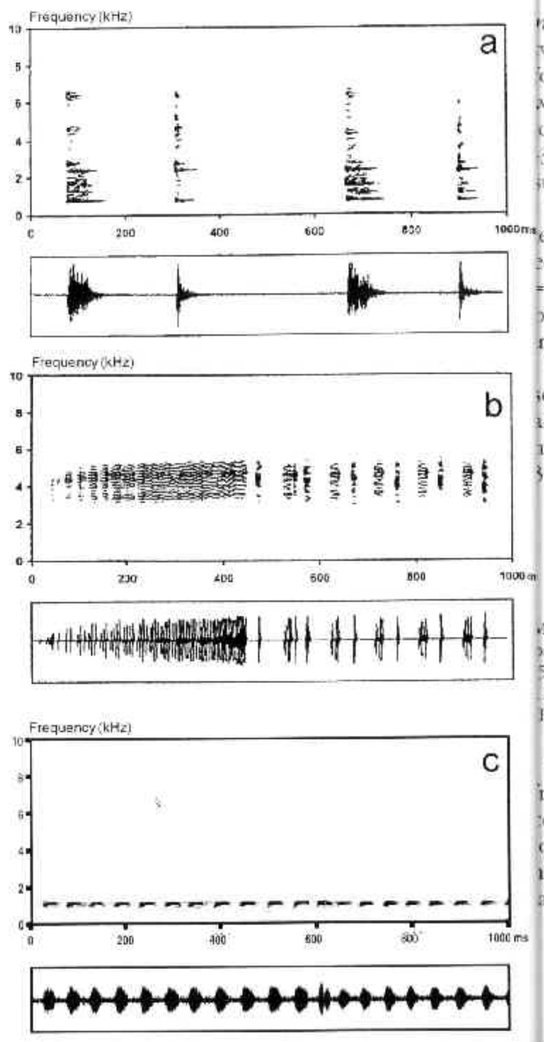

Fig. 4 - Sonagrams and oscillograms of advertisement calls of: **a**, *Boophis microtympanum* from the Ankaratra region, recorded 1992; **b**, *Mantidactylus domerguei* from Manjakatompo, recorde on 8.I.1994 at 18° C air temperature; **c**, *Scaphiophryne madag scariensis* from Manjakatompo, recorded on 11.II.2000 at 16° water temperature.

± 1 ms, n = 6). Notes of type 3 were pulse groups (4- pulses per note, pulse repetition rate ca. 200/s) of a d ration of 19-29 ms (22 ± 4 ms, n = 5). Frequency of three note types was 2900-5400 Hz, the dominant fr quency being 4100-4600 Hz.

Order and arrangement of note types was variabl Generally, each note of type 3 was followed by a no of type 2 after an interval of 16-28 ms (23 ± 5 ms, n = this combination will be called 'note pair' in what fo lows. Such note pairs were generally emitted in series 4-10 which altogether lasted 564-962 ms (786 ± 132 m n = 6), with intervals of 38-47 ms (41 ± 4 ms, n = 5) between note pairs. Also notes of type 1 were generally followed by a note of type 2, and the '1-2' combination was generally followed by several '3-2' note pairs. A typical call can be symbolized as follows: '1-2--3-2--3-2--3-2-3-2--3-2--3-2--3-2--3-2'. Duration of intervals between such series were 3159-6180 ms (4543 ± 1183 ms, n = 7).

The 1-2 note combination was sometimes also emitted in series (without notes of type 3), and then repeated after short intervals of 641-1374 ms (961 ± 258 ms, n = 11). In the field, we were able to trigger the emission of such series by playing back conspecific calls, indicating a territorial function.

Calls from Andringitra corresponded well to this description. Calls recorded in the Moramanga region were also similar but contained up to 22 note pairs. Furthermore, in the latter population the intensity of note type 3 was distinctly lower as compared to note type 2.

Mantidactylus (Blommersia) kely
Glaw & Vences, 1994

MRSN-FAZC 7929, 7989 (FA, JER, SDM, 10-11.I.1999, Manjakatompo); ZFMK 57444 (FG, MV, 8.I.1994; holotype); ZFMK 59850-59851 (FG, MV, 8.I.1994, Manjakatompo); ZSM 363/2000 (FG, MV, 11.II.2000, Ambatolampy); ZSM 364/2000 and UADBA 2000.98-100 (FG, MV, 12.II.2000, Manjakatompo).

This is a small species, which so far is only known from Manjakatompo (Glaw & Vences, 1994); in 2000 we collected the species also in a swamp area near Ambatolampy. Tadpoles from this site were identified by means of DNA sequences and will be described in detail elsewhere.

Mantidactylus (Brygoomantis) curtus
(Boulenger, 1882)

MRSN-FAZC 7912-7916, 7944, 7947, 7949-7950, 7955 (FA, JER, SDM, 8-11.I.1999, Manjakatompo); MNHN 1953.79-80 (including 79A-C and 80A-B) (Manjakatompo); MNHN 1953.76 (Tsiafajavona, 2450-2500 m elevation); MNHN 1972.1678-1684, 1972.1685-1691, 1972.1694-1714 (Ambohimirandrana); MNHN 1972.1717-1720, 1972.1722-1723 (Manjavona); MNHN 1972.1727 (Lac Froid) MNHN 1972.1730-1734 (road towards Tsiafajavona); MNHN 1972.1736-1737, 1972.1741-1742, 1972.1745 (Marizana); MNHN 1972.1750, 1972.1752-1761, 1972.1763 (Betay Forest); MNHN 1972.1767-1769 (Nosiarivo); MNHN 1984.69-77 (Manjakatompo); MRSN A391.1-3 (FA, DV, 2.II.1993); MRSN A435.1-3 (RN, 28.XII.1992-3.I.1993); UADBA 2000.89-91, 2000.94 (FG, MV, 12.II.2000, Tsiafajavona plateau); UADBA 2000.452-453 (MV, NR, 2.III.2000, Manjakatompo); ZFMK 59857 (FG, MV, 8.I.1994, Manjakatompo); ZSM 368/2000 (FG, MV, 12.II.2000, Manjakatompo); ZSM 369/2000 (FG, MV, 12.II.2000, Tsiafajavona road).

This medium-sized semi-aquatic species is probably the most common anuran above the treeline at Ankaratra, and it is also regularly found in the forest. *M. curtus* is generally observed along brooks, and we found its tadpoles in slow-running parts of the brooks, and in stagnant sidearms and puddles near them. The call of this species is unknown. Snout-vent length in the MNHN Ankaratra sample was 33.0-44.2 mm (38.4 ± 2.9 mm, n = 25) for males and 36.1-50.2 mm (43.3 ± 3.9 mm, n = 31) for females. Mean male/female size ratio was 89%. Oocytes (with a yellowish and a brownish pole) were recorded in several females after dissection (all collected in January): MNHN 1972.1698 (SVL = 50.2 mm; 48 not completely mature oocytes, 2.1 mm in diameter); MNHN 1972.1755 (SVL 49.1 mm; 84 mature oocytes, 2.2-3 mm); MNHN 1972.1763 (SVL 42.8 mm; 68 not completely mature oocytes, 2-2.2 mm in diameter); MRSN-FAZC 7950 (47.3 mm SVL; 56 mature oocytes, 3 mm in diameter).

Mantidactylus (Brygoomantis) alutus
(Peracca, 1893)

MRSN-FAZC 7917-7921, 7923-7925, 7945, 7952, 7956, 7987-7988 (FA, JER, SDM, 9-11.I.1999, Manjakatompo); MNHN 1972.1716, 1972.1721, 1972.1724-1726 (Manjavona Valley); MNHN 1972.1728 (Lac Froid, Manjakatompo); MNHN 1972.1729 (route du Tsiafajavona); MNHN 1972.1739-1740, 1972.1743-1744, 1972.1746-1749 (Marizana swamp); MNHN 1972.1766 (Nosiarivo); MRSN A401.1-2 (FA, DV, 3.II.1993); UADBA 2000.454 (MV, NR, 2.III.2000, Manjakatompo).; ZFMK 59854-59856 (FG, MV, 8.I.1994, Manjakatompo).

Mantidactylus alutus differs from *M. curtus* in its smaller body size. We typically observed it in shallow, slow-running water bodies at rather low elevations (Manjakatompo and Ambatolampy), generally not within dense forest.

Snout-vent length in the MNHN Ankaratra sample was 24.4-26.1 mm (25.5 ± 0.1 mm, n = 3) for males and 26.0-30.9 mm (28.3 ± 1.6 mm, n = 10) for females. Mean male/female size ratio was thus 90%. The females 1972.1744 (SVL = 26.6 mm), 1972.1729 (SVL = 26.0 mm) and 1972.1740 (SVL = 27.9 mm) contained 22, 27 and 30 yellowish oocytes with a dark pole, respectively. These were obviously immature in MNHN 1972.1744 and 1972.1740, but rather well developed in MNHN 1972.1729, measuring 2-2.5 mm in diameter. All three females were captured in January according to the corresponding catalogue entries.

