

## Filling the gaps – amphibian and reptile records from lowland rainforests in eastern Madagascar

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Manuscript received: 27 May 2010

**Abstract.** We report on the results of a survey of amphibians and reptiles at several primary and secondary lowland habitats along Madagascar's east coast. The survey yielded a total of 106 species (61 amphibians and 45 reptiles). Comparisons of mitochondrial DNA sequences of selected amphibian and reptile species confirmed their identification and in some cases allowed to assign them to particular intraspecific genetic lineages. The highest species diversity was found in the primary lowland rainforests of Ambodiriana and Sahafina. The littoral forests of Tampolo and Vohibola held overall a higher species diversity than the anthropogenic secondary forest formations of Vatomandry and Mahanoro. Structural differences between lowland forests and littoral forests seem to cause a difference in species composition, especially relevant for the amphibian species assemblages. Besides a number of undescribed species, the most remarkable records were those of *Mantidactylus majori*, *Uroplatus lineatus* and *Blaesodactylus antongilensis* in the Sahafina forest at Madagascar's central east coast, which constitute significant range extensions for these species. Four new unconfirmed candidate species (specimens of high genetic divergences that require further study to assess their possible species status) were recorded: *Blommersia* sp. [Ca12 HM631877] from Vatomandry, *Boophis* sp. aff. *arcanus* (*Boophis arcanus* [Ca44 HM631879]) from Marolambo, *Boophis* sp. aff. *boehmei* (*Boophis boehmei* [Ca43 HM631885]) from Sahafina, and *Guibemantis* sp. aff. *bicalcaratus* (*Guibemantis bicalcaratus* [Ca21 HM631910]) from Maroantsetra.

Key words. Herpetofauna, DNA barcoding, biodiversity, primary lowland rainforest, littoral forests, secondary habitats, Madagascar.

### Introduction

Madagascar is one of the world's most renowned zones of biological diversity. Knowledge on the diversity and distribution of Madagascar's unique herpetofauna has rapidly increased in the last two decades, yet the taxonomic status and especially the distribution of many of its highly endemic amphibians and reptiles remain poorly studied. As evaluated by VENCES et al. (2008), in amphibians, the traditional methods of morphological comparison of preserved specimens tend to identify only a small portion of the actual species richness. The recent increase in discoveries is mainly due to increased intensity of field exploration combined with the use of integrative taxonomic approaches that combine molecular genetics, comparative morphology and bioacoustics. VIEITES et al. (2009) highlighted that the actual amphibian species richness in Madagascar is in fact very incompletely represented by numbers of currently recognized nominal species.

Connected to ongoing taxonomic rearrangements, the knowledge on the distribution ranges of many species is also changing rapidly, usually because of their partition into several species. For example, the splitting of the formerly recognized widespread species *Calumma brevicorne*

by RAXWORTHY & NUSSBAUM (2006) makes it impossible to assign many of the historical records for *C. brevicorne* without extensive re-analysis and therefore left each of the newly recognized species of this complex with just a few reliable localities in the summarizing account of GLAW & VENCES (2007). Thus, partly as a consequence of taxonomic progress, important data for biogeographic studies and conservation assessments are missing for a considerable proportion of Madagascar's herpetofauna.

The intensity of herpetological surveys in Madagascar is biased towards areas included in the official network of protected areas managed by Madagascar National Parks (MNP), and still limited by time, personnel and financial resources (D'CRUZE et al. 2009). Other locality records are often clustered along main roads or near frequently visited tourist destinations (VIEITES et al. 2008). Although inventories and rapid assessments have been carried out in many regions throughout Madagascar, several larger areas still remain insufficiently studied, for example along Madagascar's east and northeast coast (e.g., ANDREONE 2005, ANDREONE et al. 2005, BOUMANS et al. 2007, VIEITES et al. 2008). Taking into account that habitat loss is rapid and ongoing in most of Madagascar's landscapes, efforts are needed to improve the knowledge on the island's fauna

and flora especially within these major geographical gaps. In this study, we contribute to the herpetological inventory in the region roughly extending from the northeastern coastal town Maroantsetra to the Mangoro River estuary at Madagascar's central east coast, which is a relatively large area that includes some major sampling gaps for Malagasy amphibians and reptiles. Our work received important assistance from several non-governmental organisations that are protecting small relicts of original forest habitat in the study area. As a general trend, the herpetofauna of most of these sites is only poorly known (e.g., RANDRIANIRINA 2005, RASELIMANANA 2005, DESCHAMPS 2007, RABEARIVONY et al. 2007)

### Materials and methods

Our surveys were carried out from 7 April to 2 May 2009 during the rainy season, when species are breeding and activity is at its highest. The four members of the herpetological field survey team were EMILE RAJERARISON, FRANÇOIS RANDRIANASOLO, FANOMEZANA M. RATSOAVINA and PHILIP-SEBASTIAN GEHRING. A preliminary survey had previously been carried out by P.-S. GEHRING from 1 July to 2 August 2008. Additionally, FANOMEZANA RATSOAVINA, EMILE RAJERARISON and FRANÇOIS RANDRIANASOLO conducted a survey around Marolambo, a small town south of the Mangoro River, from 12–25 May 2009.

### Study sites

Denomination of geographic areas within Madagascar follows BOUMANS et al. (2007) and GLAW & VENCES (2007). The following sites, all in the northern central east region except Andaparaty (northeast) and Marolambo (southern central east), were visited (from north to south; Fig. 1):

1. Andaparaty-“north” – Antainambalana River basin ( $15^{\circ}12'20.5''S$ ,  $49^{\circ}36'73.0''E$ , 247 m a.s.l.) visited on 26 July 2008. The village Andaparaty is located on the Antainambalana River, approximately 26 km northwest of Maroantsetra on the northeastern slopes of the Makira plateau. The visited site was four km north of Andaparaty, where a small farmhouse marks the boundary of the primary rainforest at an altitude of 110 m a.s.l. We here refer to this site as “Andaparaty-north”. From this point on, the slopes continue for 4 km from the river basin (56 m a.s.l.) to one of the peaks of the Anjanaharibe massif (1150 m a.s.l.). The Antainambalana River basin is densely populated and the vegetation along the river mainly consists of secondary and agricultural vegetation.

2. Antanambe ( $16^{\circ}25'47.6''S$ ,  $49^{\circ}47'04.4''E$ , 319 m a.s.l.) – visited from 16–20 July 2008. The village of Antanambe is located directly on the coast. The sampling site was 5 km southwest of Antanambe, close to the border of the Biosphere Reserve of Mananara Nord, but outside of the protected area. The Biosphere Reserve covers approximately 140,000 ha of primary low-altitude humid forest. The altitude at the sampling site was 160 m a.s.l. Many small permanent streams flow inside the forest.

