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The peculiar herpetofauna of some Tsaratanana rainforests and its affinities with Manongarivo and other massifs and forests of northern Madagascar

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Abstract

Amphibians and reptiles were surveyed at several rainforest sites on the Tsaratanana Massif and in the nearby Manongarivo Massif, NW Madagascar. Visual methods and pitfalls led to the discovery of 30 amphibian and 23 reptile species at Tsaratanana, and 30 amphibian and 17 reptile species at Manongarivo. The herpetofauna present at the investigated sites turned out to be composed (1) of typical elements of Madagascar's eastern rainforests, (2) of species widely distributed at low altitudes of the northwest, (3) of species typical for rainforests of the northeast and north (Montagne d'Ambre), and (4) of a rather large proportion of possible endemics. Beside many still undescribed species, we found some species of considerable biogeographic interest, such as the snake *Pseudoxyrhopus ambreensis* and the treefrog *Boophis blommersae* at Tsaratanana, previously known only from Montagne d'Ambre, which emphasizes a biogeographical link to this northernmost massif. At Manongarivo we also found one still unidentified species of leaf-axil dwelling mantellid frog of the subgenus *Pandamusicola*, representing the first record of this subgenus from northwestern rainforests. Comparisons of mitochondrial DNA sequences of some selected amphibian species indicate that the populations from Tsaratanana and Manongarivo show no or only a slight differentiation between the two massifs but are often strongly different from conspecific populations, or from their closest relatives, in other regions of Madagascar. Conservation at Tsaratanana should, as a priority, include an increase of field surveys and an integration of local people in the management planning of this huge massif.

Keywords: *Amphibians, biodiversity, biogeography, Madagascar, Manongarivo, reptiles, Tsaratanana*

Introduction

Slash-and-burn practices of deforestation and other anthropogenic activities destroyed or fragmented much of the primary rainforests of Madagascar since the arrival of humans, about 2000 years ago, a process much accelerated in the past decades. In many areas, only small fragments of forest remain (Vallan 2000), often only in the form of small gallery forests along streams (Andreone & Randrianirina 2000). In such a context, the montane massifs of Madagascar are crucial biodiversity areas for many groups of organisms, with the major blocks of

remaining rainforest being located in the inaccessible areas of several of the mountain chains (Raxworthy & Nussbaum 1994, 1996a). This is especially true for amphibians and reptiles, i.e. vertebrates that in the last years were subjected to increased attention and studies. In fact, recent surveys carried out by various teams across Madagascar led to an increase in the number of known species due to a fast rate of taxonomic discovery and description (Köhler et al. 2005).

Most of the field studies in some massifs clearly showed that amphibians and reptiles are also extremely sensitive to local ecological conditions,

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and even a narrow shift in altitude, trade wind exposure or mean temperature may be accompanied by a rapid turnover in species composition of herpetofaunal communities. Being non-flying vertebrates, with supposedly limited dispersal capacities, and sensitive to ecological change, amphibians and reptiles are also key organisms for biogeographical analyses, and precious indicators of conservation priorities (Raxworthy & Nussbaum 1997).

In the last decade we oriented our efforts at contributing to Madagascar's herpetological species diversity by conducting numerous surveys which allowed us to outline general biogeographical patterns, and to discover new taxa in most of the visited forests. Thus, it became evident that the identification of general biogeographical patterns is particularly important in northern Madagascar, which turned out to be a centre of biological diversity and endemism due to the presence of many ecosystems, river water basins, massifs and ecological barriers (Andreone & Randrianirina 2000; Andreone et al. 2000; Andreone 2004). After having devoted our efforts to take an inventory of some forests in the easternmost portion (such as Anjanaharibe-Sud, Ambolokopatrika, Tsararano, and Masoala), we studied the species inhabiting the Tsaratanana, a huge massif located in NW Madagascar, this being crucial in dividing the rainforests of the eastern escarpment and the forests of the Sambirano Domain (Raxworthy & Nussbaum 1996a). In addition, we also conducted a rapid survey on the neighbouring massif, Manongarivo. Although the Tsaratanana occupies a large surface area and our survey refers only to a small portion of this massif, we consider it important to summarize the data we collected on the occasion of these recent surveys. In fact, these inventories allowed the finding of many interesting species, many of which, again, still undescribed.

During our analysis of the data and identification of voucher specimens collected at Tsaratanana we noticed unexpected faunal similarities that may contribute significantly to the understanding of the biogeography of amphibians and reptiles in northern Madagascar. For this reason, the present paper reports the data on the herpetofauna of Antsahamanara, a mid-altitude rainforest, and other sites of Tsaratanana, and presents consideration on the affinities of Tsaratanana and Manongarivo with some massifs of northern Madagascar, with a special attention to the herpetofauna inhabiting the isolated rainforest Montagne d'Ambre.

Materials and methods

The Tsaratanana Massif

The Tsaratanana Massif is located in NW Madagascar, between 13°51'S and 14°07'S; and between 48°45'E and 48°59'E (Nicoll & Langrand 1989). Much of the massif is managed as a Strict Nature Reserve (Réserve Naturelle Intégrale, RNI 4), with a surface area of 48,622 ha and an altitude between 227 and 2876 m a.s.l. The reserve is included in the Antsiranana Faritany (Diégo-Suarez Province), Marotolana Fivondronana and Mangindrano Fivondronana. The climate is of the wet hot type at low altitude and is characterized by heavy rainfalls throughout the year and a maximum between the month of November and April, with a quite low year temperature variation. At high altitudes the climate is basically transitional between the western and high-plateau type (Anonymous 1999).

Our research was carried out during two different periods: RJ and GS stayed at a first campsite (here onwards named "Tsaratanana 1997", 14°02.40'S, 48°47.3'E; about 1000 m a.s.l.) from 13 to 23 February 1997, while FA, FM, JER, and MV visited Antsahamanara (14°02.70'S, 48°47.6'E; 1100 m a.s.l.) from 3 to 11 February 2001; this site is also roughly located in the Antsahamanara forest. The vegetation around both sites corresponds to the typically mid-altitude rainforest, which is crossed by several streams and deep valleys. In this site the rainforest nucleus appears apparently quite intact, although the human disturbance is constantly increasing. Complementary data were also collected at Andampy (14°02.53'S, 48°45.70'E, 730 m a.s.l.), a site visited by FA, FM, JER, and MV on 2 February 2001, and by FM and MV on 10 and 11 February 2001. In this rainforest RJ and GS briefly visited (14 and 15 February 1997) an unnamed site (14° 02.59' S, 48° 45.67'E) at an altitude of about 600 m a.s.l., here named "Tsaratanana Camp 1", while during the preliminary survey (13–26 December 2000) JER visited other Tsaratanana sites as follows: (i) Andranohofa (14°07.18'S, 48°44.08'E, 913 m a.s.l.; a herbaceous savannah crossed by a small stream), (ii) Ampiboahan'ala (14°02.45'S, 48°57.14'E, 2360 m a.s.l.; a forest typical of the altitude belt, with lichens and epiphytic plants, and subject to strong trade winds); (iii) Andavaka (14°04.34'S, 48°53.47'E, 1056 m a.s.l.; a heavily disturbed mid-altitude rainforest, with trees 20–25 m tall, epiphytic plants, lichens, arboreal ferns, and *Pandanus* screw pines); (iv) Antsahamaninty (14°03.25'S, 48°55.05'E, 1000 m a.s.l.; an apparently intact forest with a relatively thick litter); (v)

Andranomamelona (14°06.35'S, 48°43.54'E, 851 m a.s.l.; a transitional forest between the low-altitude and mid-altitude rainforest, with cattle use and extended *tavy*, i.e. slash and burn agriculture).

Further observations mentioned throughout the paper refer to some low altitude sites and villages outside of the reserve: Antsirrasira (13°56.37'S, 48°33.27'E, less than 100 m a.s.l.); Marotolana (14°01.41'S, 48°37.01'E, 104 m a.s.l.); and Marovato (13°56.24'S, 48°33.21'E, 75 m a.s.l.). Although the data are cursorial and refer to brief stays in each of these latter sites only, these observations do contribute some relevant distributional information and are therefore presented here, although not commented on in detail.

The Manongarivo Massif and other comparative sites

We compared data from Tsaratanana with other sites to draw biogeographic considerations (Figure 1). New data are reported here for Manongarivo. FG and MV conducted a rapid survey from 30 January to 6 February 2003 on this massif. This survey included three campsites, each of which was surveyed for 1–2 days by visual encounters and bioacoustic surveys (due to time constraints, no pitfall trapping was performed) (1) Camp Norbert (13°56.88'S, 48°27.47'E, 288 m a.s.l.); surrounded

by rather degraded rainforest and plantations, next to a large stream of ca. 6 m width, with numerous rocks and a sandy bottom; (2) Camp 0 (13°58.53'S, 48°25.60'E, 688 m a.s.l.), in primary rainforest, next to two small streams, with abundant understorey vegetation and some *Pandanus* plants; (3) Camp 1 (13°58.62'S, 48°25.32'E, 751 m a.s.l.), corresponding to Camp 1 of Rakotomalala (2002), in a dense primary rainforest and next to a small stream. On the way to Manongarivo, a few records were also obtained from two further localities: Antanambao village (13°53.38'S, 48°29.05', 9 m a.s.l.), and the old Anketrakabe settlement (13°55.17'S, 48°27.72'E, 117 m a.s.l.).