Calling males were observed sitting in slowly running, shallow water flowing into a larger pond at Manjakatompo. Recordings were made on 8.I.1994 at 19 h (16° C air temperature). Calls were series of 5-10 pulsed notes (17-22 pulses). Note duration was 207-351 ms (286 ± 50 ms, n = 7). Duration of intervals between notes was 195-332 ms (243 ± 49 ms, n = 6), note repetition rate was 1.8/s. Frequency was 1000-3000 Hz. Each note corresponded to one expiration; the vocal sac did not remain partly inflated between notes. Calls analysed by Blommers-Schlösser (1979a; also recorded at Manjakatompo) were similar.

Mantidactylus (Brygoomantis) pauliani Guibé, 1974

MNHN 1972.1508-1513 (CPB, I.1972, Nosiarivo; holotype and paratypes); MNHN 1972.1514-1516 (CPB, I.1972, Betay Forest, paratypes); ZMA 6803 (5 specimens, field numbers 1184-1188, R. Blommers-Schlösser, 21.III.1975, Nosiarivo, 2200 m); ZSM 756/2001 (MV, DRV, 20.III.2001, Ambohimirandrana).

The third member of the subgenus *Brygoomantis* in the Ankaratra Massif appears to be one of the strictly montane Malagasy anurans, and a regional endemic (Vences & Glaw, 1999). So far, it was known only from two independent collections, the type series (nine specimens collected by C. P. Blanc at Nosiarivo and Betay Forest) and five specimens collected by R. Blommers-Schlösser (1979a) "under rapids in boulders" at Nosiarivo. The status of this species and its close relative *M. madecassus* from Andringitra has recently been reviewed by Vences & Glaw (1999). Both species are only known from elevations above 2000 m. In March 2001, we collected one presumably subadult specimen of *M. pauliani* at Ambohimirandrana. The specimen was first observed during the day, sitting in sunlight on a stone in a fast flowing brook. Three additional specimens were also seen in the same brook, sitting a few centimetres above the water on stones in the wet area under a cascade. All these specimens were very shy and immediately dived when disturbed. At night, we collected the first observed specimen (Fig. 2e, f; see Table 1 for measurements) by placing a net under the boulder on which it had been seen during the day, and moving the boulders in this brook section. From these data, the species appears to lead a predominantly subaquatic life with some degree of site-fidelity. Dorsal colour in life of the specimen was similar to that in preservative (see description in Vences & Glaw, 1999). The venter was dirty silvery whitish without markings. The iris was uniformly light brownish with a characteristic regular pattern of dark speckles; no distinction of an upper and lower part of the iris as often seen in terrestrial or semi-aquatic *Mantidactylus* was possible, this being an evident difference from sympatric *M. curtus*.

Mantidactylus (Chonomantis) brevipalmatus Ahl, 1929

MRSN-FAZC 7926, 7943, 7948 (FA, SDM, JER, 8-11.I.1999, Manjakatompo); MNHN 1953.45 (Manjakatompo); MNHN 1972.1355-1361 (Ambohimirandrana); MNHN 1972.1362-1364 (Manjavona Valley); MNHN 1972.1365-1396 (Betay Forest); MNHN 1972.1397-1402 (Nosiarivo); MNHN 1975.392 (Manjakatompo); MRSN A434.1-4 (RN, 28.XII.1992-3.I.1993, Manjakatompo), MRSN A398.1-5 (FA, DV, 3.II.1993, Manjakatompo; ZFMK 56163 (FG, J. Müller, 13.III.1992, Manjakatompo); ZFMK 59853 (FG, MV, 8.I.1994, Manjakatompo); ZSM 371/2000 (12.II.2000, Tsiafajavona Plateau); ZSM 372/2000-374/2000 (March 2000, Manjakatompo); ZSM 753/2001 and UADBA 2001.412, 2001.414 (MV, DRV, 8.III.2001).

A relatively common species both at Manjakatompo and the high-elevation areas near the Tsiafajavona summit (Andreone & Gavetti, 1994). It was found along quiet parts of brooks. Calls were heard during the day in 1992 in Manjakatompo and in 2000 on the Tsiafajavona Plateau. A detailed call description is being published in a revision of the subgenus *Chonomantis* (Vences & Glaw, in press). The tadpoles are characterized by a specialized funnel mouth, as is typical for other representatives of this subgenus (Blommers-Schlösser, 1979a).

Family Ranidae

Ptychadena mascareniensis (Duméril & Bibron, 1841)

MNHN 1953.202 (4 adult and 2 unlabelled juvenile specimens; Manjakatompo); MRSN A400 (FA, DV, 3.II.1993, Manjakatompo); UADBA 2001.417 (MV, DRV, 9.III.2001); ZSM 359/2000-360/2000 and UADBA 2000.75 (FG, MV, 11.II.2000, Ambatolampy); ZSM 376/2000 and UADBA 2000.446-447 (MV, NR, 2.III.2000, Manjakatompo); ZSM 720/2001 (MV, DRV, 8.III.2001, Ambohimirandrana).

An ubiquitous species, as far as known not endemic to Madagascar (see Glaw & Vences, 1994). At Andringitra, we observed the species in 1994 and 2001 on the Andohariana Plateau, at about 2100 m elevation. Probably due to the lack of stagnant, warm water bodies at high elevations, at Ankaratra the species is only known from lower elevations around Manjakatompo. Here, it is a common species in and around temporary and permanent ponds, puddles and rice fields. One female belonging to the series MNHN 1953.202 (SVL = 43.9 mm) contained 389 mature oocytes (dark brown with a light pole; about 1 mm diameter).

Family Microhylidae

Plethodontohyla tuberata (Peters, 1883)

MRSN-FAZC 7942 (FA, JER, SDM, 11.I.1999, Manjakatompo); MNHN 1953.103 (holotype of *Plethodontohyla crisculum*, junior synonym of *tuberata*; Manjakatompo); MNHN 1953.207-210 and 1975.1534-1555 (16.XI.1950, Manjakatompo); MNHN 1962.918-919 (R. Paulian, IX.1948, Manjakatompo); MNHN 1973.733 (CPB, 7.I.1972, Tsiafajavona); MNHN 1973.734 (CPB, 7.I.1972, Ambohimirandrana); MNHN 1973.735 (CPB, 10.I.1972, Betay Forest); MNHN 1973.740-744 (CPB, 11.I.1972, Betay Forest); MNHN 1973.746 (A. Peyrieras, Ankaratra); MRSN A439.1-3 (RN); UADBA 2001.416 (MV, DRV, 8.III.2001, Ambohimirandrana); ZFMK 59845 (FG, MV, 10.I.1994, Manjakatompo); ZSM 375/2000 and UADBA 2000.412 (MV, NR, 3.III.2000, Tsiafajavona road).

Further material: MNHN 1891.406 (holotype of *Mantipus angeli*, junior synonym of *tuberata*); MNHN 1972.784 (23.I.1967, Angavokely); MNHN 1973.737-738 (CPB, 1.XII.1971, Camp V, Chaines Anosyennes); MNHN 1973.745 (CPB, 14.XI.1971, Camp V-summit, Chaines Anosyennes); MNHN 1975.591 (Zanzinakely, Tafia Forest, Itremo).

Besides from Ankaratra, this species is also known from a number of additional sites, among which it is worth mentioning Itremo and the high elevations of the Anosy Massif in south-eastern Madagascar. It is therefore strange that despite intensive efforts it has not yet been found at Andringitra. On the other hand, Andreone & Randriamahazo (1997) and Nussbaum *et al.* (1999) did not confirm its presence at Andohahela in the Anosy Massif. It would be therefore important to confirm the presence of this species at the Anosy Massif and test again for its existence at Andringitra.

Guibé (1952) reported on the breeding behaviour of *P. tuberata* but provided little more than the information that its tadpoles develop in a liquefied jelly mass in cavities in the leaf litter. Similar nests (Fig. 3g) were also found and described by Glaw & Vences (1994). MNHN 1953.209 is a series of 64 tadpoles, possibly collected by J. Guibé and probably the basis of his note on the reproduction of the species. These larvae, collected on 16.XI.1950, are in developmental stages 31-34. One specimen in stage 34 measured 5.7 mm SVL and 17.5 mm total length. It is not certain whether all tadpoles belong to the same clutch.

Adult specimens of *P. tuberata* collected by us were mainly found in or close to the forest, but in February 2000, one specimen was found during heavy rain active on the ground almost above the treeline close to Ambohimirandrana; remains of a nest, most probably of *P. tuberata*, were found under a stone on the Tsiafajavona Plateau on 12.II.2000. Advertisement calls of the species are unknown; however, on 4.III.2000, after long and heavy rain, isolated calls were heard during the day in Manjakatompo (with ca. 20° C air temperature); these series of melodious notes (ca. 320 ms duration; frequency ca. 1500 Hz), reminiscent of typical cophyline calls, may have belonged to *P. tuberata*. A report on the peculiar defensive behaviour of this species at Manjakatompo is provided by Nincheri & Andreone (in press).