3. Manompana–Ambodiriana forest ( $16^{\circ}40'28.4''S$ ,  $49^{\circ}42'10.0''E$ , 53 m a.s.l.) – visited from 27 April to 1 May

2009. The Réserve Privée (R.P.) d'Ambodiriana is located about 6 km northwest to the Rural Commune of Manompana ( $16^{\circ}41'23.3''S$ ,  $49^{\circ}44'40.92''E$ , 8 m a.s.l.) at Madagascar's east coast, about 200 km north of Toamasina (Tamatave). The altitude within the 67 ha of protected area starts from 45 m above sea level and reaches up to 230 m a.s.l. The R.P. d'Ambodiriana is flanked by the Antsahamangarana River to the south and by the Antsalovana River to the east. The Manompana River divides the sanctuary into two sections. This primary lowland forest is connected with the Zahamena-Mananara-Makira rainforest block. The R.P. d'Ambodiriana has been founded and is managed by the NGO “Association de Défense de la Forêt d'Ambodiriana” (ADEFA).

4. Tampolo ( $17^{\circ}17'19.2''S$ ,  $49^{\circ}24'41.6''E$ , 17 m a.s.l.) – visited from 24–26 April 2009. The 688 ha of littoral forest of Tampolo are situated directly on the coast, approximately 100 km north of the city of Toamasina. The area surrounding this small reserve is severely degraded and deforested, primarily due to the over-harvesting of trees and the practice of slash and burn agriculture. The Tampolo Forest Station is run by the Lemur Conservation Foundation and ESA-Forêts, University of Antananarivo. The Tampolo Forest Station was elevated to the status of ‘Système des Aires Protégées de Tampolo’ (Protected Area System of Tampolo) in 2006.

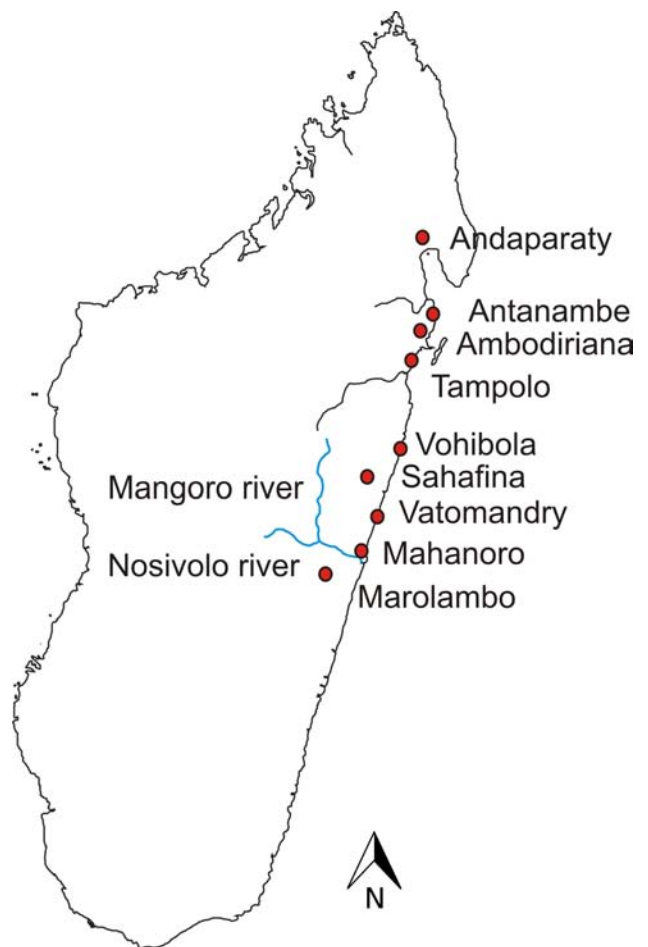


Figure 1. Map showing study sites along the east coast of Madagascar.

Vegetation types and forest classification

5. Andranokoditra – Vohibola forest (18°35'22.9"S, 49°13'50.6"E, 20 m a.s.l.) – visited from 8–15 April 2009. The littoral forest of Vohibola is a protected area 60 km south of Toamasina, under the protection of the NGO, “Man and the Environment” (MATE). The village of Andranokoditra is located at the southwestern limits of the protected area on the narrow stretch of land between the Indian Ocean and the Canal des Pangalanes. Within the protected area, different habitat types are present: primary littoral forest, secondary forest, swamp, alluvial forest and cultivated/degraded area.

6. Sahafina (18°48'38.8"S, 48°58'49.2"E, 59 m a.s.l.) – visited from 16–20 April 2009. The forest of Sahafina covers about 2500 ha of low-altitude rainforest in the Ampasimanolotra (Brickaville) district. It is located about 10 km west of Ampasimanolotra village. Its altitude varies from 50 to 240 m a.s.l. Many small permanent streams flow inside the forest. The intensive deforestation of this area during the last century (DOLCH 2003) led to the isolation of this forest fragment by ca. 30 km from the closest continuous rainforest block (Andasibe-Zahamena corridor). The NGO ‘Biodiversity Conservation Madagascar’ (BCM) took over the conservation management of the Sahafina forest fragment.

7. Vatomandry (19°20'23.2"S, 48°56'01.1"E, 33 m a.s.l.) – visited on 21 and 22 April 2009. The small town of Vatomandry is located about 140 km south of Toamasina. The vegetation in the surroundings of Vatomandry is heavily degraded and intensively used for the cultivation of crop plants. We searched for amphibians and reptiles within the remaining vegetation (mostly consisting of *Ravenala madagascariensis*) and in fields and plantations.

8. Mahanoro and Ambodiharina – northern (19°59'10.1"S, 48°47'08.3"E, 6 m a.s.l.) and southern (20°00'48.9"S, 48°45'59.1"E, 5 m a.s.l.) banks of the Mangoro River – visited on 22 and 23 April 2009. Similar to the situation in Vatomandry, the surroundings of Mahanoro and Ambodiharina are heavily degraded and intensively used for the cultivation of crop plants. Along the Mangoro River, the vegetation mainly consists of *Pandanus* and *Typhonodorum*. At its estuary, the Mangoro River has a width of nearly 3 km. Even 14 km farther inland, the river is still 700 m wide. We searched for amphibians and reptiles within the remaining original vegetation, and in fields and plantations.

9. Marolambo (20°03'08.6"S, 48°08'02.0"E, 445 m a.s.l.) – visited from 16–21 May 2009. The “Commune” of Marolambo is situated 120 km southwest of the city of Mahanoro. It includes an area of about 3764 km<sup>2</sup> and holds 125 small villages. The Nosivolo River is the major water body in this area, and it drains into the Mangoro River (Fig. 1). Due to intensive slash and burn agriculture, the surrounding forests have nearly vanished and only some small and isolated fragments have remained. Three of these last fragments were visited during our survey, named Tanin'ny Betsileo, Ambodisavoka forest and a forest close to Ambatolomakana. In the following discussion, all of these nearby localities are consolidated under “Marolambo”. The remaining primary vegetation consists of dense humid lowland evergreen forest. The altitude within the area ranges from about 400 to nearly 800 m a.s.l.