We also checked species records from the literature. Only a few bibliographic reports are available for both Tsaratanana and Manongarivo (e.g. Rakotomalala 2002). Most of the recent publications just derive from our work in the considered sites (e.g. Andreone & Greer 2002; Vences et al. 2004b). We explicitly excluded from this bibliographic list the standardized sheets available on the web under the Global Amphibian Assessment site (IUCN et al. 2006) and IUCN redlist (IUCN 2007), where most of the data and findings were the result of the current work. Except for some remarkable high-altitude endemics and for data obtained by Rakotomalala (2002), most of the species encountered by us are

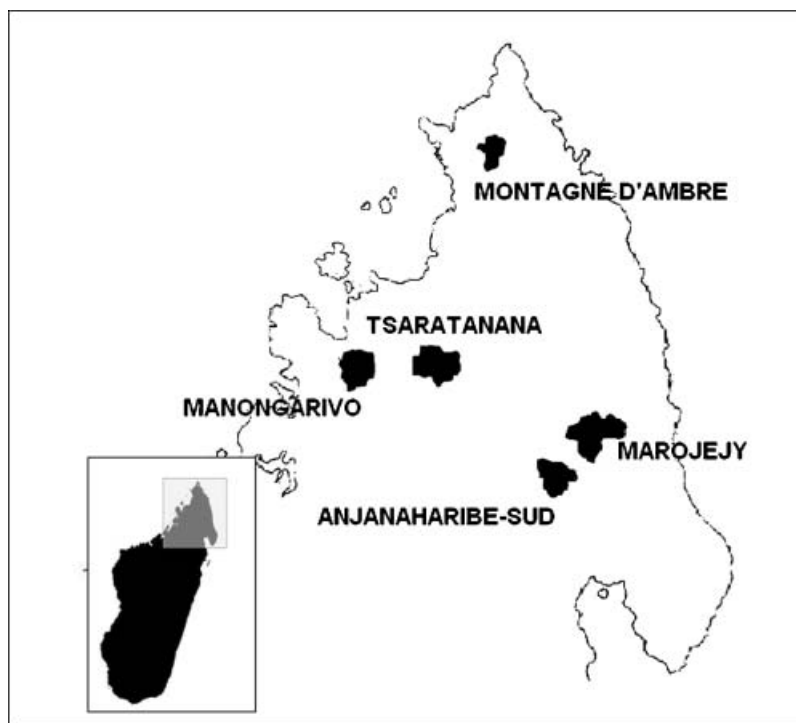


Figure 1. Map of northern Madagascar, with the main massifs and protected areas mentioned in the text.

new records for the Tsaratanana and Manongarivo areas, and the bibliographic data reported in Table I just derive from our surveys (IUCN et al. 2006; Vences et al. 2006; IUCN 2007).

Further data regard: (1) Montagne d'Ambre (largely based on Andreone 1993; Glaw & Vences 1994; Raxworthy & Nussbaum 1994, 1996b, and additional references), (2) Marojejy (Raselimanana et al. 2000), (3) Anjanaharibe-Sud (Raxworthy et al. 1998), and (4) Sambirano (Glaw & Vences 1994, and additional references).

Survey techniques

Searching methods at Tsaratanana followed established standards, including pitfall trapping and opportunistic observations, largely described by Andreone et al. (2000, 2003). Two persons were active about 6 h a day (night and day). Paths and streams were followed on alternate days, thus avoiding encountering the same individuals several times. The individuals were then counted and their habitat preferences noted, in order to get an overall abundance estimate.

Pitfalls consisted of plastic buckets (280 mm deep, 220–290 mm internal diameter), sunk into the ground at 10 m intervals along a plastic drift fence (0.5 m high and 100 m long). Holes were punched in the bottom to allow water to drain. Pitfalls were checked every morning and evening. Two fence lines were placed in different forest types: ridge (along the crest of a ridge) and valley (within 20 m of a stream in a valley bottom).

Representative individuals of almost all the species were photographed to document their colour patterns. Advertisement calls of frogs were recorded when possible, and compared to a vocalization database (mainly based on Vences et al. 2006 and personal sound collections). Voucher specimens were sacrificed (by immersion or injection of chlorobutanol solution), fixed in 10% buffered formalin or 90% ethanol, and transferred to 65–75% ethanol. Collected material is deposited in the Museo Regionale di Scienze Naturali, Torino, Italy (MRSN, MRSN-FAZC, MRSN-RJS), the Museo Civico "G. Doria" di Storia Naturale, Genova, Italy (MSNG), the Zoologische Staatssammlung München, Germany (ZSM), the Zoological Museum, Amsterdam Netherlands (ZMA), the Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar (PBZT-FAZC, PBZT-RJS), and the Université d'Antananarivo, Département de Biologie Animale, Madagascar (UADBA-FGMV, UADBA).

Taxonomy

Several amphibians and reptiles found during our surveys turned out to be new species. This was firstly assessed by the fact that they do not fit with any of the known species as reported by Glaw and Vences (1994, 2006) and the subsequent taxonomic literature. Bioacoustic comparisons were then used to characterize new amphibian species, which turned out to differ in call parameters from the recordings of known species. For some of these taxa we assign them to a known species or species-group, and they have been named as "sp. aff.", or "sp. 1", "sp. 2", and "sp. 3". For the taxonomy and nomenclature we followed Glaw and Vences (1994) and recent literature, such as the new mantellid classification provided by Glaw and Vences (2006). For the gender of the chameleon name *Calumma* we followed Lutzmann and Lutzmann (2004) in considering it neuter. More detailed data on several of the new species, including colour photos, can be found in Glaw and Vences (2007).

DNA barcoding

For some amphibian specimens from both Tsaratanana and Manongarivo we compared mitochondrial DNA sequences with an available reference database. Muscle tissue samples were taken from freshly collected specimens and preserved in 98% ethanol. DNA was extracted using different standard protocols and a fragment of the mitochondrial 16S rRNA gene amplified using the primers 16Sar-L and 16Sbr-H of Palumbi et al. (1991). After purification (Qiagen kits), the fragments were resolved on automated DNA sequencers (ABI 377, ABI 3100).

Sequences were validated and aligned with the software Sequence Navigator (Applied Biosystems), and deposited in Genbank (accession numbers of most of the newly obtained sequences are included in the batch AY847959–AY848683; details will be discussed below when adequate, see Genbank entries for voucher numbers). On the other hand, for reptiles, mitochondrial data are still scarce, and for this reason our considerations are mainly based on morphological comparisons.

Results

An overview on the amphibians and reptiles of Tsaratanana and Manongarivo

A total of 30 species of amphibians and 23 reptiles were recorded from all the Tsaratanana sites

Table I. Amphibians and reptiles found at Tsaratanana and Manongarivo; abbreviations as in the Appendix.

	Bibliography Tsaratanana	Andampy (T2)	Tsaratanana 1997 (T6)	Antsahamanara (T7)	Other sites	Bibliography Manongarivo	Camp Norbert (MCN)	Camp 0 (M0)	Camp 1 (M1)	Other sites
AMPHIBIANS										
HYPEROLIIDAE										
1					M1					
2					A, M1					
DICROGLOSSIDAE										
3					A					AB
PTYCHADENIDAE										
4					T4, A, M1					
MANTELLIDAE: BOOPHINAE										
5								+	+	
6	2			+			+		+	
7	9		+	+	T8, T5	9		+	+	
8		+								
9		+					+			
10								+	+	
11				+						
12				+		7	+	+		
13				!			!			
14					A, M1		+			
15				+				+	+	
MANTELLIDAE: LALIOSTOMINAE										
16						(5)	+			
17					A, M1					
MANTELLIDAE: MANTELLINAE										
18					A, T4 T5	5				
19								+	+	AB
20	8	+				5		+	+	
21	12		+		T5					
22		+				5		+		
23	8		+	+	T3, T5					+
24								+		
25					A, T1, T8 T3, T8, T1	5 2	+	+	+	
26		+				(2)	+			
27	2		+					+		
28	2			+	T8, T5					+
29				+	T5	(5)				+
30	10			+	T8, T5	5		+	+	
31				+	T5	(5)				+
32				+	T8, T5					
33					T3		+			
34			+	+				+		
35	2		+	+	T5, T9	(5)				
36					A					

Table I. (Continued.)

	Bibliography Tsaratana	Andampy (T2)	Tsaratana 1997 (T6)	Antsahamanara (T7)	Other sites	Bibliography Manongarivo	Camp Norbert (MCN)	Camp 0 (M0)	Camp 1 (M1)	Other sites
MICROHYLIDAE										
37					A					
38	11								+	
39								+		
40				+						
41			+	+						
42					T9					
43									+	
44			+	+						
45			+	+						
46			+	+		5				+
47							+	+		
48		+	+	+	T5	5		+		
49			+	+	A					
50		+	+	+	T5					
TOTAL AMPHIBIANS	10	7	10	19		15	11	15	17	
REPTILES										
CHAMAELEONIDAE										
1			+	+	T8					
2			+			5	+		+	
3						5	+			
4			+	+						
5		+	+	+		5			+	
6	4		+	+	T5	(5)				
7	6			+	T9					
8					A, M1, M2					
9		+	.		M1, M2, T1	5				
GEKKONIDAE										
10						5	+			
11										AB
12										AB
13		+	+		A-M1	5	+	+	+	
14				+						
15						5		+		
16							+			
17					A	5		+		AB
18					A-M1, M1-M2	5		+		AKB
19			+	+		5			+	
20			+	+	T3	5		+		
GERRHOSAURIDAE										
21					A, M1, M2					AB
22					T8	5		+		

Table I. (Continued.)