Scaphiophryne madagascariensis (Boulenger, 1882)

MRSN-FAZC 7936-7938 (FA, JER, SDM, 11.I.1999, Manjakatompo); MNHN 1953.237 (XII.1950, Manjakatompo); MNHN 1973.563-564 (Ambohimirandrana, Ankaratra, 6.I.1972); MNHN 1981.495-496, 1984.12-14 (M. Razarihelisoa, Ambatolampy); MNHN 1986.2033-2038, 1986.2146-2148 (Ambatolampy); MNHN 1984.113 (M. Razarihelisoa; no precise locality); MNHN 1987.757-764 (M. Razarihelisoa, Ambatolampy; isolated brains); UADBA 2000.71 and ZSM 387/2000 (FG, MV, 11.II.2000, Manjakatompo); ZSM 59/2001 (embryos; collected by FG and MV as eggs on 12.II.2000 and preserved on 13.II.2000).

Further material: BMNH 1947.2.7.41 (holotype of *Calophrynus madagascariensis* Boulenger, 1882; previously numbered 82.3.16.32; W.D. Cowan, East Betsileo); BMNH 1895.10.29.87-88 (P. Baron, East Imerina); BMNH 1896.10.9.38 (C. I. Forsyth-Major, Ambohimitombo); BMNH 1900.6.27.8 (C.I. Forsyth-Major, Ambohimitombo); MNHN 1945.25.27 (holotype and paratypes of *Pseudobemisus pustulosus* Angel & Guibé, 1945; no precise locality); MNHN 1890.447 (Madagascar, without precise locality); RD 452 (DR, Itremo).

Other material previously attributed to *S. madagascariensis*: MNHN 1938.245 (no precise locality in catalogue, but in same entry as the holotype of *Mantidactylus delormei* Angel, 1938, whose origin in the original description was given as "Antaranomby, l'Etang des boeufs" in the Andringitra Massif); MNHN 1972.744-752 (22.I.1971, Akiseasea pond, Ambalamarovandana, Andringitra); MNHN 1972.753-754 (22.I.1971, Bekimalao pond, Ambalamarovandana, Andringitra); MNHN 1972.755 (15.XI.1970, Andohariana Plateau, Andringitra); MNHN 1972.756 (16.I.1971, Riambavy river, Andohariana Plateau, Andringitra).

Populations of *Scaphiophryne* from the Ankaratra mountains are currently considered to belong to the species *S. pustulosa*, while the populations from the Andringitra Massif are named *S. madagascariensis* (Blommers-Schlösser & Blanc, 1991; Glaw & Vences, 1992, 1994). After re-examination of the type material of *Pseudobemisus pustulosus* Angel & Guibé 1945 (without precise locality) and of *Calophrynus madagascariensis* Boulenger, 1882 (from East Betsileo), we conclude that they are conspecific. The holotype of the senior synonym *C. madagascariensis* is a large adult female. The holotype of *P. pustulosus* is also an adult female with mature oocytes, while the two paratypes are juveniles. Coloration is largely faded in the holotype, but the original pattern and skin texture are still recognizable in the inguinal region. The type specimens of *madagascariensis* and *pustulosus* share (1) their typical colour pattern in which brown rounded blotches are encircled by green colour, in a symmetrical network-like pattern, (2) a dorsally coarsely granular skin (although only slightly recognizable in the type of *madagascariensis* due to its rather poor state of preservation), and (3) unexpanded tips of fingers and toes. We therefore conclude that the oldest available name for the *Scaphiophryne* from Ankaratra is *S. madagascariensis*, *pustulosus* being a junior synonym. Measurements of the respective holotypes are given in Table 1.

We also re-examined the available material from the Andringitra Massif, previously attributed to *S. madagascariensis*. These specimens differ from the Ankaratra material, as well as from the type material of *S. madagascariensis* and its synonym *P. pustulosus*, by (a) a consistently different colour pattern of brown blotches on a green ground colour, not distinctly arranged as network-like pattern, and with the brown patches being less rounded (e.g., generally a straight dorsolateral colour border is present on the anterior half of the body, separating a green back from a brown flank), (b) a smooth dorsal skin, and (d) slightly enlarged finger and toe disks (see also Blommers-Schlösser & Blanc, 1991). No name is currently available for the Andringitra population, which will be subject of forthcoming studies.

Disregarding the imprecise type locality "East Betsileo" (a rather large region more or less south-east of Ankaratra) and the similarly imprecise "East Imerina" (for BMNH 1895.10.29.87-88), the species is known from the Ankaratra massif, from the area between Ambatolampy and Tsinjoarivo (Bommers-Schlösser & Blanc, 1991), Itremo and Ambohimitombo.

Glaw & Vences (1994) recorded the finding of *S. madagascariensis* tadpoles in ponds near the Man-

jakatompo Forest station; no further biological data are so far known on the species. On 11.II.2000, during heavy rain, we heard a chorus of the species from a small pond at Manjakatompo. The pond measured ca. 10 m in diameter and had a maximum depth of 50 cm. At least 10 calling males were observed floating on the water surface which was largely covered with grass and debris at 16° C water temperature. They had enormously inflated single subgular vocal sacs (Fig. 3b), and were unable to deflate the sacs quickly; when trying to escape, they were unable to dive because of this air reservoir. The calls were long series of short melodious notes (Fig. 4c). Total call duration could not be ascertained as the calls of single specimens were very difficult to analyse considering the intense background noise of the chorus. Note duration was 28-32 ms (30 ± 1 ms, n = 10), duration of intervals between notes was 15-26 ms (22 ± 5 ms, n = 10). Note repetition rate was 19.5 per second. Notes were slightly frequency modulated, the frequency rising slightly towards the end of each note. Frequency was 750-1250 Hz.

One couple was observed at the pond in axillary amplexus. On 12.II.2000, a large number of *Scaphiophryne* eggs were observed floating on the surface and partly lying on the bottom of the pond (Fig. 3c). Eggs hatched after less than three days; embryonal and larval development will be the subject of a further publication. On 4 March, after long and heavy rains, the pond was much larger (ca. 15 m diameter; maximum depth about 150 cm), and many *Scaphiophryne* tadpoles of different sizes were observed floating in the free water (Fig. 3d). No *Scaphiophryne* calls were heard between 1 and 4.III.2000, despite the heavy and prolonged rains falling during this period.

Guibé (1952) reported having found one specimen of *S. madagascariensis* under a fallen tree trunk. Several additional indications on distribution, ecology and biology of *S. madagascariensis* are included in the unpublished thesis of M. Razarihelisoa. This Author found the species at Nosiarivo and close to the villages of Ambatondrakalavao and Antsampandrano (SE of Ambatolampy). At the latter locality, she observed *S. madagascariensis* on alluvial plains formed by a soil of very fine mud, with fruit trees and other cultivations, and moor land areas. In the rainy season, specimens were found under fallen logs and similar structures, and gathered in noisy choruses at night in water bodies. In the dry season, specimens were collected 40-50 cm deep in the soil of dried swamp areas, where they were hidden in more or less circular holes of 8-10 cm in diameter (M. Razarihelisoa, 1979, unpubl. diss., Univ. Paris VII). This locality may be identical to the record "Ambatolampy-Tsinjoarivo" indicated by Blommers-Schlösser & Blanc (1991), and MNHN specimens from Ambatolampy may have been collected at this site.

Family Hyperoliidae

Heterixalus betsileo (Grandidier, 1872)

MRSN A399.1-9 (FA, DV 1-4.II.1993, Manjakatompo); MRSN A433.1-2 (RN 28.XII.1992 - 3.I.1993, Manjakatompo); ZFMK 59849 (FG, MV, 8.I.1994, Manjakatompo); ZSM 356/2000-358/2000 and UADBA 2000.66-67 (FG, MV, 11.II.2000, Ambatolampy).

A common species in swamps and rice fields of the central highlands of Madagascar. Its typical call is regularly heard around Ambatolampy and in Manjakatompo (Andreone *et al.*, 1995). At the latter site, specimens were also found around a small pond, close to the forestry station, surrounded by dense vegetation, but they do not seem to penetrate into areas of dense forest. Detailed comparative call descriptions of this species have been published by Vences *et al.* (2000a). On 11.II.2000, during sudden and heavy rain, F. Glaw and M. Vences observed territorial behaviour between two *H. betsileo* males at Manjakatompo. Both specimens were fighting ca. 1.5 m high on a leaf (Fig. 3a). Similar observations (and call recordings) were also made by F. Andreone and D. Vallan on 2.II.1993. Besides aggressive clasping with the forelegs, the hindlegs were constantly used trying to kick off the rival from the leaf. During the fight, which lasted several minutes until one specimen left, both were regularly emitting long calls (second note type as described by Glaw & Vences, 1994), confirming that this type of vocalisation is to be regarded as a territorial call in *Heterixalus* (Glaw & Vences, 1994). On 11.II.2000, a clutch of 254 eggs was obtained in the collection bag from ZSM 357/2000 (male) and 358/2000 (female) from Ambatolampy; embryonic development was observed.