The forest formations of the eastern escarpments of Madagascar are often referred to as a single continuous stretch of rainforest, with parts of it being more pristine or more disturbed. Although the lowland areas are restricted to a comparatively narrow stretch along to the coastline from north to south, they contain a variety of significantly different habitats. Structural differences between forests can have important implications for the composition of amphibian and reptile communities. We therefore will here give a short review on the different vegetation types within the visited study sites (Fig. 2). A detailed summary of all vegetation types within each locality is given in Table 1. Six major vegetation types could be recognized, following the forest classification of LOWRY et al. (1997) and GAUTIER & GOODMAN (2003).

1. Primary forest formations: Moist evergreen littoral forest (LF). Due to intensive deforestation, littoral forests today persist only as small fragments. They are no more than a few kilometres and never more than 10 km in width (DE GOUVENAIN & SILANDER 2003, GANZHORN et al. 2000), located close to the coastline on shallow sandy soils, with a canopy height of 6 to 20 m on average. Dominant plant genera in these forests are, amongst others, *Canarium*, *Eugenia*, *Intsia*, *Dyopsis*, *Raphia*, *Pandanus*, and *Uapaca* (DE GOUVENAIN & SILANDER 2003, BOLLEN & DONATI 2005). Littoral forests were once contiguous with the dense humid lowland evergreen forests that cover the adjacent eastern hills. Directly along the coastline, the vegetation changes to a typical “beach” forest type, with *Calophyllum*, *Faucherea*, *Mimusops*, *Pandanus*, and *Terminalia* being the dominant plant genera (DE GOUVENAIN & SILANDER 2003).

Swamp forest and coastal marshland (SWF). Swamps can be found adjacent to the beach behind frontal dunes, along forest streams, or along the coastline close to the Canal de Pangalanes. The Pangalanes is a chain of fresh water lakes and lagoons parallel to the coast of the Indian Ocean, separated by a narrow stretch of land. The lakes are connected by a man-made channel system that forms an inland waterway from Toamasina through to Farafangana,

Table 1. Distribution of different vegetation types at the study sites. LF = littoral forest, SWF = Swamp forest and coastal marshland, LEF = Low-elevation moist evergreen forest (0-800m), ST = secondary thicket, SG = secondary grassland, CA = cultivated area.

Locality	Vegetation type					
	LF	SWF	LEF	ST	SG	CA
Andaparaty “north”			*	*		
Antanambe			*	*		*
Ambodiriana		*	*	*		*
Tampolo	*	*		*		*
Vohibola	*	*		*		*
Sahafina			*	*		*
Vatomandry				*	*	*
Mahanoro / Ambodiharina		*		*		*
Marolambo			*	*		

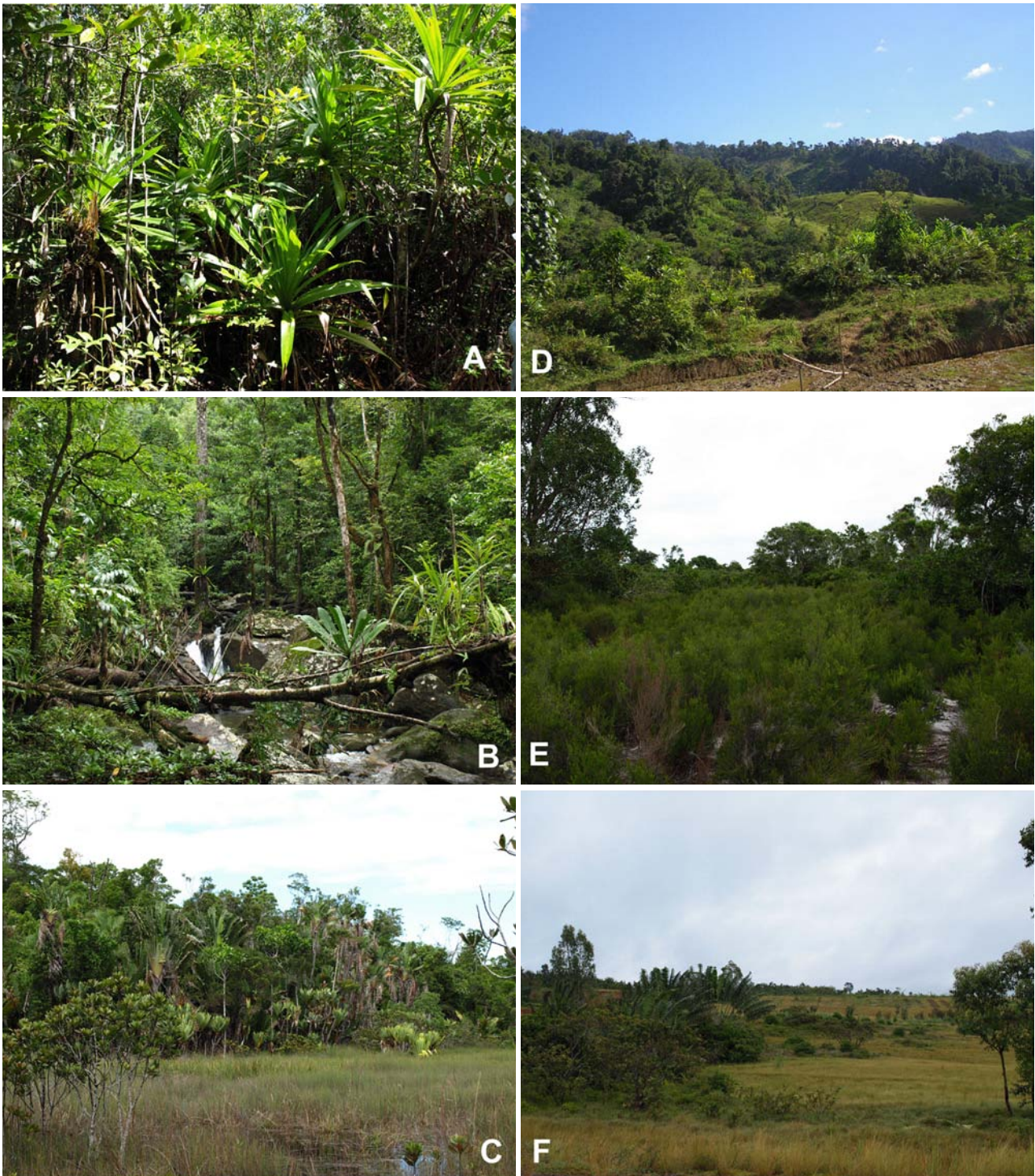


Figure 2. Overview of the different vegetation types. Primary vegetation: (A) Littoral forest, Vohibola; (B) Low-altitude moist evergreen forest (0–800 m), Ambodiriana; (C) Swamp forest and coastal marshland, Vohibola; Secondary vegetation: (D) Cultivated area, Andaparaty; (E) Secondary thicket, Vohibola; (F) Secondary grassland, Vatomandry.

covering a distance of about 600 km from north to south. Heavy rainfall during the annual rainy season cause the water level of the Canal des Pangalanes to rise and spill over into wide floodplains. The dominant plant genera of this vegetation are *Pandanus*, *Ravenala*, *Typhonodorum*, *Raphia*, *Carex*, *Cyperus*, and the invasive plant *Melaleuca quinquenervia*.