	Bibliography Tsaratanana	Andampy (T2)	Tsaratanana 1997 (T6)	Antsahamanara (T7)	Other sites	Bibliography Manongarivo	Camp Norbert (MCN)	Camp 0 (M0)	Camp 1 (M1)	Other sites
IGUANIDAE										
23	<i>Oplurus cuvieri</i>				A, M1, M2					
SCINCIDAE										
24	<i>Amphiglossus tanysona</i>				A					
25	<i>Madascincus melanopleura</i>	1	+	+		5				
26	<i>Madascincus mouroundavae</i>	1		+	A	5				
27	<i>Madascincus polleni</i>				A-M1					AB
28	<i>Trachylepis elegans</i>	1			T4	5				
29	<i>Paracontias manify</i>	1	+	+						
TYPHLOPIDAE										
30	<i>Typhlops microcephalus</i>			+						
31	<i>Typhlops</i> sp.								+	
BOIDAE										
32	<i>Sanzinia madagascariensis</i>		+			5	+	+		
COLUBRIDAE (SENSU LATO)										
33	<i>Alluaudina bellyi</i>					5			+	
34	<i>Bibilava stumpffi</i>		+			5	a		+	
35	<i>Compsophis fatsibe</i>	3		+						
36	<i>Dromicodryas quadrilineatus</i>		+		A, M1	5				
37	<i>Leioheterodon madagascariensis</i>				A, M1					
38	<i>Leioheterodon modestus</i>				A					
39	<i>Madagascarophis colubrinus</i>	+				5		+		
40	<i>Pseudoxyrhopus ambreensis</i>			+						
41	<i>Stenophis betsileanus</i>						+			
	TOTAL REPTILES	7	4	13	14	21	9	11	6	
	OVERALL TOTAL (AMPHIBIANS + REPTILES)	17	10	22	33	36	19	26	23	

The numbers in the bibliography columns refer to published references (we did not consider reports made available on the web), as follows: 1, Andreone and Greer (2002); 2, Glaw and Vences (1994); 3, Mercurio and Andreone (2005); 4, Nečas (2004); 5, Rakotomalala (2002); 6, Raxworthy and Nussbaum (2006); 7, Vences and Glaw (2005); 8, Vences et al. (2003); 9, Vences et al. (2005b); 10, Vences et al. (2004b); 11, Vences et al. (2005b); 12, Vences et al. (2002). The exclamation marks (!) refer to acoustic records that are not supported by voucher specimens. The number within round parentheses [e.g. (1), (5)] indicates the possible occurrence of a taxon in another site, but not yet confirmed by unequivocal data (e.g. voucher specimens, call records); a, between Manongarivo, Camp Norbert and Camp 0. Abbreviations for the columns "Other sites" are given in the appendix.

(Table I). Only a few of these findings were already known in bibliography. Furthermore, 144 pitfall trap-days yielded 41 captures at Antsahamanara, corresponding to six species of amphibians, and three of reptiles (Table III). The overall mean daily pitfall capture rate of amphibians and reptiles was 28.48% (22.92% for amphibians and 5.56% for reptiles).

We also observed some other taxa in the habitats around the Antsirasa village and during the transfer to the Antsahamanara Forest: *Heterixalus luteostriatus*, *H. variabilis*, *Hoplobatrachus tigerinus*, *Ptychadena*

mascareniensis, *Boophis tephraeomystax*, *Laliostoma labrosum*, *Mantella ebenau*, *Wakea madinika*, *Blommersia wittei*, *Dyscophus insularis*, *Stumpffia gimmeli*, *Lygodactylus* sp. 2, *Phelsuma laticauda*, *P. madagascariensis*, *Madascincus stumpffi*, *Amphiglossus tanysona*, *Trachylepis elegans*, *Zonosaurus laticaudatus*, *Furcifer oustaleti*, *F. pardalis*, *Oplurus cuvieri*, *Dromicodryas quadrilineatus*, *Leioheterodon madagascariensis*, and *L. modestus*.

At Manongarivo we found 30 amphibian and 18 reptile species. In addition, we found several other

Table II. Herpetofaunal species (alphabetical within order) shared between Tsaratanana (data from the present study and bibliography) and other sites: Manongarivo (data from Rakotomalala 2002 and present study), Sambirano (other than Manongarivo, including Nosy Be) (data from Andreone et al. 2003 and own records), PN de la Montagne d'Ambre (data from Raxworthy & Nussbaum 1994 and Glaw & Vences 1994), RS d'Anjanaharibe-Sud and Marojejy (data from Raxworthy et al. 1998 and Raselimanana et al. 2000). Presence of species with question mark (?) is so far dubious.

Tsaratanana/Manongarivo	Tsaratanana/Sambirano	Tsaratanana/Marojejy	Tsaratanana/M. d'Ambre
AMPHIBIANS			
<i>Boophis albilabris</i>	<i>Blommersia wittei</i>	<i>Boophis albilabris</i>	<i>Boophis blommersae</i>
<i>Boophis andreonei</i>	<i>Boophis albilabris</i>	<i>Boophis axelmeyeri</i>	(<i>Boophis</i> sp.1 aff. <i>brachychir</i>)
<i>Boophis axelmeyeri</i>	<i>Boophis andreonei</i>	<i>Boophis marojezensis</i>	<i>Boophis septentrionalis</i>
(<i>Boophis</i> sp.1 aff. <i>brachychir</i>)	(<i>Boophis</i> sp.1 aff. <i>brachychir</i>)	<i>Boophis septentrionalis</i>	<i>Boophis tephraeomystax</i>
<i>Boophis sambirano</i>	<i>Boophis sambirano</i>	<i>Boophis tephraeomystax</i>	<i>Gephyromantis granulatus</i>
<i>Boophis septentrionalis</i>	<i>Boophis tephraeomystax</i>	<i>Boophis vittatus</i>	<i>Gephyromantis horridus</i>
<i>Boophis tephraeomystax</i>	<i>Gephyromantis granulatus</i>	<i>Mantella ebenau</i>	<i>Gephyromantis pseudoasper</i>
<i>Boophis vittatus</i>	<i>Gephyromantis horridus</i>	<i>Gephyromantis granulatus</i>	<i>Mantidactylus ambreensis</i>
<i>Gephyromantis ambohitra</i>	<i>Gephyromantis pseudoasper</i>	<i>Gephyromantis pseudoasper</i>	(<i>Mantidactylus</i> sp. aff. <i>femoralis</i>)
<i>Gephyromantis granulatus</i>	<i>Mantella ebenau</i>	<i>Mantidactylus opiparis</i>	(<i>Mantidactylus</i> sp. aff. <i>mocquardi</i>)?
<i>Gephyromantis pseudoasper</i>	<i>Mantidactylus ambreensis</i>	(<i>Mantidactylus</i> sp. aff. <i>biporus</i>)?	<i>Rhombophryne laevipes</i>
<i>Gephyromantis zavona</i>	<i>Mantidactylus ulcerosus</i>	(<i>Mantidactylus</i> sp. aff. <i>femoralis</i>)	
<i>Mantella ebenau</i>	<i>Ptychadena mascareniensis</i>	(<i>Mantidactylus</i> sp. aff. <i>guttulatus</i>)	
<i>Mantidactylus ambreensis</i>	<i>Spinomantis massorum</i>	(<i>Mantidactylus</i> sp. aff. <i>mocquardi</i>)	
<i>Mantidactylus</i> sp. aff. <i>betsileamus</i>	<i>Stumpffia psologlossa</i>	<i>Ptychadena mascareniensis</i>	
<i>Mantidactylus</i> sp. aff. <i>biporus</i>		(<i>Spinomantis</i> sp. aff. <i>peraccae</i>)	
<i>Mantidactylus</i> sp. aff. <i>femoralis</i>			
<i>Mantidactylus</i> sp. aff. <i>guttulatus</i>			
<i>Mantidactylus</i> sp. aff. <i>mocquardi</i>			
<i>Mantidactylus ulcerosus</i>			
<i>Ptychadena mascareniensis</i>			
<i>Rhombophryne laevipes</i>			
<i>Spinomantis massorum</i>			
(<i>Spinomantis</i> sp. aff. <i>peraccae</i>)			
<i>Stumpffia psologlossa</i>			
REPTILES			
<i>Alluaudina bellyi</i>	<i>Alluaudina bellyi</i>	<i>Alluaudina bellyi</i>	<i>Alluaudina bellyi</i>
<i>Brookesia minima</i>	<i>Brookesia minima</i>	<i>Brookesia thieli</i> (?)	<i>Calumma boettgeri</i>
<i>Brookesia lineata</i> (?)	<i>Calumma boettgeri</i>	<i>Calumma guillaumeti</i>	<i>Calumma ambreense</i>
<i>Calumma boettgeri</i>	<i>Dromicodryas quadrilineatus</i>	<i>Madascincus melanopleura</i>	<i>Furcifer pardalis</i>
<i>Furcifer pardalis</i>	<i>Furcifer pardalis</i>	<i>Furcifer pardalis</i>	(<i>Lygodactylus madagascariensis</i> *)
<i>Bibilava stumpffi</i>	<i>Bibilava stumpffi</i>	<i>Sanzinia madagascariensis</i>	<i>Pseudoxyrhopus ambreensis</i>
<i>Lygodactylus madagascariensis</i>	<i>Madagascarophis colubrinus</i>	<i>Uroplatus sikorae</i>	<i>Uroplatus sikorae</i>
<i>Madagascarophis colubrinus</i>	<i>Sanzinia madagascariensis</i>	<i>Zonosaurus madagascariensis</i>	
<i>Sanzinia madagascariensis</i>	<i>Uroplatus</i> cf. <i>ebenau</i>		
<i>Uroplatus ebenau</i>	<i>Zonosaurus madagascariensis</i>		
<i>Uroplatus sikorae</i>			
<i>Zonosaurus madagascariensis</i>			

The species in parentheses indicate a possible shared presence between the two considered massifs, but without a sound biomolecular confirmation (they could belong to two still undistinguished separate taxa). (*) The *Lygodactylus madagascariensis* population from Montagne d'Ambre is considered as a separate subspecies, *L. m. petteri*.

species on the way to this reserve that were not collected in most cases. A detailed list of specimens from both Tsaratanana, Manongarivo, and nearby low-altitude areas, housed in the above-quoted herpetological collections, is given in the Appendix.