Heterixalus rutenbergi (Boettger, 1881)

ZSM 361/2000 (FG, MV, 11.II.2000, Ambatolampy). MRSN A1981 (MV, III.2000, Ambatolampy); ZFMK 59844-59845 (FG, MV, 11.I.1994, Ambatolampy).

This species is known from a number of localities in the central highlands of Madagascar (Blommers-Schlösser & Blanc, 1991), but so far very little is known on its ecology and biology. Glaw & Vences (1994) described for the first time the call from a swamp area near Ambatolampy. In 2000, we visited this area again, and collected two further specimens. ZSM 361/2000 was found on 11 February during the day, together with at least 25 specimens of *H. betsileo*; MRSN A1981 was found on 25 March, calling from a freshly conditioned rice field at night, within a large chorus of *H. betsileo*. A hybrid clutch *rutenbergi* × *betsileo* of 166 eggs was obtained in the collection bag on 11.II.2000 from the specimens ZSM 361/2000 and 356/2000 (preserved in the ZSM). No development of the eggs was recorded.

Angel (1934) and Guibé (1952) reported the species from Manjakatompo, but did not list any voucher specimens. There are no Manjakatompo vouchers in the MNHN, but, as this conspicuous species is easy to identify and the report of Guibé (1952) refers to his own field observations, its presence at some spots close to Manjakatompo is probable.

Class REPTILIA
Order SQUAMATA
Family Chamaeleonidae

Calumma hilleniusi (Brygoo, Blanc & Domergue, 1973)

MRSN FAZC 7932, 7934-7935 (FA, JER, SDM, 8.I.1999, Manjakatompo); MNHN 1972.53 (male, holotype) MNHN 1972.49-52, 1972.55 (females, paratypes) and MNHN 1972.48, 1972.54 (males, paratypes) (CPB, January and February 1972, Ankaratra); MNHN 1970.1049, (Manjakatompo); MNHN 1989.2874 (CPB, January/February 1972, Ankaratra); ZSM 380/2000 and UADBA 2000.421 (MV, NR, 2.III.2000, Manjakatompo); ZSM 545/2001 (MV, DRV, 8.III.2001, Nosiarivo).

Described as a subspecies of *C. brevicornis* from Ankaratra (Brygoo *et al.*, 1973), this taxon was elevated to full species rank by Glaw & Vences (1994). We observed several specimens in the forest and at forest edges around Manjakatompo. Females collected in March (UADBA 2000.421) and January-February (MRSN-FAZC 7932, MNHN 1972.50) contain large eggs (10 in the case of MRSN-FAZC 7932). Glaw & Vences (1994) reported on a clutch of seven eggs found in January; a young hatched in mid-April. Raxworthy & Nussbaum (1996a) report this species from the Andringitra mountains; it also has been found at Ivohibe (Raselimanana, 1999; Rasolonandrasana & Goodman, 2000) but the identity of these populations is to be confirmed. Snout-vent length of the MNHN specimens was 57-63 mm (males) and 59-71 mm (females).

Furcifer campani (Grandidier, 1872)

MNHN 5465 (holotype; from Ankaratra according to Brygoo, 1971); MNHN 1957.221 (Manjakatompo); MNHN 1957.222-223 (Tsiafajavona; MNHN 1957.225 bearing a label indicating its collection on July 1947); MNHN 1970.1058 (no locality information); MNHN 1991.2995-2997 (ex 8884; Manjakatompo according to MNHN catalogue, although MNHN 1991.2996 bears a label "Andringitra"); ZSM 386/2000 and UADBA 2000.472 and 2000.474 (MV, NR, 3.III.2000, Tsiafajavona road); ZSM 537/2001 (MV, DRV, 9.III.2001, Tsiafajavona road).

Further material: MNHN 1891.391 (no locality information); MNHN 1929.47 (G. Petit, 1926, Antananarivo); MNHN 1950.361 (J. Millot, "region des plateaux" of the Andringitra massif); ZSM 538/2001-539/2001 and UADBA 2001.563-564 (MV, DRV, DR, 13.III.2001, Andohariana Plateau, Andringitra).

In contrast to *C. hilleniusi*, this chameleon does not appear to occur normally in the forested areas of Manjakatompo but mainly in savannah situations. We found three dead specimens after very heavy and prolonged rain on 3.III.2000 on the road to the Tsiafajavona. One of these specimens (ZSM 386/2000) had four eggs (9.0-9.2 × 5.1-5.7 mm), in part hanging out of the cloaca (possibly naturally aborted). At Analamilona, in savannah situations, we found *F. campani* in sympatry with *F. lateralis* (see below), with a higher relative abundance of *F. campani*. One uncatalogued MRSN-FAZC female specimen (from Analamilona) measured 68.5 mm SVL and is one of the largest individuals known.

The poor voucher material of this species available in the Paris museum is surprising, considering that Brygoo (1971) reported that he collected the species himself at several localities which are not represented in the MNHN collection: Ibity, Antobeba, Ambohimitombo, Ambatolampy.

Furcifer lateralis (Gray, 1831)

MRSN-FAZC 7931 and 7933 (FA, JER, SDM, 8-9.I.1999, Manjakatompo).

This relative of *F. campani* (see Brygoo, 1971) had previously been recorded for Manjakatompo, but no voucher specimens were so far available. The two specimens reported here confirm the presence of the species within the area of the Manjakatompo forestry station. Both specimens were females; MRSN-FAZC 7931 contained 15 eggs, MRSN-FAZC 7933 12 eggs. At Analamilona, the species occurs in sympatry with *F. campani*.

Family Gekkonidae

Lygodactylus mirabilis (Pasteur, 1962)

MNHN 1966.1000 (holotype) and 1966.999, 1990.3572-3598 (paratypes) (J. Millot, 8.IX.1959, Tsiafajavona); MNHN 1990.3601-3630 (CPB, Tsiafajavona, 2300-2500 m); MNHN 1990.3631-3636 (D. Linares, 21.II.1973, high-elevation prairie habitat close to the Tsiafajavona summit, 2500 m); MNHN 1990.3637 (D. Linares, 13.VIII.1973, Tsiafajavona); UADBA 2001.406 (MV, DRV, 8.III.2001, Tsiafajavona Plateau); ZSM 388/2000 (FG, MV, 12.II.2000, Tsiafajavona Plateau); ZSM 389/2000 and UADBA 2000.429 (MV, NR, 3.III.2000, Tsiafajavona Plateau); ZSM 946/2000 and 947/2000 (two juveniles, hatched from eggs collected on 3.III.2000 on the Tsiafajavona Plateau).

Originally described as *Millotisaurus mirabilis*, this small gekkonid was placed in *Lygodactylus* by Pasteur (1995) because of the discovery of a species (*L. intermedius*) from Andringitra with characters intermediate between *mirabilis* and other species of *Lygodactylus*. *Lygodactylus mirabilis* is a small gecko, as far as known endemic to the high elevation area around the Tsiafajavona, where it lives on and under stones. We observed several specimens under stones on 12.II and 3.III.2000. Two pairs of eggs (one pair already hatched) were found under a stone on 3.III.2000, and several others in March 2001 (Fig. 3h). The two eggs measured 6 × 4 mm and 6 × 4.5 mm; they had been laid singly.

not attached to each other. On 7 and 8 March, two young (ZSM 946/2000 and 947/2000, hatched from the collected eggs measuring 11.2 and 11.9 mm SVL and 15.3 and 14.5 mm total length, respectively).

Of the series preserved in the MNHN, several specimens are informative regarding the reproductive biology of *L. mirabilis*. Very small, apparently recently hatched juveniles were collected in September (MNHN 1990.3594-3598; 11.7-13.4 mm SVL) and in January (MNHN 1990.3611-3630; 9.8-13.7 mm SVL). An uncatalogued egg (5.8 × 4.6 mm) is preserved with the former of these two series. One female specimen collected in August (MNHN 1990.3637; 26.2 mm SVL) contained two large eggs (ca. 5.7 × 4 mm).

Phelsuma barbouri Loveridge, 1942

MNHN 1948.8-9, 1994.789-794 (J. Millot, Tsiafajavona); MNHN 1984.425 (J. Millot, 1.1959, Tsiafajavona); MNHN 1984.427 (J. Millot, 8-9.IX.1959, Tsiafajavona, 2300-2500 m); MNHN 1984.428, 429, 431, 434-436 (J. Millot, Tsiafajavona); MNHN 1984.438 (CPB, Tsiafajavona); ZSM 385/2000 and UADBA 2000.86 (FG, MV, 12.II.2000, Tsiafajavona road); ZFMK 62333 (FG, MV 8-10.I.1994); ZSM 384/2000 and UADBA 2000.425 and 2000.427 (MV, N. Raminosa, 3.III.2000, Tsiafajavona road); ZSM 788/2001 and UADBA 2001.434 (MV, DRV, 9.III.2001, Tsiafajavona Plateau).