Low-altitude moist evergreen forest (0–800 m) (LEF). This forest type often has trees of 25–30 m in height with several strata and a diffuse understorey. It is very rich in species; some of the dominant genera are *Calophyllum*, *Ocotea*, *Dalbergia*, *Anthostema*, and *Pandanus*.

2. Degraded and secondary forest formations: Secondary thickets (ST). Large areas of Madagascar’s east coast

are covered by secondary woody vegetation representing a number of successive stages. After the clearing of a forest without cultivating the area, secondary thickets arise. On sandy soils close to the coastline, these thickets mainly consist of *Phyllippia* sp., *Helichrysum*, *Ravenala madagascariensis* and *Harungana*. The vegetation of fallow fields (“savoka”) more inland consists mainly of heliophilous species like *Ravenala madagascariensis*, *Aframomum* sp., *Lantana camara*, *Rubus* sp., and ferns (*Pteridium* spp.) (HLADIK et al. 2000).

Secondary grassland (savanna) (SG). Areas with poor drainage or where many years of cultivation and erosion have impoverished soils are usually covered by savannah vegetation dominated by fire-resistant grasses, sedges, ferns (*Pteridium* spp.), *Erica* sp., and *Ravenala madagascariensis* (HLADIK et al. 2000, DE GOUVENAIN & SILANDER 2003).

Cultivated area (CA). Owing to high annual rainfall throughout the year, the east coast is one of the most fertile regions of Madagascar. The majority of the cultivated area consists of small plantations for coffee, clove, litchi, banana, bamboo, *Eucalyptus*, and along the floodplains of most streams, rice paddies.

#### Search and collecting methods

We searched for amphibians and reptiles by making direct opportunistic observations during day and night, with special attention to particular kinds of microhabitats known to be suitable for these animals, usually for three hours in the morning, three to four hours in the afternoon and three hours in the night, along particular transects (paths and streams). Transects were searched on alternate days at different times, thereby largely avoiding encountering the same individuals several times. Secretive species were searched for in their natural refuges (e.g., fallen logs, under bark and in leaf litter, soil and leaf axils of screw pines (*Pandanus* sp.)). Most searches were done close to existing forest trails, but also away from paths on ridges and in streams. Night searches were made using torchlights and headlamps. This procedure does not exactly correspond to randomised visual encounter surveys as described by CRUMP & SCOTT (1994). Nevertheless, comparisons of the herpetofaunal diversity across sites in this paper maintain their validity because data collection was carried out by the same persons during the 2009 survey and is therefore comparable across the sites of Ambohidriana, Tampolo, Vohibola, Sahafina, Vatomandry and Mahanoro. Exceptions to this are the sites visited during the preliminary survey in 2008 (Andaparaty-“north” and Antanambe) and the Marolambo sites visited in 2009, which are therefore not included in any statistical analyses.

For genetic analyses, tissue samples (tail tips, toes) were taken from each specimen and preserved in 99% ethanol. Most of the animals were immediately released after sampling. The tissue samples are deposited at the Zoological Institute of the Technical University of Brunswick (Germany). Specimens that could not be identified in the field were first photographed to document their colouration in life and then euthanized with chlorobutanol, fixed in 90% ethanol, and preserved in 70% ethanol for later lab-

oratory identification. Specimens and/or tissue samples were labelled with field numbers of M. VENCES (ZCMV) or P.-S. GEHRING (PSG). These specimens are deposited at the University of Antananarivo, Département de Biologie Animale, Madagascar (UADBA-ZCMV, UADBA) and the Zoologische Staatssammlung München, Germany (ZSM), respectively.

#### Bioacoustics and morphology

The calls of several amphibian species were recorded with an Edirol R-09 handheld digital voice recorder. For some reptile specimens, especially of taxa imperfectly known or of special interest, we also took biometric measurements with dial callipers with a precision of 0.1 mm (snout-vent length SVL; total length TL; tail length TaL).

#### Identification, nomenclature and DNA barcoding

Species identification in the field was based on GLAW & VENCES (2007). Taxonomy is based on GLAW & VENCES (2007) and subsequent updates such as the synonymisation of the genus *Bibilava* with *Thamnosophis* by CADLE & INEICH (2008), and the revision of the former snake genus *Stenophis* by NAGY et al. (2010).

Several amphibians found during our survey could not be assigned to any described species. To refer to these we use the terms and abbreviations, confirmed candidate species (CCS), unconfirmed candidate species (UCS), and deep conspecific lineage (DCL) as defined by VIEITES et al. (2009). Candidate species are named with numbers as in VIEITES et al. (2009) for frogs, and/or newly identified CCS and UCS are named after PADIAL et al. (2010) with the genus name and respective candidate number and GenBank accession number: e.g., *Boophis arcanus* [Ca44 HM631879]. For unidentified reptiles, we used the names as in GLAW & VENCES (2007) with “sp. aff.” or “cf.” preceding the name of the morphologically closest described species and a descriptor that is either geographic or refers to a characteristic trait of the candidate species. We do not apply the new scheme of PADIAL et al. (2010) to all candidate species, but rather adopt here the system used for the existing comprehensive listing in VIEITES et al. (2009) for consistency, and because the paper of PADIAL et al. (2010) was published after the present work was finalized and sequences submitted to GenBank. However, we suggest applying the new scheme wherever possible in the future. For a number of frog specimens, we determined mitochondrial DNA sequences and compared them with a reference database. Tissue samples were taken from freshly collected specimens and preserved in 100% ethanol. After extraction of total genomic DNA, using different standard protocols, fragments of the mitochondrial 16S rRNA gene were PCR-amplified using the newly designed primers 16S-FrogL1 (5' CATAATCACTTGTTCTTTAAA 3') and 16S-FrogH1 (5' GATCCAACATCGAGGTCG 3') for amphibians, and for reptiles, the primers 16S-AL and 16S-BH (PALUMBI et al. 1991), following standard protocols (see VENCES et al. 2005). After purification (EXOAP), the fragments were re-

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Table 2. List of fieldnumbers and localities of specimens used for DNA barcoding and their respective Genbank accession numbers.