Taxonomic identity and remarkable records

We mention here a number of species and records, which are either remarkable new records from the Tsaratanana and Manongarivo massifs, or where

DNA barcoding data provided some information on the degree of differentiation from populations in other massifs, mainly for a number of frog species (Figure 2).

Boophis albilabris. This species had been recorded before from Benavony in the Sambirano region, but at Berara (Sahamalaza Peninsula), the encountered specimens were attributable to its western sibling species, *B. occidentalis* (Andreone et al. 2001). We also found specimens of *B. albilabris* at



Figure 2. Some of the most remarkable amphibians and reptiles found in the Antsahamanara Forest, Tsaratanana. (A) *Boophis andreonei* (MRSN A4255); (B) *Boophis vittatus* (MRSN A4395); (C) *Mantidactylus* sp. aff. *guttulatus* (MRSN A5481); (D) *Spinomantis massorum* (MRSN A3517); (E) *Brookesia lineata* (MRSN-FAZC 11042); (F) *Calumma ambreense* (MRSN R2864); (G) *Calumma peltierorum* (MRSN-FAZC 11092); (H) *Uroplatus ebenau* (MRSN R2932 and R2936).

Manongarivo, and the 16S DNA sequence of one of these specimens (sequence AY848556) had only two substitutions as compared to that of a specimen from the southeastern locality Ranomafana (AY848557; 0.4% divergence).

Boophis andreonei. So far only known from Benavony in the lowlands of the Sambirano region (Glaw & Vences 1994), but specimens with an identical advertisement call were collected at Manongarivo. The 16S DNA sequences of one Manongarivo specimen (sequence AY848449) were fully identical to a specimen from Tsaratanana (sequence AY848450), which we therefore assign to this species too.

Boophis axelmeyeri. This species has been recently described from Antsahamanara (Vences et al. 2005b). The 16S differences are 1.9% when compared to a specimen from Marojejy, and 0% (identical sequences) as compared to a conspecific specimen from Manongarivo (Vences et al. 2005b).

Boophis blommersae. This species had been described from Montagne d'Ambre and was so far known only from this northernmost massif (Glaw et al. 2001). Specimens from Tsaratanana (sequence AY848558) were genetically strongly differentiated from the Montagne d'Ambre specimens (sequence AY848451–AY848454), with 23 substitutions in the 16S fragments studied (4.3% pairwise difference), although their advertisement calls and morphology were similar.

Boophis sp. 1 aff. *brachychir*/*B.* sp. 2 aff. *brachychir*. The taxonomy of *B. brachychir* is not yet well settled; thus, we follow the general description based on Glaw and Vences (1994). We noted that at Manongarivo, two species of similar morphology (but with different advertisement calls) occur, one of which is genetically similar to specimens from Tsaratanana. Which of these two species is to be assigned to *B. brachychir* can only be decided after careful taxonomic revision and comparison with the original description and topotypic material from Nosy Be, since the types of this species are lost.

Boophis marojezensis. This frog was known to have a wide range from its type locality Marojejy in the northwest to the Ranomafana area in the southeast (Glaw et al. 2001). The record from Tsaratanana constitutes a considerable range extension into the northwest. Compared to a 16S sequence from a specimen from a southeastern population, Vohiparara (AY848594), the sequence from a

Tsaratanana specimen (sequence AY848595) differed by 28 substitutions (5.3%).

Boophis septentrionalis. At both Tsaratanana and Manongarivo we recorded calls of a green *Boophis* that is here attributed to *B. septentrionalis*. If this determination turns out to be correct, it stresses a further biogeographic relationship between these massifs and Montagne d'Ambre.

Boophis vittatus. Described from Marojejy in northeastern Madagascar it was found to be common both at Manongarivo and Tsaratanana, and Masoala (F. Andreone, unpublished). 16S sequences from the former two areas (sequences AY848524–AY848525) differed by a single substitution (0.2% pairwise differentiation), while sequences from Marojejy were not available for comparison.

Gephyromantis ambohitra. Originally described (and so far only reliably known) from Montagne d'Ambre (Vences & Glaw 2001), we recorded this species also at Manongarivo and probably (two individuals, without advertisement call recording, MRSN-RJS 0099 and MRSN-RJS 0112) from Tsaratanana (Antsahamanintsy). The genetic differentiation in the 16S fragment between Manongarivo (sequence AY848311) and Montagne d'Ambre (sequence AY848309) was of 31 substitutions (5.8% divergence).

Gephyromantis granulatus. Differences were 0.7–1.4% as compared to specimens from northeastern, northern and northwestern Madagascar (Vences et al. 2003).

Gephyromantis zavona. This species had been described from Tsaratanana (Vences et al. 2003) and hitherto was only known from this massif. However, specimens reported here from Manongarivo were identified unambiguously by bioacoustics and morphology, indicating that this species occurs at both Tsaratanana and Manongarivo.

Guibemantis sp. aff. *bicalcaratus*. This phytotelmic frog was found at Manongarivo in the leaf axils of a *Pandanus* screw pine. This is the first record of a *Pandanus*-dwelling species from northwestern Madagascar, although such species are known from Marojejy and from Montagne d'Ambre. However, the taxonomy of this whole complex is in urgent need of revision, and the specific identity of the

Manongarivo specimen (sequence AY848033) remains to be clarified.

Mantidactylus sp. aff. *guttulatus*. The individuals found at Tsaratanana (sequence AY848171) belong to a species with broad terminal disks on fingers and toes (see also Vences et al. 2004b), which seems to be exclusive of the northern part of Madagascar (present at least at Tsaratanana, Manongarivo, Besariaka, and Ambolokopatrika: see Andreone et al. 2000), and genetically distinct from specimens distributed along the central and southeastern coast. A comprehensive revision of the *Mantidactylus guttulatus* species complex is currently in preparation.

Mantidactylus sp. aff. *betsileanus*. This undescribed frog of the subgenus *Brygoomantis* was found at the Andampy campsite at Tsaratanana and at the campsite 0 at Manongarivo. The 16S mtDNA sequence of one specimen from Tsaratanana (AY848223) was totally identical to those from Manongarivo specimens (AY848263).

Mantidactylus sp. aff. *biporus*. This further undescribed and small species of the subgenus *Brygoomantis* was found at both Manongarivo and Tsaratanana at a higher altitude when compared to the previous species. The sequence of one specimen from Tsaratanana (sequence AY848276) had 3 substitutions (0.5% divergence) as compared to a specimen from Manongarivo (sequence AY848245).

Spinomantis massorum. This species was so far known only from its type locality Benavony in the lowland Sambirano region (Glaw & Vences 1994), but occurred up to 1100 m a.s.l. at Antsahamanana. 16S sequences from Manongarivo (sequence AY848412) differed by eight substitutions from those obtained from a Tsaratanana specimen (sequence AY848413; 1.5% divergence).

Cophyla phyllodactyla. One male specimen was recorded calling at Manongarivo, and based on bioacoustics the attribution was clearly conspecific with populations of this species from the type locality Nosy Be, and differed from *C. berara* which occurs further south at Berara (Andreone et al. 2001; Vences et al. 2005a).

Platypelis spp. The taxonomy of the genus *Platypelis* is in strong need of revision, and many new species still wait to be described. During our surveys we collected three undescribed species from Tsaratanana and one from Manongarivo. We are

currently unable to provide a diagnosis of these species which were partly included in a phylogenetic study on cophylina microhylids (Andreone et al. 2005).

Plethodontohyla spp. Similarly to the taxonomic situation observed for *Platypelis*, also in this case we discovered three unidentified “*Plethodontohyla*” species. At present data are insufficient to decide whether these specimens belong to *Plethodontohyla* s.str. or to *Rhombophryne* (according to Frost et al. 2006).

Brookesia minima. Based on the examination of the hemipenial morphology, the small *Brookesia* found at Manongarivo are attributed to this species, and not to *B. tuberculata*, which is typical from Montagne d’Ambre, or to *B. peyrierasi*, which is known from the northeast of Madagascar (Glaw et al. 1999). A single female from Tsaratanana 1997 is preliminarily assigned to this taxon, although further confirmation is needed.

Brookesia thieli/*B. lineata*. The medium-sized *Brookesia* specimens found at Tsaratanana are herein ascribed in a preliminary way to *B. lineata*, but it is likely that this assignation (see also photos in Nečas & Schmidt 2004 and Glaw & Vences 2007, which refer to one of the Manarikoba specimens) is to be changed in the future. In fact, our specimens (and *B. lineata* in general) also show strong similarities to *B. thieli*. According to molecular data by T. Townsend (in progress), *thieli* appears to be paraphyletic relative to *lineata*, and one of our samples from Tsaratanana clusters most closely to the sequence of *B. lineata* obtained by Raxworthy et al. (2002). It should also be considered that the type specimen of *B. lineata* (from Manongarivo) is quite big in size (37.7 mm average SVL for *B. thieli* vs. 46.7 for the type specimen of *B. lineata*), whereas our specimens collected at Tsaratanana agree fully with *thieli* in size (average SVL 37.7 mm). The presence of *B. thieli* at Marojejy is corroborated by a series within the Paris collection (MNHN 1974 1087–1088), but it has not been studied whether these specimens may bear morphological characters of *B. lineata*. Clearly, this whole complex is in need of revision and may contain several new species.