Further material: MNHN 1924.72-75 (M.G. Petit, Andringitra Massif); MNHN 1950.339-340 (J. Millot, Cirque Boby, Andringitra); MNHN 1950.389-391 (J. Millot, Andringitra "plateaux"); MNHN 1956.48 (J. Millot, "Andranontily"); MNHN 1984.432 (C. A. Domergue, 13.XII.1960, Mt. Ibity); MNHN 1984.433 (Pic Boby, Andringitra, 2680 m); MNHN 1993-2780-2786, 1994.7269-7276 (no locality); UADBA 2001.595 (MV, DRV, DR, 13.III.2001, Andohariana Plateau, Andringitra); ZSM 474/2001 and 475/2001 and UADBA 2001.602 and 2001.604 (MV, DRV, DR, 14.III.2001, Cuvette Boby, Andringitra).

In contrast to most other Malagasy *Phelsuma* which are mostly arboreal, *P. barbouri* is strictly a rock-dwelling species. During the day, the species is active on the exposed rocks of the Ankaratra mountains above the treeline; during rainy weather, it hides under stones.

Pasteur (1959) reported on the discovery of eggs of this species in September. On 12.II and 3.III.2000 we found eggs (egg pairs, i.e. two eggs attached to each other) glued onto the underside of stones and in rock crevices, along the Tsiafajavona road. Four measured eggs had sizes of 13 × 11 mm, 12 × 11 m, 10 × 10 mm and 12 × 10 mm, in close agreement with the data of Pasteur (1959) on two eggs; the weight of one egg pair was 1.4 g. At one site, a communal nest of a total of about 10 eggs in different developmental stages (partly hatched) was found. We also found a large communal egg deposition site of the species at the "Cuvette Boby" in the Andringitra Massif, under a flat stone lying on granitic rock surface on 14.III.2001. Winter breeding is demonstrated by a single preserved specimen, a juvenile (MNHN 1984.427) which according to the catalogue was obtained from an egg collected in September 1959. Furthermore, Pasteur (1959) reported on evidence for winter breeding: one clutch found in June 1946, and several eggs found in September 1959. Snout-vent length in the available MNHN sample (pooled for all localities) was 42.1-59.3 mm (54.4 ± 4.2 mm, n = 19) for males and 48.2-57.5 mm (52.8 ± 2.7 mm, n = 13). Although the largest recorded specimens are females (see also Pasteur 1959: 151), males of this species appear to grow larger on average, as in most *Phelsuma* (Glaw & Vences, 1994).

Although we found *P. barbouri* in Ankaratra only above the treeline (above 2200 m elevation), and it seems to be absent from Manjakatompo, the species also occurs in suitable habitats at lower elevations. The type locality (forest between Toamasina and Antananarivo) has not been confirmed so far, but the types and all specimens examined (see list above) clearly correspond to *P. barbouri* and not to the closely related *P. pronki* (pers. obs.) based on their spiny supraocular scales and slightly overlapping ventral scales (Seipp, 1994). Berghof (2000) found the species on a rocky crest on the National Road 7, about midway between Antananarivo and Ambatolampy (35 km south of Anatananarivo), at ca. 1700-1800 m elevation. Glaw & Vences (1994) and Raxworthy & Nussbaum (1996a) had already reported the occurrence of the species on the Andringitra Massif.

Family Scincidae

Amphiglossus macrocercus (Günther, 1882)

MRSN R1775-1781 (FA, JER, SDM, 11.I.1999, Manjakatompo); MNHN 1933.74 (Manjakatompo); MNHN 1948.24, 24A, 25, 25A (Tsiafajavona); MNHN 1956.52, 54, 56 (Manjakatompo); MNHN 1965.295 (Manjakatompo); MNHN 1974.1026-1029 (Manjakatompo); MNHN 1980.1194 (Tsiafajavona, 2400 m); MNHN 1984.174 (Ambatolampy); MNHN 1984.175 (Tsiafajavona 2300-2500 m); UADBA 2001.431 (MV, DRV, 8.III.2001, Tsiafajavona Plateau); ZSM 382/2000-383/2000 and UADBA 2000.82 - 2000.84 (FG, MV, 12.II.2000, Tsiafajavona road); ZSM 381/2000 and UADBA 2000.475 (MV, NR, 2.III.2000, Manjakatompo).

These medium-sized *Amphiglossus* specimens from Ankaratra were previously assigned to *Amphiglossus melanurus* (e.g., Brygoo, 1984; Glaw & Vences, 1994), but according to Andreone & Greer (in press), they are to be assigned to the species *A. macrocercus*. Clearly the *A. melanurus* complex, which includes *A. melanurus*, *A. macrocercus*, *A. gastrosticutus* and *A. poecilopus* according to Brygoo (1984), is in need of revision. By superficial examination the Ankaratra specimens appear to be conspecific or at least closely related to specimens collected at Andringitra (pers. obs.), higher elevations of Andohahela (MNHN 1980.1170-1175), Antananarivo (MNHN 1980.1191-1193, 1982.1259), the "Col des Tapias" (close to Mt Ibity; MNHN 1980.1178) and other localities.

Amphiglossus macrocercus is probably the most common lizard in the Ankaratra region. It is regularly found during the day hidden under stones and logs, both in the forested areas and above the treeline, up to the Tsiafajavona Plateau.

In the genus *Amphiglossus*, one species has so far been demonstrated to be live-bearing (*A. punctatus*) while others are oviparous (*A. igneocaudatus*, *A. mouroundavae*, *A. melanopleura*) (Blanc & Blanc, 1967b; Raxworthy & Nussbaum, 1993; Glaw & Vences, 1996). Almost nothing is known on the reproduction of *A. macrocercus*, except the mention of Pasteur (1959) who found three very large oocytes in one specimen from Ankaratra. We observed, in the dissected specimen MRSN-FAZC 7959 (a female of 92.3 mm SVL) five rather well-developed juveniles which, however, were not yet ready to hatch as indicated by the broad and large head, still not fully transformed from the embryonal stage. One of these juveniles had a SVL of 24 mm and a tail length of 27 mm. Taking into account that no *Amphiglossus* eggs have so far been found at Manjakatompo despite the high population densities observed, we assume that *A. macrocercus* is obligatorily live bearing at least in the Ankaratra region.

Mabuya boettgeri (Boulenger, 1887)

MRSN R1782-1784 (FA, JER, SDM, 9.I.1999, Manjakatompo); MRSN R1883-1884 (JER, 3-10.X.1998, Ankaratra); MNHN 1993.73 (M.G. Petit, Manjakatompo); MNHN 1965.296-297, (Manjakatompo); MNHN 1980.1202 (22.IV.1962, Manjakatompo, "dans un petit etang"); MNHN 1990.368-369 (1 and 7.III.1960, Ambatolampy); UADBA 2001.433 (MV, DRV, 9.III.2001, Nosiarivo); UADBA 2000.424 (MV, NR, 2.III.2000, Manjakatompo); ZSM 362/2000 and UADBA 2000.116-117 (FG, MV, 11.II.2000, Ambatolampy); ZFMK 46777 (R. Seipp, IV.1987, Ankaratra); ZFMK 62332 (FG, MV, 8-10.I.1994, Ankaratra); ZSM 513/2001 (MV, DRV, 9.III.2001, Ambohimirandrana).

Further material: MNHN 1906.168 (Betafo); MNHN 1933.225 (R. Canala, Sahambavy brook, east of Fianarantsoa); MNHN 1936.14 (R. Heim, no locality); MNHN 1950.328 (J. Millot, Andringitra Plateau); MNHN 1983.871 (2.VI.1961, Ampasampito, Antananarivo); ZFMK 61541 (J. Krüger, 19.IX.1994, 30 km E Ambositra); ZFMK 62328 (FG, Andringitra); ZSM 581/2001 (MV, DRV, DR, 13.III.2001, Andohariana Plateau, Andringitra); ZSM 511/2001-512/2001 and UADBA 2001.605-607 (MV, DRV, DR, 13.III.2001, Gîte Soaitambara, Andringitra).

This diurnal lizard is known from a number of localities in the central highlands of Madagascar (Brygoo, 1983). At Ambatolampy and Manjakatompo, we found the species at rather humid spots, generally in grassland around swamps and flooded areas. We did not observe specimens above the treeline at Ankaratra. The female MRSN-FAZC 7957 (49.0 mm SVL) contained three apparently almost mature oocytes, which measured 11.2 × 5.1 mm, 10.8 × 5.8 mm, and 10.0 × 5.9 mm, respectively. In the sample examined, the dorsolateral light lines appeared to be more intensively whitish in specimens from Andringitra, but more data are necessary for statements on variation among populations of *M. boettgeri*.

Mabuya madagascariensis (Mocquard, 1908)

MRSN R1785 (FA, SDM, JER, 9.I.1999, Manjakatompo); MRSN R1885-1886 (JER, 3-10.X.1998, Ankaratra); MNHN 1965.300 (J. Millot, IX.1953, Ambatolampy road); MNHN 1984.176-1984.179 (J. Millot, 8-9.IX.1959, Tsiafajavona); MRSN uncatalogued (JER, X.1998, Analamilona); ZFMK 46776 (R. Seipp, IV.1987, Ankaratra); ZFMK 50564-50565 (F. W. Henkel, W. Schmidt, V. Müller, V.1989, Ankaratra); ZFMK 62331 (FG, MV, 8-10.I.1994, Ankaratra).