Genbank accession number	Field-number	Taxon	Locality	Genbank accession number	Field-number	Taxon	Locality
GU984751	PSG-825	<i>Blommersia</i> sp. aff. <i>blommersae</i> "Nosy Boraha" ( <i>B.</i> sp. 3)	Tampolo	HM631910	PSG-29	<i>Guibemantis</i> sp.aff. <i>liber</i>	15 km south of Maroantsetra Marolambo
HM631876	PSG-20	<i>Aglyptodactylus</i> sp. aff. <i>madagascariensis</i> "East" ( <i>A.</i> sp. 2)	Andaparaty north	HM631911	PSG-31		
HM631877	ZCMV-8943	<i>Blommersia</i> sp. aff. <i>blommersae</i> "Nosy Boraha" ( <i>B.</i> sp. 3)	Vatomandry	HM631912	ZCMV 8988		
HM631878	ZCMV-8942		Vatomandry	HM631913	PSG-46	<i>Mantidactylus</i> sp. aff. <i>betsileanus</i> ( <i>M.</i> sp. 25)	Antanambe
HM631879	PSG 1515	<i>Boophis</i> sp. aff. <i>arcanus</i>	Marolambo	HM631914	PSG-970		Ambodiriana
HM631880	PSG 1516		Marolambo	HM631915	PSG-1017		Ambodiriana
HM631881	PSG 1517		Marolambo	HM631917	PSG-1080		Ambodiriana
HM631882	PSG 1518		Marolambo	HM631916	PSG-1088		Ambodiriana
HM631883	ZCMV-8975		Marolambo	HM631918	ZCMV-8959		Ambodiriana
HM631884	PSG-8	<i>Boophis axelmeyeri</i>	Andaparaty north	HM631919	PSG-288	<i>Mantidactylus</i> sp. aff. <i>betsileanus</i> ( <i>M.</i> sp. 34)	Sahafina
HM631885	PSG-313	<i>Boophis</i> cf. <i>boehmei</i>	Sahafina	HM631920	ZCMV-8945		Mahanoro
HM631886	PSG-414		Sahafina	HM631921	PSG-610	<i>Mantidactylus</i> sp. aff. <i>betsileanus</i> ( <i>M.</i> sp. 36)	20 km north of Vatomandry
HM631887	PSG-418		Sahafina	HM631922	PSG-778		Sahafina
HM631888	PSG-1367		Marolambo	HM631923	ZCMV-8925		
HM631889	PSG-996	<i>Boophis englaenderi</i>	Ambodiriana	HM631924	PSG-1299	<i>Mantidactylus</i> <i>betsileanus</i> "slow calls"	Ambodisavoka
HM631890	PSG-1497	<i>Boophis pyrrhus</i>	Marolambo	HM631925	PSG-1389		Marolambo
HM631891	PSG-54	<i>Boophis roseipalmatus</i>	Antanambe	HM631926	PSG-1522		Marolambo
HM631892	PSG-61		Antanambe	HM631927	PSG-962	<i>Mantidactylus</i> sp. aff. <i>charlotteae</i> ( <i>M.</i> sp. 10)	Ambodiriana
HM631893	PSG-1005		Ambodiriana	HM631928	PSG-1009		Ambodiriana
HM631894	ZCMV-8926	<i>Gephyromantis</i> sp. aff. <i>boulengeri</i> ( <i>G.</i> sp. 24)	Sahafina	HM631929	PSG-1294	<i>Mantidactylus</i> sp. aff. <i>femoralis</i>	Ambodisavoka
HM631895	SG-282		Sahafina	HM631930	PSG-9	<i>Mantidactylus grandidieri</i>	Andaparaty
HM631896	ZCMV-8961	<i>Gephyromantis</i> sp. aff. <i>boulengeri</i> ( <i>G.</i> sp. 25)	Sahafina	HM631931	PSG-416	<i>Mantidactylus majori</i>	Sahafina
HM631897	ZCMV-8905		Ankanin'ny Nofy	HM631934	PSG-1295		Marolambo
HM631898	ZCMV-8990	<i>Gephyromantis</i> sp. aff. <i>boulengeri</i>	Marolambo	HM631935	PSG-1296		Marolambo
HM631899	ZCMV-8991		Marolambo	HM631932	ZCMV-8924		Sahafina
HM631900	PSG-10	<i>Gephyromantis luteus</i>	Andaparaty north	HM631933	ZCMV-8927		Sahafina
HM631901	PSG-11		Andaparaty north	HM631936	ZCMV-8923	<i>Mantidactylus femoralis</i>	Sahafina
HM631902	PSG-977		Ambodiriana	HM631937	ZCMV-8929		Sahafina
HM631903	PSG-49	<i>Gephyromantis malagasius</i>	Antanambe	HM631938	PSG-295	<i>Mantidactylus opiparis</i>	Sahafina
HM631904	PSG-1015		Ambodiriana	HM631939	PSG-392	<i>Spinomantis aglavei</i>	Sahafina
HM631905	PSG-5	<i>Gephyromantis</i> sp. aff. <i>moseri</i> ( <i>G.</i> sp. 18)	Andaparaty north	HM631940	PSG-234	<i>Anodonthyla boulengeri</i>	Vohibola
HM631906	PSG-6	<i>Gephyromantis redimitus</i>	Andaparaty north	HM631941	PSG-1101		Ambodiriana
HM631907	PSG-48	<i>Gephyromantis webbi</i>	Antanambe	HM631942	PSG-1134		Ambodiriana
HM631908	PSG-242	<i>Guibemantis bicalcaratus</i>	Vohibola	HM631943	PSG-1127		Ambodiriana
HM631909	PSG-242	<i>Guibemantis bicalcaratus</i>	Vohibola	HM631944	ZCMV-8963		Ambodiriana
HM631910	PSG-242	<i>Guibemantis bicalcaratus</i>	Vohibola	HM631945	ZCMV-8921		Sahafina
				HM631946	ZCMV-8922		Sahafina
				HM631947	ZCMV-8913		Vohibola
				HM631948	ZCMV-8912		Vohibola
				HM631949	ZCMV-8911		Vohibola
				HM631950	ZCMV-8901		Ankanin'ny Nofy
				HM631951	ZCMV 8962	<i>Platypelis</i> cf. <i>tetra</i>	Ambodiriana

solved on an automated DNA sequencer (ABI 3130 XL, Applied Biosystems). For some reptile species, comparisons of other mitochondrial genes (12S rRNA, cytochrome *b*, NADH dehydrogenase subunit 2 and NADH dehydrogenase subunit 4) were supplied by collaborators or obtained

in the framework of other projects and are only briefly reported on here.

Sequences were validated and aligned with the software CodonCode Aligner (CodonCode Corporation), and have been deposited in GenBank under the Accession Nos.