Calumma boettgeri/*C. guibei*. *C. guibei* has been described from Tsaratanana, and apparently it differs from *C. boettgeri* for having completely divided occipital lobes and for the rostral appendix that appears shorter than in *boettgeri* (Glaw & Vences 1994). The specimens we found at Manarikoba did

not exhibit these characters, and for this reason they probably do not belong to *C. guibei*. However, some of these specimens do have slightly separated lobes (see photos in Glaw & Vences 2007 as *C. guibei*), and therefore are probably also distinct from *C. boettgeri*, which have completely undivided lobes. Clearly, this whole complex of small forest chameleons (the *Calumma nasutum* group) contains numerous undescribed species and is in need of fundamental taxonomic revision.

Calumma guillaumeti. Known from Marojejy and Anjanaharibe-Sud (Andreone 1997; Raxworthy et al. 1998; Raselimanana et al. 2000), although generically reported for Tsaratanana too (Nečas 2004). Five specimens found at Tsaratanana (MRSN-FAZC 11154, PBZT-FAZC 11163, PBZT-RJS 0108, 0128, MSNG 49104) clearly belong to this species (see Andreone et al. 2001).

Calumma ambreense. According to Glaw and Vences (1994), the taxon *ambreense* appears morphologically more similar to *C. globifer* than to *C. oshaughnessyi*. We agree with this observation. For this reason, Glaw and Vences (2007) elevated *ambreense* at specific level. We here formally accept this species rank elevation.

Calumma peltierorum. According to the revision of the occipitally lobed *Calumma* chameleons by Raxworthy and Nussbaum (2006), we identified the female MRSN-FAZC 11092 as *C. peltierorum*: this finding at Antsahamanara lowers considerably the minimum range elevation of this species to 1100 m. The male MRSN-RJS 0107 was assigned to this taxon too.

Lygodactylus madagascariensis/L. sp. aff. *madagascariensis*. Based on the 16S mtDNA phylogenetical analyses of Puente et al. (2005), the specimen ZSM 782/2001 from Andampy resulted to be the sister species to *Lygodactylus madagascariensis* from Manongarivo, and this clade is sister to *L. madagascariensis petteri* from N. Madagascar. Although Puente et al. (2005) had no genetic data for specimens from the type locality of *L. madagascariensis* (Nosy Be), it is therefore very likely that ZSM 782/2001 is to be attributed to *L. madagascariensis*. We preliminarily assume the same for other specimens from Manongarivo and other Tsaratanana localities (see Appendix). On the other hand, a sample of ZSM 781/2001 from Antsahamanara was highly divergent. Subsequent morphological analysis revealed no detectable morphological differences between these two specimens (M. Puente, personal communication).

Although we here list ZSM 781/2001, as well as the specimen MRSN-FAZC 11044 from Antsahamanara (for which no tissue sample for genetic analysis was available), as a separate taxon (*L.* sp. aff. *madagascariensis*), we stress that the available evidence based on one sequenced individual only is not yet sufficient to draw definitive taxonomic conclusions.

Uroplatus cf. *ebenau*. The small *Uroplatus* we found at Tsaratanana and Manongarivo are here ascribed to *U. ebenau*. Morphologically they bear similarities to specimens from the type locality Nosy Be, but differ from the comparatively large individuals found at Montagne d'Ambre and in the NE of Madagascar. From data presented by Greenbaum et al. (2007) it is clear, however, that *U. ebenau* is a complex of numerous genetically deeply divergent species and that the taxonomy of this complex is in need of revision.

Sanzinia madagascariensis. Based on preliminary DNA data, to be published elsewhere, two samples from Manongarivo belong to the subspecies *S. m. voluntary* (see Vences & Glaw 2004).

Pseudoxyrhopus ambreensis. We found a single individual of *Pseudoxyrhopus* at Antsahamanara, which fitted with the morphology and lepidosis of *P. ambreensis* (SVL=344 mm; 21 scale rows at mid-body; 159 ventrals, 49 subcaudals (1st and 2nd scales divided, scales 3–6 undivided, from the 7th onwards divided); anal plate divided and 7 supralabials. This colubrid was so far known from Montagne d'Ambre only, and its finding at Tsaratanana constitutes a significant range expansion into the south. Anyhow, the relationships of this species with *P. analabe* from NE Madagascar (Nussbaum et al. 1998), which is morphologically similar, should also be investigated.

Stenophis betsileanus. The collection of this snake at Manongarivo extends its distribution area into the northwest of Madagascar from where, until now, no reliable records were available (Vences et al. 2004c).

Discussion

Sampling methods

Pitfall trapping allowed the capture of only some amphibian species, all of which were also found with direct search. This shows that pitfalls were not useful for obtaining information on the presence of frogs in the habitat we studied, limiting it to secretive and

fossorial frogs. In our case the fossorial species were also detected with the visual encounter system and found by searching in refuges and under dead roots and trunks. In contrast, pitfalls were much more relevant for ground-dwelling or fossorial reptiles: we captured *Madascincus melanopleura*, *M. mouroundavae*, and *Typhlops microcephalus* by pitfall trapping only. In general, pitfalls are even more successful for small mammal capture, as already discussed by Andreone et al. (2001). During the Tsaratanana survey we also captured some small mammals (mainly tenrecs), and a list of them is available in Andreone et al. (2006).

Amphibians were discovered at a high rate during the first days of sampling, while reptiles followed a less steep slope, as previously evidenced by Andreone and Randrianirina (2000). Anyhow, for both groups it is possible to state that the highest peak of sampling was reached, respectively, on the 7th and 8th days, and that after this there was no further species increase. The number of amphibians remains stable for five days, while reptiles remained so for four days (Figure 3). We believe that, at least for the analysed site, the total numbers of observed amphibian and reptile species is not so far from the reality, and can be considered for further argumentations. The apparently low abundance of many reptiles makes them difficult to find in a short time, and it is therefore likely that only a longer survey

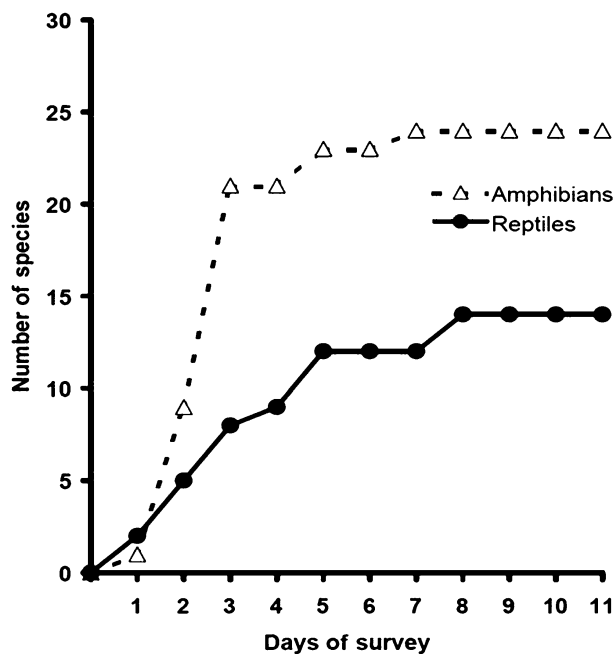


Figure 3. Species accumulation curves of amphibians and reptiles in the Antsahamanara Forest, Tsaratanana (all sample techniques combined).

period will yield a more realistic picture of reptile diversity.

This daily trap success for amphibians and reptiles is much higher than formerly detected values in eastern rainforest sites: 3.0%, 3.5%, and 2.1%, respectively, at Andohahela, Andringitra, and Anjanaharibe-Sud (Raxworthy & Nussbaum 1996b; Raxworthy et al. 1998; Nussbaum et al. 1999).

Ecological aspects and abundance

We largely ignore how the abundances of amphibians and reptiles follow the seasonal and geographic changes, although Andreone and Randriamahazo (1997) and Andreone et al. (2000) already indicated some differences. At Antsahamanara the survey was conducted in the warm rainy period (January) and should have given results comparable to former surveys carried out in the same season. This was not the case, since we found a very limited number of individuals per species.

It is also difficult to make reliable statements on the relative or absolute abundances of the various species at Antsahamanara: the short study period and the variance in secretiveness among species prevent to establish such indications, and it is clear that a longer survey would be likely necessary. As a rough approximation, and judging from the absolute number of observed and/or captured specimens, the most abundant amphibian species at Tsaratanana was *Plethodontohyla* sp. 2, with 22 adult specimens captured in pitfalls, followed by *Gephyromantis zavona*, with 14 individuals counted during the nocturnal surveys. The least frequent amphibian was *Gephyromantis pseudoasper* with a single specimen, but this species was commonly heard at the Andampy campsite and in further low-elevation sites on the way to Antsahamanara.

The observed abundance patterns were different in lizards and snakes; while lizards were sometimes quite abundant, with only *Madascincus mouroundavae*, *Uroplatus* cf. *ebenau*, and *Brookesia* cf. *lineata* with a number of at least four individuals each, snakes were only rarely observed. Our survey recorded a single *Compsophis*, one *Pseudoxyrhopus*, and two *Typhlops*. The overall scarcity of snakes in Malagasy rainforests is in agreement with the considerations by Andreone and Luiselli (2000), that rainforest snakes appear in general to be elusive in Madagascar.