Further material: MNHN 1907.85 (lectotype) and 1907.86 (paralectotype) (no precise locality).

Like *M. boettgeri*, this species has been recorded from a number of localities in the central highlands (Brygoo, 1985). At Ankaratra, we found only one specimen (ZFMK 62331), just above the treeline close to the Tsiafajavona road in 1994. The specimen deposited five eggs (16-19 × 12-14 mm) which hatched at the beginning of March (Glaw & Vences, 1994).

Besides the larger body size and different subocular shape, *M. madagascariensis* can be distinguished from *M. boettgeri* by coloration: The most conspicuous dorsal pattern of *M. madagascariensis* are two light dorsolateral and one vertebral stripes, while the pattern of *M. boettgeri* is mainly marked by dark stripes.

Zonosaurus ornatus (Gray, 1831)

ZSM 379/2000 (MV, NR, 3.III.2000, close to Nosiarivo).

Zonosaurus ornatus has often been found in savannah habitat (Andringitra, Isalo: Glaw & Vences, 1994) and is known from a number of localities in the Central highlands of Madagascar (Brygoo, 1985). At Ankaratra, we captured one specimen (ZSM 379/2000) at the edge of a recently cleared pine plantation, and on 13.II.2000 we observed several specimens in highly degraded remains of natural forest near the "Rova" palace of Tsinjoarivo.

Family Colubridae

Geodipsas infralineata (Günther, 1882)

MNHN 1957.731 (Manjakatompo); ZSM 378/2000 (FG, MV, 11.II.2000, Manjakatompo); UADBA 2000.419 (MV, NR, 2.III.2000, Manjakatompo); MRSN-FAZC 7971, 7973 (FA, JER, SDM, 10.I.1999, Manjakatompo).

This mainly nocturnal snake appears to be rather common at Manjakatompo. In 1994, we observed several juvenile specimens at night, active on the ground. On 11.II.2000, we found one specimen active at night on a road during heavy rain, and on 2.III.2000 we found a second specimen during the day hidden under a stone. The specimens collected by us clearly belong to *G. infralineata*, and not to the recently described (Cadle, 1996b) *G. laphystia* (scale counts of ZSM 378/2000: 19

dorsal, 180 ventral scales). MNHN 1957.731 is a damaged juvenile specimen, and counts of ventral scales are therefore not possible; nevertheless it seems to fit well with ZSM and UADBA specimens.

Liopholidophis lateralis (Duméril, Bibron & Duméril, 1854)

MRSN-FAZC 7972 (FA, JER, SDM, 10.I.1999, Manjakatompo); MNHN 1989.2851 (R. Vionnet, 12 June 1962, Ambatolampy).

This diurnal snake species has previously been observed around the ponds of the piscicultural station of Manjakatompo by Glaw & Vences (1994), but no voucher specimens have so far been available. It occurs syntopically with *L. sexlineatus* in a swamp area near Ambatolampy. *L. lateralis* is oviparous; a road-killed specimen from Andasibe (ZSM 578/2001) contained eight eggs.

Liopholidophis sexlineatus (Günther, 1882)

MNHN 1965.259 (December 1950, Manjakatompo); ZFMK 62334 (FG, MV, 8-10.I.1994, Ankaratra).

Further material: ZSM 576/2001 and UADBA 2001.596 (MV, DRV, DR, 13-14.III.2001, Andohariana Plateau, Andringitra).

This colubrid is clearly a more aquatic species than *L. lateralis*. At Ambatolampy we observed several specimens in and close to water in a larger swamp area. MNHN 1965.259 (catalogued as *L. pinguis*) is a male with everted hemipenes, and its coloration and scale counts agree with *L. sexlineatus* (see Cadle, 1996a): 17 dorsal, 154 ventral, 135 subcaudal scales; anal and all subcaudal scales divided. The two specimens from the Andohariana Plateau (Andringitra), collected at ca. 2110 m, so far represent the highest elevational record of any colubrid snake in Madagascar. Glaw & Vences (1994) discussed the possibility of a viviparous reproductive mode in *L. sexlineatus*, upon personal communication of C. A. Domergue. Then Cadle (1996a) quoted the occurrence in five analysed females from Ranomafana National Park (Fianarantsoa Province) of a variable number of embryos (4-10), surrounded by fetal membranes, but without thickened shells. This observation, although preliminary and in need of confirmation upon other specimens, would support the viviparity in this species.

DISCUSSION

Biogeography

Guibé (1952) was the first to give a list of the amphibians known from the Manjakatompo Forest station, reporting 10 species: *Ptychadena mascareniensis* (as *Rana mascareniensis*), *Mantidactylus curtus*, *M. ulcerosus*, *M. brevipalmatus*, *Boophis goudoti* (as *Rhacophorus Goudoti*), *B. ankaratra* (probably; as *Rhacophorus luteus longicrus*), *Heterixalus betsileo* (probably; as *Megalixalus tricolor*), *H. rutenbergi* (as *Hyperolius Rutenbergi*), *Scaphiophryne madagascariensis* (as *Pseudohemisus pustulosus*), and *Plethodontohyla tuberata*. While the record of *Mantidactylus ulcerosus* is almost certainly based on a confusion with *M. curtus*, the other species were recorded by us as well. Pasteur (1959, 1962) provided information on the Ankaratra lizards, but only reported on four species occurring in the montane areas close to the Tsiafajavona (*Mabuya madagascariensis*, *Amphiglossus macrocercus*, *Phelsuma barbouri*, and *Lygodactylus mirabilis*). Two additional dubious amphibian records may be mentioned here: *Laliostoma labrosum* was reported by Angel (1934) but was based on a poorly preserved voucher according to him; since this species occurs mainly in the dry areas of Madagascar, the record was probably based on a misidentification. *Mantidactylus blanci* is based on the specimen MNHN 1975.780 from "Nosiarivo" according to the MNHN catalogue, which is most probably a mislabelling.

According to the present knowledge, a total of 14 species of amphibians and 10 species of reptiles are known from the Ankaratra Massif (Table II). Considering the fact that the central mountain chain of Madagascar largely acts as a division between the humid eastern rainforests and the dry western regions, the herpetofauna of Ankaratra could be expected to be a mixture of eastern and western elements. In what follows we will review the affinities of the Ankaratra herpetofauna based on current knowledge.

(A) Species with eastern affinities. Among amphibians, *Boophis ankaratra* belongs to the *B. luteus* group. Species of this group occur along rainforest brooks and are present only in a few humid enclaves of the west such as Isalo and Sahamalaza (Andreone *et al.*, 2001). *Boophis williamsi* and *B. microtympanum* are likely related to the *B. goudoti* group which is largely restricted to eastern Madagascar (Glaw & Vences, 1994). *Mantidactylus pauliani* is the sister species of *M. madecassus*, and is probably also related to *M. curtus* because of similarities in its femoral gland morphology (Vences & Glaw, 1999); *M. curtus* itself is restricted to humid high- and mid-elevation rainforests and montane areas, since the records from the west (as given by Blommers-Schlösser & Blanc, 1991) refer to other species of the subgenus *Brygoomantis* (pers. obs.). *M. brevipalmatus* belongs to a group (subgenus *Chonomantis*) absent from large parts of western Madagascar (Vences & Glaw, in press). *Plethodontohyla tuberata*, like almost all the cophylines, is restricted to humid zones. Among the reptiles, *Calumma hilleniusi* belongs to a group (*C. brevicornis* group) restricted to rainforests and montane areas (Brygoo, 1971). The same is true for the snake genera *Geodipsas* and *Liopholidophis* (Cadle, 1996a, b). Most localities of the *Amphiglossus melanurus* complex are located in the east (Brygoo, 1984).