HM631876–HM631951 and GU984751 (Table 2). For identification of sequences, we used BLAST searches against sequences deposited in GenBank that include 16S rDNA sequences from a near-complete sampling of Madagascar frogs from VIEITES et al. (2009) as well as large series of specimens of some species from additional localities (e.g., from VENCES et al. 2005). In addition, we used MAFFT (KATO et al. 2002) to align the newly obtained sequences with the original data set of VIEITES et al. (2009) that contained all but seven species of Madagascar anurans, as well as numerous candidate species and deep conspecific lineages. Subsequently, we used this alignment to produce a Neighbour-joining tree in MEGA 4.0 (KUMAR et al. 2008) based on K2P-distances, in order to obtain first hypotheses on the probable phylogenetic clustering of the newly sequenced specimens with any of the nominal species or previously identified candidate species.

Because the 16S fragment amplified was shorter than the fragment to which previous barcoding results refer (e.g., VENCES et al. 2005), genetic distances are not directly comparable and are therefore not reported here for most species in order to avoid confusion: the fragment sequenced herein contains a large part of two very variable regions for loops of the secondary structure of the 16S rRNA molecule, and lacks several conserved stem regions; comparisons would therefore yield substantially higher genetic divergence values than in previous comparisons (VENCES et al. 2005, FOUQUET et al. 2007, VIEITES et al. 2009).

## Results and discussion

### Taxonomic identity and remarkable records

A complete list of sampled, collected and observed taxa is provided in supporting information S1. Families are sorted according to GLAW & VENCES (2007), while lower taxa (genera, species, and subspecies) are reported in alphabetically order. In total, we identified 61 species and candidate species of amphibians and 45 species of reptiles, giving a total of 106 species. Only a few of these findings were previously known from the above-mentioned localities. In the following, we provide more detailed information on several species records, which are either new records for a locality, or of interest ecologically and/or ethologically. Where DNA barcoding data are available, we furthermore provide some information on the degree of differentiation in the 16S rRNA gene from populations known from other localities, mainly for a number of frog species.

### Pelomedusidae

#### *Pelusios subniger* (LACÉPÈDE, 1788)

We found this species in rice paddies close to the villages of Manompana and Maroantsetra. Morphometric measurements of specimens from Maroantsetra and Manompana are as follows (minimum-maximum values and mean;  $n = 13$ ): Plastron: length 42.0–113.0 mm, mean 90.6 mm; width 27.3–65.5 mm, mean 54.7 mm; carapace: length 48.6–127.7 mm, mean 101.0 mm; width 37.1–87.4 mm, mean 71.7 mm; height: 20.7–55.0 mm, mean 40.9 mm. The colouration of the plastron was rather uniform dark brown while the carapace showed a light yellow colouration.

### Chamaeleonidae

#### *Brookesia superciliaris* (KÜHL, 1820)

This species is widely distributed along the rainforest band of Madagascar's east coast and can be found from lowland to altitudes up to about 1000 m a.s.l., thus occupying one of the largest distribution areas in this genus. This species is one of the largest leaf chameleons with a maximum total length of 120 mm (GLAW & VENCES 2007). Analyses of the 12S rRNA gene in the samples obtained, as reported on in RATSOAVINA et al. (2010), yielded four major clades of *B. superciliaris*, with samples from Ambodiriana in a basal position. Samples from Sahafina formed a well-supported clade and are the sister group of the *B. superciliaris* lineages from Andasibe/Marolambo, and among these localities no haplotype-sharing occurred. Interestingly, a close relationship among *B. superciliaris* from moderate-altitude localities (Andasibe/Marolambo and Ranomafana) was observed, although based on geographic distances, a closer sister group relationship between samples from Andasibe and Sahafina (ca. 70 km distance between localities) was expected a priori.

#### *Calumma cucullatum* (GRAY, 1831)

One female specimen was found in a rainforest fragment close to Marolambo. Being stressed from being captured, it showed a unique yellow body colouration with dark dorsoventral grid-like lines and the specific distinct dark blotch at the insertion of the arms (Fig. 4F).

#### *Calumma* sp. aff. *gallus* "south"

This chameleon was found south of the Mangoro River in secondary vegetation as well as in fragments of primary lowland rainforests. At a first glance, it looks quite similar to *Calumma gallus* from the lowland and moderately elevated areas north of the Mangoro. Nevertheless, it differs in several morphological characters from this species. The rostral appendage of the male is not as elongated as in *Calumma gallus*, and its tip is more or less rounded and not as pointed as in male *Calumma gallus*. Moreover, there are upright spine-like scales on the outer edge of the appendage, so the rostral appendage resembles the blade of a chain saw. These spine-like scales are also present in the smaller rostral appendage of the female. This *Calumma* probably represents a new species and its formal description is in progress.

#### *Calumma* cf. *marojezense* "Ambodivoahangy"

This species represents a form of the *Calumma gastrotaenia* group, which is composed of morphologically similar small, green chameleons from Madagascar's east coast. *Calumma marojezense* (BRYGOO, BLANC & DOMERGUE, 1970) is characterized by a very low casque and the absence of occipital lobes, a rostral appendage and a parietal crest. Its colouration is described as uniformly green with a white lateral line in males, interrupted by two or three small light spots (GLAW & VENCES 2007). The single male specimen we found in the low-altitude forest of Andaparaty-north differed from this colouration by showing a conspicuous pattern of blackish dorsoventral lines and a dark lateral band along the flanks with three white spots within. The venter showed a light-blue colouration with single blue spots that extended to the lateral band. Several blue spots

were present on the hind- and forelimbs and on the throat as well. Two distinct white spots were present on the neck, while occipital lobes, parietal and rostral appendage were absent, and lateral and temporal crests were indistinct. The lack of a dorsal crest in this adult male indicates that it does probably not represent the similar *Calumma vencesi*.

*Calumma* sp. aff. *nasutum* "Vohibola"

This chameleon is quite similar to *Calumma nasutum*, but differs from this species in different aspects. Both sexes have a very low casque without any occipital lobes. Males have a lateral crest of eight distinct spines, and the rostral appendage is quite short. Females lack a lateral crest and the rostral appendage is almost absent. The colouration is bluish-grey with single red and light spots (Fig. 4H). Data of the mitochondrial NADH dehydrogenase subunit 2 and NADH dehydrogenase subunit 4 genes and of the nuclear Phosducine gene showed a distinct differentiation from other *Calumma nasutum* populations. Therefore, this *Calumma* certainly represents a new species and its formal description is in progress. In general, the whole *Calumma nasutum* group contains numerous additional undescribed species and is in need of fundamental taxonomic revision.

*Furcifer willsii* (GÜNTHER, 1890)

This species is known from several moderately elevated rainforests especially in Madagascar's central east (GLAW & VENCES 2007). Generally thought of as an inhabitant of the rainforest canopy, we found a female roosting in a bush 1.5 m above the ground at Vohibola. The littoral forest of Vohibola differs from other reported localities of *Furcifer willsii* mainly in its low canopy height.