The ratio of 30 amphibians and 23 reptiles observed at Tsaratanana (1.30) is apparently lower than that observed in another northern rainforest, Ambolokopatrika, where Andreone et al. (2000)

found 42 amphibians and 23 reptiles (ratio=1.82). At Anjanaharibe-Sud, Raxworthy et al. (1998) found 53 amphibians and 40 reptiles, giving a quite similar value (1.32) to that observed at Tsaratanana. Using the same search methodologies (direct observation and pitfall trapping) and for the same number of days (11 days) at a site characterized by Sambirano forest (Lokobe, Nosy Be Island), Andreone et al. (2003) found 8 amphibians and 34 reptiles, while in the transitional Berara Forest Andreone et al. (2001) found a further bias in favour of reptiles, with 10 amphibians and 26 reptiles during a 12-day period. Data from Tsaratanana therefore so far appear more similar to those from typical eastern rainforests, in particular when compared with comparable time lapses: at the campsite of Ambolokopatrika named Antsinjorano (12 days), at Ambolokopatrika-Andranomamelona (8 days), Andohahela (15 day) there are, respectively, 27, 31, and 22 amphibians, and 15, 18, and 16 reptiles (Andreone & Randriamahazo 1997; Andreone et al. 2000).

Biogeographical relationships

Combining the distributional data and data on molecular differentiation of Tsaratanana and Manongarivo specimens as presented above, it is possible to identify in a preliminary way some biogeographical patterns for the fauna of these localities, especially when compared to other northern massifs (Table II).

The faunas of the two massifs (western versant of Tsaratanana and eastern versant of Manongarivo) appear to be remarkably similar, leading to the conclusion that these two rainforest areas must have been in contact until recently. This is supported by further observations. First, there is a number of species which so far have only been found in these two massifs and at Benavony which can be seen as geographically belonging to the Tsaratanana mountain chain, and which may constitute regional endemics (*Boophis andreonei*, *Boophis sambirano*, *Gephyromantis zavona*, *Mantidactylus* sp. aff. *biporus*, *M.* sp. aff. *betsileanus*, *Spinomantis massorum*). Second, populations of several frog species, among them all of the above-mentioned potential endemics, except for *G. zavona*, as well as non-endemics, such as *Boophis axelmeyeri* and *B. vittatus*, show only a negligible genetic differentiation between the massifs (pairwise divergences <1% in all cases except for *S. massorum* which had a 1.5% divergence).

A second observed pattern is the existence of a biogeographical link between Tsaratanana-Manongarivo with Montagne d'Ambre in the north.

Table III. Characteristics and captures (Amphibia, Reptilia) for all pitfall lines at Antsahamanara, Tsaratanana (NW Madagascar).

Dates	3–11 February 2001		Total
	A	B	
Pitfall lines			
Altitude range of pitfall lines (m)	1000	1150	
Length	110	110	
Trap position	Valley	Ridge	
Number of nights	6	6	12
Pitfall number	12	12	24
Trap-nights	72	72	144
	Number of captured specimens		
Amphibians			
<i>Gephyromantis zavona</i>	2	1	3
<i>Mantidactylus opiparis</i>	–	1	1
<i>Platypelis</i> sp. 1	1	–	1
<i>Plethodontohyla</i> sp.2	8	14	22
<i>Rhombophryne laevipes</i>	–	1	1
<i>Stumpffia</i> sp. 1	–	5	5
Reptiles			
<i>Madascincus melanopleura</i>	2	–	2
<i>Madascincus mouroundavae</i>	1	3	4
<i>Typhlops microcephalus</i>		2	2
Total amphibians	11	22	33
Total reptiles	3	5	8
Overall total	14	27	41

This is supported by the occurrence of species like *Boophis blommersae*, *Mantidactylus ambreensis*, *Gephyromantis ambohitra*, *Rhombophryne laevipes*, *Pseudoxyrhopus ambreensis*, and *Calumma ambreense* at Tsaratanana. However, for two species in which we tested the genetic differentiation (*B. blommersae*, *G. ambohitra*), the pairwise divergence between Tsaratanana and Montagne d'Ambre was very high (4.3% and 5.8%, respectively). This suggests that the connection between the two rainforest blocks is relatively ancient, but this hypothesis needs to be tested with other species common to the two areas. The relationships between Manongarivo and Montagne d'Ambre are also supported by the recent discovery of *Amphiglossus mandokava* at the latter massif (ZSM 208/2003, ZSM 312/2004).

A further biogeographic link is that with the Marojejy/Anjanaharibe-Sud complex in the north-east (including the Ambolokopatrika ridge), supported by the occurrence of species like *Boophis axelmeyeri* and *Mantidactylus guttulatus* at Marojejy/Anjanaharibe-Sud, and of several other species including reptiles (e.g. *Phelsuma laticauda*, *Calumma guillaumeti*, and *Furcifer pardalis*) as summarized in Table II. However, also in this case, at least for some mid-altitude species such as *B. axelmeyeri*, the genetic and also morphological differentiation between the two areas is relatively strong (1.9%; Vences et al. 2005b).

As a last category of species, it is worthwhile mentioning those of a rather widespread distribution that occur also at Tsaratanana/Manongarivo. Into this category fall *Boophis albilabris*, *B. marojezensis*, and *Mantidactylus opiparis*, which have a very wide distribution over most of Madagascar's eastern rainforests, as well as *Gephyromantis pseudoasper* and *G. granulatus* which are widespread in the north. Although one of these species, *B. marojezensis*, seems to show a large interpopulational differentiation (see above) – and thus hiding a complex of species – in two others (*B. albilabris*, *G. granulatus*) the differentiation of the Tsaratanana/Manongarivo populations and those from other sites seems to be low, indicating a recent gene flow across their distribution area. At least two of these species (*G. pseudoasper* and *G. granulatus*) are indeed common lowland species.

As a general hypothesis from our data on mid- and low-elevation herpetofaunas, and assuming a general and very rough estimate of 0.3–1.0% pairwise 16S divergence per million years, it appears that the Tsaratanana and Manongarivo massifs had ancient connections with both Marojejy/Anjanaharibe-Sud and Montagne d'Ambre around 15–5 mya, which were severed long ago, maybe earlier with Montagne d'Ambre than with Marojejy/Anjanaharibe-Sud. Faunal exchange was then limited to species adapted to lowland rainforest that may still have been able to maintain some gene flow until recently. Some of these species evolved into local endemics, but gene flow was uninterrupted between Tsaratanana and Manongarivo, accounting for the high similarities of specimens of many species from both massifs. The fauna were then complemented by several recently arriving species from eastern Madagascar which indicates that connections between eastern and northwestern rainforests have existed, and that it was the complex geographical topology of northern Madagascar which inhibited more extensive faunal exchanges.

However, this hypothesis clearly needs further refinement from data on the herpetofaunal elements known to occur at higher altitudes of both Tsaratanana and Manongarivo, several of which are likely to be endemics (e.g. *Plethodontohyla guentherpetersi*, *Amphiglossus tsaratananensis*). Once that more complete data on the phylogeny and phylogeography, and elevational distribution of the Tsaratanana and Manongarivo herpetofauna get available, it will be possible to draw more comprehensive hypotheses on their origins and relationships.

Conservation and fields for further research

The Tsaratanana Massif, with its peak of 2876 m a.s.l., is an obvious biogeographic refuge and

radiation centre for many animals and plants, and likely an endemism centre, as witnessed by the high number of endemics or presumable endemics. Tsaratanana is currently managed as a Strict Nature Reserve, and this should prevent further degradations (Association Nationale pour la Gestion des Aires Protégées 2003). Anyhow, a large part of the surface area is highly degraded, with virtually no forest coverage, and only the inner part of the reserve covered by forest. Curiously not so many inventories have been carried out so far at Tsaratanana. This is likely due mainly to the difficulties of access and distance from towns, and a reduced tourist interest. It is therefore important that further surveys are made, in order to give an overall assessment of the area's biodiversity, and also to suggest management practices in more detail. Concerning the herpetofauna and small mammal fauna, such data will be soon available (C.J. Raxworthy, personal communication). This will hopefully fill the gap of knowledge at Tsaratanana, and will also provide information badly needed to get a full biogeographic and conservation assessment.

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Appendix

List of voucher specimens from Tsaratanana and Manongarivo and low-altitude nearby areas, and currently conserved in the Museo Regionale di Scienze Naturali (Torino, Italy; MRSN-FAZC), Parc Botanique et Zoologique de Tsimbazaza (Antananarivo, Madagascar; PBZT-FAZC), Université d'Antananarivo, Département de Biologie Animale (UADBA-MV, UADBA-FGMV), Zoological Museum Amsterdam (ZMA), Zoologische Staatssammlung München (München, Germany; ZSM and ZSM-FGMV). For each specimen we provide the abbreviation of the site name, the coordinates and the altitude. Abbreviations are as follows: A, Antsirasia (13°56.37'S, 48°33.27'E, <100 m a.s.l.); M1, Marotolana (14°01.41'S, 48°37.01'E, 104 m a.s.l.); M2, Marovato (13°56.24'S, 48°33.21'E, 75 m a.s.l.); T1, Tsaratanana/Camp 1 (14°02.59'S, 48°45.67'E, 600 m a.s.l.); T2, Tsaratanana/Andampy (14°02.53'S, 48°45.70'E, 730 m a.s.l.); T3, Tsaratanana/Andranomamelona (14°06.35'S, 48°43.54'E, 851 m a.s.l.); T4, Tsaratanana/Andranohofa (14°07.18'S, 48°44.08'E, 913 m a.s.l.); T5, Tsaratanana/Antsahamanintsy (14°03.25'S, 48°55.05'E, 1000 m a.s.l.); T6, Tsaratanana 1997 (14°02.40'S, 48°47.3'E; about 1000 m a.s.l.); T7, Tsaratanana/Antsahamanara (14°02.70'S, 48°47.6'E; 1100 m a.s.l.); T8, Tsaratanana/Andavaka (14°04.34'S, 48°53.47'E, 1056 m a.s.l.); T9, Tsaratanana/Ampiboahan'ala (14°02.45'S, 48°57.14'E, 2360 m a.s.l.); AB, Antanambao (13°53.38'S, 48°29.05'E, 9 m a.s.l.); MCN, Manongarivo Camp Norbert (13°56'53"S, 48°27'28"E, 288 m a.s.l.); M0, Manongarivo, campsite 0 (13°58.53'S, 48°25.60'E, 688 m a.s.l.); M1, Manongarivo Camp 1 (13°58.62'S, 48°25.32'E, 751 m a.s.l.).