(B) Species with western affinities. Among amphibians, *Scaphiophryne madagascariensis* is probably related to species occurring in the Central East such as *Scaphiophryne* sp. from Andringitra (Vences & Glaw, 1999), but the genus *Scaphiophryne* has several representatives in the west, and furthermore displays a breeding behaviour (explosive reproduction, small pigmented and fast-developing eggs deposited in lotic waterbodies) typical for dry areas (see Vences

TABLE II - *Amphibians and reptiles of the Ankaratra massif, their occurrence in the submontane (1500-2000 m) and montane areas (2000-2640 m), and natural history.*

Species	Submontane	Montane	Activity	Call	Reproduction
AMPHIBIA					
Mantellidae					
Boophis ankaratra	BF	-	N	N	tadpoles in brooks
Boophis goudoti	BF, P, PF	B	N	N	tadpoles in brooks and ponds
Boophis microtympanum	-	B	D/N	N	tadpoles in brooks
Boophis williamsi	-	B	N	?	tadpoles in fast-flowing brooks
Mantidactylus domerguei	P, PF	-	D/N	(D)/N	tadpoles in ponds
Mantidactylus kely	P, PF, M	-	D/N	D/(N)	tadpoles in ponds
Mantidactylus alutus	P, M	-	D/N	D/N	tadpoles in ponds and slow-moving brooks
Mantidactylus curtus	B, BF	-	D/N	?	tadpoles in brooks
Mantidactylus pauliani	-	B	D/N	?	unknown
Mantidactylus brevipalmatus	BF	B	D/N	D/N	funnel-mouth-tadpoles in brooks
Ranidae					
Ptychadena mascareniensis	P, PF, M	-	D/N	D/N	tadpoles in ponds
Microhylidae					
Plethodontohyla tuberata	F	H	D/N	D?	non-feeding tadpoles in jelly nests
Scaphiophryne madagascariensis	F, PF	-	N	N	filter-feeding tadpoles in ponds
Hyperoliidae					
Heterixalus betsileo	P, PF, M	-	N	N	tadpoles in ponds
Heterixalus rutenbergi	M	-	N	N	tadpoles in ponds
SQUAMATA					
Chamaeleonidae					
Calumma hilleniusi	F	F	D	-	oviparous - eggs burrowed into the ground
Furcifer campani	-	H	D	-	oviparous
Furcifer lateralis	D	-	D	-	oviparous
Gekkonidae					
Phelsuma barbouri	-	H	D	-	oviparous - egg pairs attached in crevices and under stones
Lygodactylus mirabilis	-	H	D	-	oviparous - egg pairs burrowed under stones
Scincidae					
Amphiglossus macrocercus	F	H	D	-	viviparous
Mabuya boettgeri	D, M	-	D	-	probably oviparous
Mabuya madagascariensis	-	H	D	-	oviparous
Gerrhosauridae					
Zonosaurus ornatus	D, F	-	D	-	probably oviparous
Colubridae					
Geodipsas infralineata	F	-	N	-	Unknown
Liopholidophis lateralis	P, M	-	D	-	oviparous
Liopholidophis sexlineatus	P, M	-	D	-	viviparous

B, brooks outside of forest; BF, brooks in forest; D, degraded/deforested areas below 2000 m; F, forest independent from brooks; H, montane heathland and savannah, independent from brooks; M, moorland out of the forest; P, ponds and swamps outside of the forest; PF, ponds and swamps in forest. Habitat information refers only to our observations at Ankaratra; in some cases, the respective species may have been found in other habitat types at other sites. Data on calling (mating calls – only in frogs) and general activity are categorized as diurnal (D) or nocturnal (N) – parentheses refer to less regular activity.

et al., 2000b). *Lygodactylus mirabilis* displays a mental scale arrangement typical for the occidental lineage of *Lygodactylus* of Pasteur (1965). By the shape of its subocular scale, *Mabuya boettgeri* belongs to the *M. aureopunctata* group which largely occurs in western Madagascar (Brygoo, 1983).

No reliable statement can be made on the remaining Ankaratra amphibians and reptiles, as their phylogeny is so far unresolved. Considering the species discussed above, 12 show more or less distinctly biogeographic affinities to the east, while only three show affinities to the west. However, it should be taken in mind that the surveys so far carried out were centred on the eastern slope of Ankaratra (Manjakatompo) and the summit. Some further species may be recorded in the area when the western Ankaratra slopes are surveyed more intensively; here, in possibly more xeric situations, species adapted to the arid conditions of western Madagascar may reach relatively high elevations, as is the case on Mount Ibity (ca. 45 km south of Ankaratra), where reptiles such as *Paroedura bastardi*, *Oplurus quadrimaculatus* and *Mabuya vato* occur at elevations near 2000 m (pers. obs.) and probably also higher. Nevertheless, the general picture of a montane species community largely influenced by eastern groups is unlikely to change for Ankaratra. A similar situation can be predicted for the Andringitra Massif, where the rather intensive surveys so far carried out (see Glaw & Vences, 1994; Raxworthy & Nussbaum, 1996a) identified no endemic montane taxa with clear western affinities, perhaps except for *Lygodactylus intermedius* and *L. montanus*.

The Ankaratra and Andringitra Massifs have a high proportion of amphibian and reptile species in common (*Boophis ankaratra*, *B. microtympanum*, *Mantidactylus curtus*, *M. brevipalmatus*, *M. domerguei*, *Phelsuma barbouri*, *Amphiglossus macrocercus*, *Furcifer campani*, *Calumma brilleniusi*), some pairs of possible allopatric sister taxa (*Mantidactylus pauliani* - *M. madecassus*, *Scaphiophryne madagascariensis* - *Scaphiophryne* sp., and *Lygodactylus mirabilis* - *L. intermedius*), and a few species on one of the massifs without close relationships to a taxon on the other massif (Andringitra: *Mantidactylus elegans*, *Anodonthyla montana*; Ankaratra: *Plethodontohyla tuberata*, *Boophis williamsi*) (Raxworthy & Nussbaum, 1996a, b; Vences & Glaw, 1999). These different patterns are probably related to past climatic changes which led to an oscillation of the extension of montane habitats; vicariance caused by fragmentation of a previously continuous montane savannah and heathland area in central Madagascar (Battistini, 1996; Burney, 1996) may account for the presence of sister species on both massifs. In this context, the populations of species occurring on both massifs would have been less strictly or more recently isolated. The discovery of *Boophis ankaratra* – previously only known from Ankaratra and Andringitra – at further localities, as well as the confirmation of the occurrence of *B. microtympanum* and *Mantidactylus curtus* at a locality – the "Col des Tapias" – geographically intermediate between the two massifs confirms this scenario. Apparently, these species do depend less strictly on high elevation conditions and are distributed more or less continuously in suited areas between Ankaratra and Andringitra.

Community analysis

In Table III, the relative species richness of different amphibian and reptile groups at Ankaratra is compared to their importance in the total herpetofauna of Madagascar. The percentage of species of most groups at Ankaratra corresponds roughly to their overall proportion but some deviations are apparent. Two of the most speciose amphibian groups, *Boophis* and *Mantidactylus* are over-represented at Ankaratra, while the third large group, cophyline microhylids, is under-represented with a single species. Among reptiles, most speciose groups are under-represented at Ankaratra: chameleons, skinks other than *Mabuya*, gekkonids, and colubrids. Considering the montane fauna only (species occurring regularly above 2000 m elevation), the over-representation of mantellines and *Boophis* among amphibians becomes still more distinct, while the cophyline percentage is similar to the overall value. Of the large reptile groups, the percentages of skinks and geckos approach the overall values, while colubrids are lacking in montane areas of Ankaratra. Altogether, the proportion of amphibians to reptiles (index of number of amphibian/reptile species = 1.4) corresponds to that of eastern rainforest areas (e.g., Andreone & Randrianirina, 2000 and Andreone *et al.*, 2000: 0.9-1.8 in forests of north-eastern Madagascar; Raselimanana, 1998: 1.0 at Anjozorobe in central-eastern Madagascar) rather to that of western sites with generally their much higher reptile proportion (e.g., 0.2 at Isoky-Vohimena and Zombitse; Raxworthy *et al.*, 1994; Goodman *et al.*, 1997).

One important aspect in the Ankaratra community is the apparent lack of nocturnal gekkonids. The Gekkonidae family is only represented by the diurnal genera *Phelsuma* and *Lygodactylus*, but the nocturnal *Uroplatus* and *Paroedura*, present at mid-elevation localities (such as Andasibe), are absent (like other nocturnal genera such as *Hemidactylus*, common on houses and walls of Antananarivo, and *Geckolepis*, present at lower altitudes). Furthermore, the two Ankaratra gekkonids are restricted to sun exposed areas above the treeline; there are no gekkonids at all in the forest. The same regards the forest-dwelling dwarf chameleons, genus *Brookesia* (Brygoo, 1978). Even Ambatolampy apparently does not harbour any species of gekkonid; the geographically closest gecko population that we observed were *Phelsuma* specimens on the Rova palace of Tsinjoarivo (*P.* cf. *quadricocellata*: ZSM 390/2000). On the Andringitra Massif, the situation appears similar, with no forest-dwelling *Phelsuma* recorded at high elevations (Raxworthy & Nussbaum, 1996b). On the Tsaratanana Massif, *P. lineata punctulata* occurs above 2700 m and has rupicolous habits (Raxworthy & Nussbaum, 1996a). We suppose that this lack of nocturnal and arboreal lizards is caused by the low temperatures which are common at Ankaratra during the night, in combination with the high humidity. At drier sites, such as Mt. Ibity, at least one nocturnal gekkonid (*Paroedura bastardi ibityensis*) is present around 2000 m altitude. This indicates that the lack of such species at Ankaratra is not only caused by a general altitudinal limit, but is also influenced by other factors. We suppose that at Ibity the rocks, heated by the sun during the day, act as a thermal buffer in the evening and night, allowing nocturnal reptiles to be active. This is probably less so at Ankaratra where during the (warm) rainy season clouds, mist, and rain are common and thus the (few) rocks are not heated, which 'forces' lizards to be active during the day.