**Scincidae**

*Amphiglossus* sp. "phaeurus"

Preliminary data of the mitochondrial NADH dehydrogenase subunit 1 gene confirmed the existence of a genetically somewhat differentiated population of this candidate species (which is probably closely related to, or conspecific with, *A. melanurus*) at Sahafina (A. MIRALLES pers. comm.).

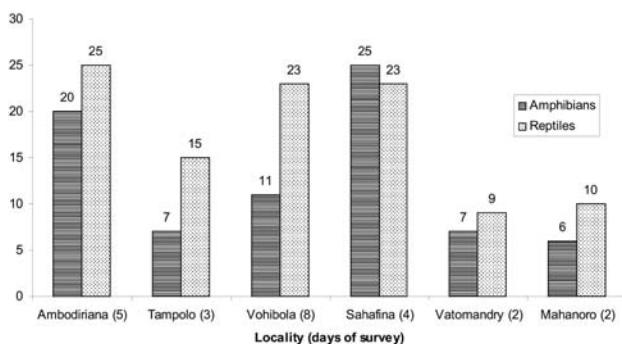


Figure 3. Diagram showing the total numbers of amphibian and reptile species found at each locality. The number of survey days at each locality is given as well.

**Gekkonidae**

*Blaesodactylus antongilensis* (BÖHME & MEIER, 1980)

At daytime, these geckos were found resting in rotten tree trunks that were still standing upright. We could find this species only within primary rainforest habitats. The finding of this species at Sahafina constitutes a significant range expansion towards the south (see distributional information in GLAW & VENCES 2007, SCHÖNECKER 2008).

*Paroedura gracilis* (BOULENGER, 1896)

Within the distribution range of this species, the dorsal blackish pattern varies from vertical crossbands (at Montagne d'Ambre, Marojejy), via an irregular pattern (at Mananara, Antanambe, Ambodiriana), to longitudinal blackish lines (at Sahafina, Andasibe), but polymorphism can occur within populations. The findings of *Paroedura gracilis* at Ambodiriana and Antanambe fill major gaps in the known range of this species.

*Phelsuma guttata* KAUDERN, 1922

Mainly found within primary rainforests of Madagascar's east coast between Sambava in the north and Toamasina in the south (GLAW & VENCES 2007), this species was observed in the low-altitude rainforests of Ambodiriana and Sahafina as well as in the littoral forests of Tampolo and Vohibola. Concerning its ecological preferences, we emphasize that *Phelsuma guttata* was also found outside the primary forest in a cultivated area along the Route National 5 between Rantabe and Fananehana and does not appear to be restricted to primary rainforest habitats. In April of 2009, a gravid female was observed in the Ambodiriana forest. Morphometric measurements of adult specimens from Ambodiriana and Sahafina are as follows (n = 28): TL: 51.8–130.8 mm, mean 107.8 mm; SVL: 29.7–68.0 mm, mean 49.2 mm; TaL: 73.3–22.1 mm, mean 58.2 mm.

*Phelsuma hoeschi* BERGHOF & TRAUTMANN, 2009

This species has so far been known only from its type locality a few kilometres south of Ampasimalotra (Brickaville) and little is known about its ecology (BERGHOF & TRAUTMANN 2009). BERGHOF & TRAUTMANN (2009) describe *Phelsuma hoeschi* as living exclusively on and close to *Atafana* trees (*Terminalia catappa*) directly at the coastline. We collected a male (ZCMV 8938) and a female (ZCMV 8939) 60 km south of Ampasimalotra in a degraded cultivated area near Vatomandry, approximately 3 km from the coast. The animals were observed living in groups of one male and several females on the branches and trunks of larger trees (*Canarium* sp., *Mangifera indica*). Preliminary data on mitochondrial 16S rRNA sequences show that *Phelsuma hoeschi* is deeply nested within the *P. lineata* clade, as sister species of, but not identical to, *Phelsuma kely*, providing some support for its status as a separate species although its differentiation from *P. pusilla hallmanni* needs further study.

*Phelsuma laticauda laticauda* (BOETTGER, 1880)

This species is very abundant in the humid regions of northern Madagascar (Sambirano and the coastal north-east) (GLAW & VENCES 2007). We found it in the village of Andaranokoditra and on palm trees around Lac Ampitabe, which forms part of the Canal des Pangalanes in eastern



Madagascar. PEARSON & RAXWORTHY (2009) report that this species has been introduced to this region of Madagascar and is now expanding its range. The impact of this introduction on the original species assemblage of this region remains unclear. *Phelsuma l. laticauda* was observed living syntopically with *Phelsuma lineata* and *Phelsuma m. madagascariensis*.

*Phelsuma lineata lineata* GRAY, 1842

This species is widely distributed along Madagascar's east coast, also at higher altitudes, and can be found in a variety of habitats, ranging from primary rainforests to villages and houses. Morphometric measurements taken from adult specimens from Mahavelona, Tampolo, Vohibola, Sahafina, Vatmandry, and Mahanoro are as follows (n = 41): TL 62.3–117.1 mm, mean 96.8 mm; SVL 28.8–54.4 mm, mean 45.3 mm; TaL 33.5–64.8 mm, mean 51.5 mm.

*Phelsuma quadriocellata bimaculata* KAUDERN, 1922

KAUDERN (1922) described this taxon - which probably merits recognition as separate species (see ROCHA et al. 2010) - based on specimens from northeastern Madagascar (Fandrarazana). We discovered populations, which we assign to this taxon, north of its type locality in *Ravenala madagascariensis* plants within the intact primary lowland rainforests of Antanambe and Ambodiriana. In the coastal forest of Tampolo (approximately 60 km south of Fandrarazana), we found these geckos mainly on *Typhonodorum lindleyanum* and *Pandanus* sp., and in Andrangazaha (approximately 18 km south of Fandrarazana) in *Pandanus* sp. in heavily degraded vegetation along the beachside. Data of the mitochondrial 16S rRNA gene revealed that the populations from Tampolo are highly differentiated from those of Antanambe, Ambodiriana and Andrangazaha. Compared to specimens from the nearby island of Nosy Boraha, we found only little genetic differentiation.

*Phelsuma serraticauda* MERTENS, 1963

*Phelsuma serraticauda* was found living high up on coconut trees (*Cocos nucifera*) in the village of Manompana and Mananara. Although we found *Phelsuma pusilla pusilla* sympatrically living in coconut trees at Manompana and Mananara, we never saw both species on the same tree. Morphometric measurements of adult specimens from Manompana are as follows (n = 5): TL 88.8–145.5 mm, mean 119.0 mm; SVL 49–65.7 mm, mean 57.4 mm; TaL 39.8–79.8 mm, mean 61.5 mm.