Amphibia

Hyperoliidae

Heterixalus luteostriatus, MRSN-RJS 0056 (M1), 0058 (M1), PBZT-RJS 0057 (M1); *Heterixalus variabilis*, PBZT-RJS 0059 (M1), MRSN-RJS 0060 (M1); UADBA-MV 2001.45 (A), ZSM 608/2001–609/2001 (A).

Dicroglossidae

Hoplobatrachus tigerinus, PBZT-FAZC 11213 (A), 11214 (A).

Ptychadenidae

Ptychadena mascareniensis, MRSN-FAZC 11225 (A), PBZT-FAZC 11224 (A), MRSN-RJS 0055 (M1), PBZT-RJS 0141–0142 (T4).

Mantellidae – Boophinae

Boophis albilabris, UADBA-FGMV 2002.794 (M0), UADBA-FGMV 2002.807 (M1); *Boophis andreonei*, MRSN A4255 (T7) MRSN-FAZC 11067 (T7), ZSM 625/2001 (T7), ZMA 19369 (M0); *Boophis axelmeyeri*, MRSN-FAZC 11001 (T7), 11004 (T7), 11027 (T7), 11028 (T7), 11029 (T7), 11057 (T7), 11116 (T7), 11121 (T7), PBZT-FAZC 11030 (T7), 11031 (T7), 11114 (T7), 11115 (T7), MRSN-RJS 0076 (T8), 0105 (T5), UADBA-MV 2001.120–2001.121 (T7), 2001.125 (T7), 2001.135 (T7), 626/2001–631/2001 (T7), MSNG 49124A-B (T6), UADBA 10022 (T6), ZSM 837/2003 (M0); *Boophis blommersae*, UADBA-MV 2001.146–2001.149 (T2), 2001.52–2001.54 (T2), ZSM 617/2001–623/2001 (T2); *Boophis* sp. aff. *brachyichir* 1, UADBA-MV 2001.49 (T2), ZSM 624/2001 (T2), ZSM 993/2003 (MCN); *Boophis* sp. aff. *brachyichir* 2, ZSM 830–831/2003 (M0), ZSM 852/2003 (M1), ZSM 858/2003 (M1), ZMA 19543 (M0); *Boophis marojezensis*, MRSN-FAZC 11011 (T7), 11090 (T7), 11140 (T7), PBZT-FAZC 11061 (T7), UADBA-MV 2001.65–2001.67 (T7), ZSM 614/2001–616/2001 (T7); *Boophis sambirano* MRSN-FAZC 11124 (T7); ZSM 810–811/2003 (MCN); ZSM 815/2003 (MCN-M0), ZSM 995–996/2003 (MCN), ZMA 19569–19570 (MCN); *Boophis tephraeomystax*, MRSN-FAZC 11222 (A), 11223 (A), MRSN-RJS 0061 (M1), PBZT-FAZC 11221 (A), PBZT-RJS 0062 (M1); *Boophis vittatus*, MRSN A4395 (T7), UADBA-MV 2001.82 (T7), 2001.92–2001.93 (T7), ZSM 610/2001–613/2001 (T7); ZSM 819/2003 (M0), ZSM 835–836/2003 (M0), ZSM 978–981/2003 (M0), ZMA 19373, 19580 (M0), ZSM 840/2003 (M1), ZMA 19371–19372 (M1).

Mantellidae – Laliostominae

Aglyptodactylus securifer, ZSM 812/2003 (MCN), ZSM 19588 (MCN); *Laliostoma labrosum*, MRSN-FAZC 11227 (A); PBZT-FAZC 11226 (A), MRSN-RJS 0053 (M1); PBZT-RJS 0054 (M1).

Mantellidae – Mantellinae

Blommersia wittei, MRSN-FAZC 11229 (A), 11230 (A), 11244 (A), PBZT-FAZC 11228 (A), MRSN-RJS 0139 (T4), PBZT-RJS 0138 (T4), 0140 (T4), UADBA-MV 2001.35 (A), ZSM 589/2001 (A); *Gephyromantis ambohitra*, MRSN-RJS 0112 (T5), 0099 (T5); ZSM 820/2003 (M0), ZSM 838/2003 (M1), ZSM 848–851/2003 (M1); *Gephyromantis granulatus*, UADBA-MV 2001.152 (T2), ZSM 645/2001–646/2001 (T2), ZSM 818/2003 (M0), ZSM 834/2003 (M0), ZSM 839/2003 (M1); ZSM 845/2003 (M1); *Gephyromantis horridus*, MRSN-RJS 0125 (T5), MSNG 49125A-C (T6), UADBA 10001–10002 (T6), 10027 (T6); *Gephyromantis pseudoasper*, UADBA-MV 2001.139 (T2), 2001.140 (T2), ZSM 642/2001 (T2); ZSM 827–828/2003 (M0), ZSM 982/2003 (M0), ZMA 19376 (M0); *Gephyromantis zavona*, MRSN-FAZC 11003 (T7), 11005 (T7), 11015 (T7), 11024 (T7), 11025 (T7), 11051 (T7), 11087 (T7), 11088 (T7), 11089 (T7), 11119 (T7), 11142 (T7), 11168 (T7), MRSN-RJS 0063 (T3), PBZT-FAZC 11022 (T7), 11023 (T7), 11026 (T7), 11052 (T7), 11053 (T7), 11054 (T7), 11118 (T7), 11120 (T7), 11148

(T7), PBZT-RJS 0064 (T3), MRSN-RJS 0097 (T5), PBZT-RJS 0098 (T5), UADBA-MV 2001.57 (T7), 2001.85 (T7), 2001.89 (T7), ZSM 647/2001–650/2001 (T7), MSNG 49128 (T6), UADBA 10020.10021 (T6), ZSM 846–847/2003 (M1); *Guibemantis* sp. aff. *albolineatus*, ZSM 816/2003 (M0), ZMA 19582 (M0); *Mantella ebenau*, MRSN-FAZC 11236 (A), MRSN-RJS 0069 (T8), ZSM 593/2001 (A), MSNG 49120A-B (T1), UADBA 10023–10024 (T1), ZSM 992/2003 (MCN-M0), ZMA 19811 (M0–M1); *Mantidactylus ambreensis*, MRSN-RJS 0066 (T3), MRSN-RJS 0073 (T8), PBZT-RJS 0072 (T8), 00740075 (T8), UADBA-MV 2001.143–2001.144 (T2), ZSM 634/2001–635/2001 (T2); UADBA-MV 2001.138 (T2), ZSM 651/2001–654/2001 (T2), 639/2001–640/2001 (T7), MSNG 49121 (T1); ZSM 807–808/2003 (MCN); *Mantidactylus* sp. aff. *betsileanus*, MSNG 49122A-B (T6), UADBA 10025–10026 (T6), ZSM 821–826/2003 (M0), ZMA 19374–19375 (M0); *Mantidactylus* sp. aff. *biporus*, MRSN-FAZC 11008 (T7), 11009 (T7), 11034 (T7), 11066 (T7), 11071 (T7), 11072 (T7), 11074 (T7), 11075 (T7), 11077 (T7), 11079 (T7), 11080 (T7), PBZT-FAZC 11032 (T7), 11033 (T7), 11035 (T7), 11070 (T7), 11073 (T7), 11076 (T7), 11078 (T7), 11081 (T7), 11123 (T7), MRSN-RJS 0088 (T8), 0091–0093 (T8), 0094–0095 (T5), PBZT-RJS 0084–0087 (T8), 0089–0090 (T8), 0116–0117 (T5), UADBA-MV 2001.100–2001.102 (T7), 2001.108–2001.109 (T7), 2001.111 (T7), 2001.115 (T7), 2001.128 (T7), 2001.60 (T7), 2001.76–2001.78 (T7), 2001.96–2001.97 (T7), 2001.99 (T7), ZSM 655/2001–663/2001 (T7); ZSM 843–844/2003 (M1), ZSM 989/2003 (M1), ZMS 19567–19568 (M1); *Mantidactylus* sp. aff. *femoralis* and *M.* sp. aff. *mocquardi*, MRSN-FAZC 11014 (T7), 11143 (T7), PBZT-FAZC 11068 (T7), 11069 (T7), 11112 (T7), MRSN-RJS 0103 (T5), 0118 (T5), 0120–0121 (T5), PBZT-RJS 0102 (T5), 0119 (T5), 0122–0123 (T5), ZSM 632/2001 (T7), 633/2001 (T7), 643/2001 (T7), ZSM 844/2003 (M1, aff. *femoralis*), ZSM 845/2003 (M1, aff. *mocquardi*), ZSM 857/2003 (M1, aff. *femoralis*); *Mantidactylus* sp. aff. *guttulatus*, MRSN A5481, MRSN-FAZC 11017 (T7), 11097 (T7), 11098 (T7), 11117 (T7), PBZT-FAZC 11099 (T7), 11016 (T7), MRSN-RJS 0070–0071 (T8), 0101 (T5), PBZT-RJS 0100 (T5), UADBA-MV 2001.133 (T7), 2001.69 (T7), ZSM 644/2001 (T7); *Mantidactylus opiparis*, MRSN-FAZC 11065 (T7), 11082 (T7), 11122 (T7), 11138 (T7), 11150 (T7), PBZT-FAZC 11036 (T7), 11139 (T7), 11149 (T7), MRSN-RJS 0079 (T8), 0081 (T8), 0113 (T5), 0115 (T5), PBZT-RJS 0078 (T8), 0080 (T8), 0082–0083 (T8), 0114 (T5), UADBA-MV 2001.103 (T7), 2001.59 (T7), ZSM 641/2001 (T7); *Mantidactylus ulcerosus*, MRSN-RJS 0065 (T3); ZSM 809/2003 (MCN); *Spinomantis massorum* MRSN A3517 (T7), MRSN-FAZC 11013 (T7), 11147 (T7), 11166 (T7), 11167 (T7), MSNG 49127 (T6), UADBA 10029 (T6); ZSM 829/2003 (M0); *Spinomantis* sp. aff. *peracca*, MRSN-FAZC 11000 (T7), 11007 (T7), 11018 (T7), 11020 (T7), 11055 (T7), 11056 (T7), 11105 (eggs) (T7), 11106 (eggs) (T7), 11113 (T7), 11126 (T7), 11127 (T7), PBZT-FAZC 11019 (T7), 11021 (T7), MRSN-RJS 0104 (T5), 0109 (T9), 0110 (T9), 0126 (T5), UADBA-MV 2001.127 (T7), 2001.86 (T7), ZSM 636/2001–638/2001 (T7), 796/2001 (ATH), MSNG 49126A-B (T6), UADBA 10028 (T6); *Waka madinika*, MRSN-FAZC 11234 (A), UADBA-MV 2001.40 (A), ZSM 600/2001–607/2001 (A).