TABLE III. *Species numbers and relative diversity of different amphibian and reptile groups at Ankaratra, and on montane sites of Ankaratra (2000-2642 m) only, compared to the overall values for Madagascar.*

	Ankaratra	Ankaratra montane	Madagascar
Amphibians			
Microhylidae: Dyscophinae	0 (0%)	0 (0%)	3 (1%)
Microhylidae: Scaphiophryninae	1 (4%)	0 (0%)	7 (1%)
Microhylidae: Cophylinae	1 (4%)	1 (8%)	36 (7%)
Ranidae: Raninae	1 (4%)	0 (0%)	2 (1%)
Mantellidae: *Mantidactylus*	6 (22%)	3 (25%)	67 (13%)
Mantellidae: *Mantella*	0 (0%)	0 (0%)	17 (3%)
Mantellidae: *Boophis*	4 (15%)	2 (17%)	46 (9%)
Mantellidae: Laliostominae	0 (0%)	0 (0%)	4 (1%)
Hyperoliidae	2 (7%)	0 (0%)	10 (2%)
Reptiles			
Opluridae	0 (0%)	0 (0%)	7 (1%)
Chamaeleonidae	3 (11%)	1 (8%)	68 (13%)
Gerrhosauridae	1 (4%)	1 (8%)	18 (3%)
Scincidae: *Mabuya*	2 (7%)	1 (8%)	14 (3%)
Scincidae: remaining genera	1 (4%)	1 (8%)	46 (9%)
Gekkonidae	2 (7%)	2 (17%)	88 (17%)
Colubridae	3 (11%)	0 (0%)	74 (14%)
Boidae	0 (0%)	0 (0%)	3 (1%)
Typhlopidae	0 (0%)	0 (0%)	10 (2%)
Chelonia and Crocodylia	0 (0%)	0 (0%)	10 (2%)
Total	27 (100%)	12 (100%)	530 (100%)

Snakes are also rare in Ankaratra. Although colubrids are generally relatively speciose in Madagascan herpetofaunas, no endemic montane snakes were listed by Raxworthy & Nussbaum (1996b). This is surprising, as potential preys (lizards, frogs) are common at high elevations in Madagascar. The highest elevational colubrid records in Madagascar regard *Liopholidophis sexlineatus* at 2110 m on the Andringitra Massif (see the section regarding that species), a *Geodipsas* species at 2050 m on the Tsaratanana Massif (Raxworthy & Nussbaum, 1996a), and *Pseudoxyrhopus imerinae* at 2200 m altitude at Mount Ibity and Ananokely, Ankaratra (Raxworthy & Nussbaum, 1994). *Liopholidophis sexlineatus* is a semi-aquatic species that probably mostly feeds on frogs, and is live-bearing (C. A. Domergue, pers. comm.). No data are available on the *Geodipsas* species from Tsaratanana, but it is possible that evolutionary constraints related to reproduction inhibited many lizard-eating Malagasy colubrids from populating high mountain areas. The *Pseudoxyrhopus* record at Ankaratra was not considered herein because we did not examine the voucher specimens and because the species was not recorded any more by the same authors in their comprehensive treatments of montane herpetofaunas (Raxworthy & Nussbaum, 1996b).

On the other hand, a number of amphibian and reptile species can be considered as adapted and, at least partly, endemic to montane habitats in Madagascar. At Ankaratra, this regards the frogs *Boophis microtympanum*, *B. williamsi*, *Mantidactylus pauliani*, and to a lesser degree *M. brevipalmatus*, *Scaphiophryne madagascariensis* and *Plethodontohyla tuberata*; among the reptiles, it regards the two geckos (*Lygodactylus mirabilis*, *Phelsuma barbouri*), *Mabuya madagascariensis*, and, to a lesser degree, *Furcifer campani*, *Mabuya boettgeri*, *Amphiglossus macrocercus* and *Calumma brilleniusi*. Reproductive biology of most of these species largely resembles that of their low-elevation relatives. Live-bearing, which is generally common in high-elevation reptiles, is found in *A. macrocercus* and *Liopholidophis sex-*

lineatus. However, these two species are also common at lower elevations, and at least in *Amphiglossus* one further species is live-bearing. Their reproductive mode is more likely to be explained as pre-adaptation than as specialization to high-elevation habitat. The tadpoles of *Boophis microtympanum* and *B. williamsi* grow to large size before metamorphosis and partly complete it only in their second year, as often observed in tadpoles growing in cold running water (Ultsch *et al.*, 1999).

Altogether, the main conclusion of Raxworthy & Nussbaum (1996b) is corroborated by our data (see also Vences & Glaw, 1999): high-elevation habitats in Madagascar (generally montane heathlands above the treeline) are not populated by a depauperate herpetofauna but harbour a relatively large number of species, several of which are endemic to this type of habitat. This is especially obvious in comparison to the Ankaratra rainforest, which appears to contain very few reptile species and no endemic herpetofaunal elements.

Phenology

As summarized by Glaw & Vences (1996), Malagasy reptiles generally reproduce during the (warm) rainy season (November to April), a trend which is typical for tropical reptiles (Fitch, 1982). The same is also true in amphibians which mostly depend on humidity for embryonal and larval development; most observations on calling and reproducing Malagasy amphibians (see Glaw & Vences, 1994) refer to the rainy season. A conspicuous exception from this general rule are the observations of Pasteur (1959, 1962) of eggs of *Pheisuma barbouri* and *Lygodactylus mirabilis* in September-October in the high-elevation regions of Ankaratra. Compared to those of Glaw & Vences (1996), the data summarized here provide new reproductional data for the reptiles *Furcifer campani, Calumma billenitusi, Amphiglossus macrocercus, Mabuya boettgeri, P. barbouri*, and *L. mirabilis*. Altogether, the data demonstrate reproduction in the rainy season in all Ankaratra reptiles except for the snakes (for which no data are available). Summarizing, it can be excluded that *P. barbouri* and *L. mirabilis* are specialized to breed during the dry season, although these and possibly other Ankaratra reptiles maintain (at least some) reproductive activity during this period.

Conservation

Herpetofaunal conservation recommendations in Madagascar are generally focused on areas of eastern rainforest or western dry deciduous forest (Ganzhorn *et al.*, 1997), and on species that are threatened either by commercial collection for the pet trade or by hunting for local consumption (e.g., Raxworthy & Nussbaum, 2000). Only few other taxa, such as *Liophidium apperti* and *Pseudoxyrhopus ankafinaensis*, have been mentioned as endangered or even potentially extinct species (Raxworthy & Nussbaum, 2000). Although the importance of montane herpetofaunal diversity has been repeatedly stressed (Raxworthy & Nussbaum, 1996a, b; Vences & Glaw, 1999), they have not generally been considered to merit special attention for conservation purposes. Most of the relevant massifs (Ambre, Tsaratanana, Marojejy, Andringitra, Ivohibe, Anosy) are included in Madagascar's network of protected areas, but Ankaratra is an outstanding exception to this rule.

Of the 27 species here considered to form part of the Ankaratra herpetofauna, four are so far only known from the area: *Boophis williamsi, Mantidactylus pauliani, M. kely, Lygodactylus mirabilis*. While the minute *M. kely* may in the future be found also in other highland localities, the remaining three species are likely to be Ankaratra endemics because of their habitat specialization. The rather high proportion of endemics (11-15%) may even increase in the future, as our preliminary, unpublished observations indicate a possible cryptic differentiation within species such as *B. microtympanum, M. curtus* and *M. brevipalmatus* over their distribution range.

The high intensity of herpetological survey work in Madagascar's remains of primary habitat resulted in the discovery that many species believed to be local endemics are actually also present elsewhere (Raxworthy & Nussbaum, 2000), probably occupying rather wide distribution areas in scattered populations. However, this does not hold true for montane species. Considering their habitat specializiation, several taxa (*B. williamsi, M. pauliani, L. mirabilis* in Ankaratra; *Anodonthyla montana, M. madecassus* in Andringitra) may have distribution areas which rank among the most restricted of Malagasy amphibians and reptiles. Several of the global decline phenomena in Amphibia have been recorded in montane species, e. g. in North America (Blaustein & Wake, 1995) or the Andes (La Marca & Lötters, 1997). These high-elevation specialists may suffer from increased ultraviolet radiation due to a decreasing ozone layer (Blaustein & Wake, 1995). Taking these indications into account, we consider a more thorough monitoring of Madagascar's montane faunas as urgent, especially in non-protected areas such as Ankaratra, Ibity and Itremo.

The montane amphibians and reptiles of Ankaratra have so far been able to survive substantial human habitat alterations (deforestation, regular fires, cattle grazing). No indications of imminent changes of land-use or agricultural practice in their habitats are available. However, as the high-elevation areas of the massif are not included in a protected area, any such change appears conceivable and may pass unnoticed by conservation authorities. We believe that potential innovations such as use of pesticides, aquaculture (trouts already have been released from the Manjakatompo station; Arnoult, 1959), or increased cattle density would result in serious threats of the endemics if implemented at Ankaratra. We therefore recommend to set up a monitoring program that includes assessment of actual distribution, population densities, and natural history of the species concerned.

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