Microhylidae – Cophylinae

Cophyla phyllodactyla, ZSM 842/2003 (M1); *Platypelis milloti*, ZSM 817/2003 (M0), ZSM 984/2003 (M0); *Platypelis* sp. 1 MRSN-FAZC 11064 (T7), 11170 (T7), PBZT-FAZC 11091 (T7), 11104 (T7); *Platypelis* sp. 2, MRSN-FAZC 11058 (T7),

MSNG 49119A-B (T6), UADBA 10004–10005 (T6), 10032 (T6); *Platypelis* sp. 3, MRSN-FAZC 11103 (T7); MRSN-RJS 0111 (T9); *Platypelis* sp. 4, ZSM 841/2003 (M1); *Rhombophryne laevipes*, MRSN-FAZC 11002 (T7), MRSN-FAZC 11086 (T7), 11135 (T7), PBZT-FAZC 11063 (T7), 11085 (T7), MSNG 49118 (T6), UADBA 10030–10031 (T6), ZSM 853/2003 (M1); *Plethodontohyla* sp. 1 and sp. 2, MRSN-FAZC 11062 (T7), 11084 (T7), 11129 (T7), 11131 (T7), 11133 (T7), 11134 (T7), 11146 (T7), 11151 (T7), 11161 (T7), 11169 (T7), 11048 (T7), 11059 (T7), 11060 (T7), 11145 (T7), PBZT-FAZC 11083 (T7), 11128 (T7), 11130 (T7), 11132 (T7), 11152 (T7), UADBA-MV 2001.134 (T7), ZSM 664/2001 (T7), MSNG 49123A-C (T6), UADBA 10006–10007 (T6), 10033 (T6); *Stumpffia gimmeli*, ZSM 833/2003 (M0), ZMA 19574 (MCN); *Stumpffia* sp. aff. *gimmeli*, MRSN-FAZC 11237 (A), 11238 (A), 11239 (A), 11240 (A), 11241 (A), 11242 (A), 11243 (A), UADBA-MV 2001.37 (A), ZSM 597/2001 (A); *Stumpffia psologlossa*, ZSM 983/2003 (M0), ZSM 991/2003 (M0); *Stumpffia* sp. 1, MRSN-FAZC 11046 (T7), PBZT-FAZC 11047 (T7), UADBA-MV 2001.50 (T2), ZSM 665/2001–668/2001 (T7); MRSN-RJS 0096 (T5), MSNG 49117 (T6).

Microhylidae – Dyscophinae

Dyscophus insularis, MRSN-FAZC 11231 (A), 11231/b (A), 11231/c (A), UADBA-MV 2001.38 (A), ZSM 592/2001 (A).

Reptilia

Chamaeleonidae

Brookesia minima, ZSM 814/2003 (MCN), ZSM 990/2003 (M1); *Brookesia* cf. *minima*, MSNG 49115 (T6); *Brookesia stumpffi*, ZSM 977/2003 (MCN); *Brookesia lineata/thieli*, MRSN-FAZC 11037 (T7), 11042 (T7), 11043 (T7), 11100 (T7), PBZT-FAZC 11039 (T7), 11101 (T7), 11144 (T7), 11155 (T7), 11165 (T7), PBZT-RJS 0077 (T8), MSNG 49105 A-C (T6), UADBA 10041–10043 (T6); *Calumma boettgeri/guibeii*, MRSN-FAZC 11038 (T7), 11102 (T7), ZSM 551/2001 (T2), MSNG 49102 A-C (T6), UADBA 10039–10040 (T6), UADBA-FGMV 2002.813 (M1); *Calumma guillaumeti*, MRSN-FAZC 11154 (T7), PBZT-FAZC 11163 (T7), PBZT-RJS 0108 (T5), 0128 (T5), MSNG 49104 (T6); *Calumma peltierorum*, MRSN-FAZC 11092 (T7), MRSN-RJS 0052 (T9); *Calumma ambreense*, MRSN R2864 (T7), MSNG 49107 (T6), UADBA 10008 (T6); *Furcifer oustaleti*, MRSN-FAZC 11217 (A), PBZT-FAZC 11218 (A); PBZT-RJS 0049 (MV); PBZT-RJS 0051 (M1), PBZT-RJS 0144 (M1); *Furcifer pardalis*, MRSN-FAZC 11216 (A), UADBA-MV 2001.160 (T2); MSNG 49083 (T1), UADBA-FGMV 2210–2211 (MCN).

Gekkonidae

Lygodactylus madagascariensis, ZSM 813/2003 (MCN) ZSM 782/2001 (T2); MRSN-FAZC 11153 (A–M1), ZSM 832/2003 (M0), ZMA 19581 (M1); *Lygodactylus* sp. aff. *madagascariensis*,

MRSN-FAZC 11044 (T7), ZSM 783/2001 (T7); *Paroedura oviceps*, ZSM 987/2003 (M0); *Paroedura stumpffi*, ZSM 994/2003 (MCN); *Phelsuma laticauda*, MRSN-FAZC 11219 (A), UADBA-FGMV 2002.782 (M0); *Phelsuma grandis*; PBZT-FAZC 11208 (A–M1), UADBA-FGMV 2002.797 (M0); 11251 M1–M2, PBZT-RJS 0145 (M1); *Uroplatus* cf. *ebenau*, MRSN R2932 (T7), MRSN R2936 (T7), MRSN-FAZC 11164 (T7), PBZT-FAZC 11049 (T7), MSNG 49106 A-C (T6), UADBA 10036–10037 (T6), ZSM 856/2003 (M1), ZSM 997/2003 (M1); *Uroplatus sikorae*, MRSN-FAZC 11094 (T7), MRSN-RJS 0067 (T3), PBZT-FAZC 11095 (T7), 11141 (T7); MSNG 49108 (T6), UADBA 10035 (T6), UADBA-FGMV 2002.783 (M0).

Gerrhosauridae

Zonosaurus laticaudatus, MRSN-FAZC 11207 (A–M1), 11247 M1–M2, 11250 M1–M2; PBZT-FAZC 11220 (A); PBZT-RJS 0050 (MV), UADBA-MV 2001.163 (M1–A); *Zonosaurus madagascariensis*, MRSN-RJS 0068 (T8), UADBA-FGMV 2002.785 (M0).

Iguanidae

Ophurus cuvieri, MRSN-FAZC 11202 (A–M1), 11203 (A–M1), 11204 (A–M1), PBZT-FAZC 11205 (A–M1), 11206 (A–M1), 11246 (M1).

Scincidae

Madascincus melanopleura, MRSN-FAZC 11040 (T7), 11110 (T7), 11137 (T7), MSNG 49110–49111 (T6), UADBA 10038 (T6); *Madascincus mouroundavae*, MRSN-FAZC 11111 (T7), 11157 (T7), 11159 (T7), 11160 (T7), PBZT-FAZC 11158 (T7); *Madascincus polleni*, MRSN-FAZC 11232 (A); *Amphiglossus tanysona*, MRSN-FAZC 11233 (A); *Trachylepis elegans*, MRSN-FAZC 11212 (A–M1), PBZT-RJS 0146 (T4); *Paracontias manify*, MRSN-FAZC 11109 (T7) (holotype), MSNG 49112 (T6).

Typhlopidae

Typhlops microcephalus, MRSN-FAZC 11125 (T7), 11136 (T7), 11162 (T7); *Typhlops* sp., ZSM 985/2003 (M1).

Colubridae sensu lato

Alluaudina bellyi, ZSM 988/2003 (M1); *Compsophis fatsibe*, MRSN-FAZC 11045 (T7); *Dromicodryas quadrilineatus*, MRSN-FAZC 11211 (A–M1), ZSM 568/2001 (T2); *Leioheterodon madagascariensis*, MRSN-FAZC 11209 (A–M1), PBZT-FAZC 11210 (A–M1); *Leioheterodon modestus*, MRSN-FAZC 11215 (A); *Bibilava stumpffi*, ZSM 986/2003 (M1), ZMA 19589 (AB-MCN) MSNG 49113 (T6), UADBA 10034 (T6); *Madagascarophis colubrinus*, UADBA-MV 2001.161 (T2), ZSM 571/2001 (T2); *Pseudoxyrhopus ambreensis*, MRSN-FAZC 11156 (T7).