*Uroplatus fimbriatus* (SCHNEIDER, 1797)

GLAW & VENCES (2007) reported a maximum TL of 295.0 mm for females of *Uroplatus fimbriatus*. In the forest of Ambodiriana, we measured a female with a TL of 305.0 mm (SVL 195.0 mm; TaL 110.0 mm). Because of the yellowish iris with reddish-brown stripes around the pupil we referred this specimen to *U. fimbriatus* rather than to the generally larger *Uroplatus giganteus* from the Montagne d'Ambre or *Uroplatus* cf. *giganteus* from Marojejy, although the taxonomic status of these northern populations remains uncertain and *U. giganteus* was tentatively not recognized as a valid species by RAXWORTHY et al. (2008). Morphometric measurements of adult specimens from Ambodiriana and Marolambo are as follows (n = 9):

TL 106.3–305.0 mm, mean 208.6 mm; SVL 71.6–195.0 mm, mean 134.4 mm; TaL 34.7–114.7 mm, mean 74.2 mm.

*Uroplatus lineatus* (DUMÉRIL & BIBRON, 1836)

At Sahafina forest, we found one juvenile and three adult specimens in or close to *Pandanus* plants (Fig. 4E), which constitutes a significant extension of the known range of more than 85 km to the south for this species. Morphometric measurements of the specimens from Sahafina are as follows (n = 4): TL 175.7–260.0 mm, mean 213.2 mm; SVL 109.3–150.0 mm, mean 126.1 mm; TaL 58.6–110.0 mm, mean 87.8 mm.

*Uroplatus sameiti* BÖHME & IBISCH, 1990

This species is closely related to *Uroplatus sikorae*. Morphologically, these taxa can be distinguished by the absence or presence of dark pigment in the lining of the mouth (present in *U. sikorae* and absent in *U. sameiti*). Furthermore, they show a parapatric distribution, with *U. sikorae* apparently being restricted to moderate altitudes whereas *U. sameiti* occupies lowland habitats. There is a possible narrow region of sympatry (RAXWORTHY et al. 2008). We found *U. sameiti* in all primary vegetation types within the surveyed area. This implies that the species is much more widely distributed than suggested by recently published distribution maps in which its range is mainly limited to the island Nosy Boraha off the northeast coast (GLAW & VENCES 2007, SCHÖNECKER 2008). Morphometric measurements of adult specimens from Ambodiriana, Tampolo, Vohibola, and Sahafina (n = 11): TL 68.5–170.3 mm, mean 138.3 mm; SVL 47.7–115.7 mm, mean 92.9 mm; TaL 41.7–59.5 mm, mean 38.1 mm.

**Boidae**

*Acrantophis madagascariensis* (DUMÉRIL & BIBRON, 1844)

In eastern Madagascar, the southernmost distribution record of this species so far was the Tampolo forest (RASELIMANANA et al. 1998). We now recorded *A. madagascariensis* also from the littoral forest of Vohibola, approximately 150 km south of Tampolo.

**Colubridae sensu lato**

*Ithycyphus perineti* DOMERGUE, 1986

In the eastern regions of Madagascar, records of this snake are limited to rainforests at moderate altitudes (e.g., Andasibe, Ranomafana) (GLAW & VENCES 2007). With the record of *I. perineti* from the littoral forest of Vohibola, we add lowland and coastal forests to the habitat range of the species. A further unpublished record (P.-S. GEHRING in 2006) is from the coastal village of Antalaha in northeastern Madagascar. Species identification was confirmed by molecular data of mitochondrial cytochrome *b* sequences (Z. T. NAGY, pers. comm.).

*Langaha madagascariensis* BONNATERRE, 1790

In the littoral forest of Vohibola and Tampolo, we found a male and a female of this species. The find of this species at Vohibola enlarges considerably its known distribution range along Madagascar's central east coast. Species identification was confirmed by molecular data on mitochondrial cytochrome *b* sequences (Z. T. NAGY, pers. comm.).



Figure 4. Some of the remarkable amphibians and reptiles found during the survey. (A) *Boophis englaenderi* from the Ambodiriana forest; (B) *Boophis axelmeyeri* from Andaparaty; (C) Juvenile of *Boophis roseipalmatus* from Antanambe (ZCMV 8408); (D) *Mantidactylus majori* from the Sahafina forest (ZCMV 8927); (E) *Uroplatus lineatus* from Sahafina; (F) *Calumma cucullatum* from Marolambo; (G) *Lycodryas gaimardi* from the Tampolo forest; (H) *Calumma* sp. aff. *nasutum* from the Vohibola forest (ZCMV 8915).

*Liophidium rhodogaster* SCHLEGEL, 1837

This species has so far been recorded from rainforests at moderate altitudes in central and southern Madagascar and from forests in Madagascar's far north, such as Marojejy and the Montagne d'Ambre (GLAW & VENCES 2007). A single specimen was observed at daytime foraging on the forest floor in the lowland rainforest at Antanambe. This record fills a major gap in the known range of this snake. Species identification was confirmed by molecular data on mitochondrial cytochrome *b* sequences (Z. T. NAGY, pers. comm.).

*Lycodyras gaimardi* (SCHLEGEL, 1837)

In the littoral forest of Tampolo, an adult specimen was spotted foraging at night in a *Pandanus* sp. at a height of 2 m above the ground (Fig. 4G). To our knowledge, this species has been unknown from littoral forests so far, although it occurs in coastal localities (Maroantsetra, Toamasina). A juvenile specimen tentatively assigned to this species was found at night in Sahafina.

**Typhlopidae***Ramphotyphlops braminus* DAUDIN, 1803

Specimens tentatively assigned to this species of worm snake were found under a rotten tree trunk in a cultivated area close to Rantabe (Bay of Antongil), and in Andoharina, on the southern banks of the Mangoro River in the central east.

**Ptychadenidae and Hyperoliidae**

These two anuran families were represented in our sampling by the three species to be expected in the lowlands of central eastern Madagascar: *Ptychadena mascareniensis*, *Heterixalus madagascariensis* and *H. alboguttatus*.

**Microhylidae***Anodonthyla boulengeri* MÜLLER, 1892 (new UCS)

Specimens of *Anodonthyla* were commonly encountered in many of the surveyed sites. Based on molecular results, there were high mitochondrial divergences between sites (but divergent haplotypes were never found at the same locality). All sequences clustered with *A. boulengeri* as defined by VENCES et al. (2010a), a species that was known to have significant intraspecific genetic variability. Specimens from Ambodiriana were genetically very similar to a previously sequenced specimen (ZSM 264/2002) from Foulpointe, whereas specimens from Vohibola (Fig. 5J) and Sahafina formed two previously unknown deep conspecific lineages within *A. boulengeri*, respectively.

*Platypelis* cf. *tetra*

By its colouration and morphology, one specimen from Ambodiriana largely agreed with *P. tetra*, especially by its characteristic two pairs of larger tubercles on the lower back, of which the upper pair was of white colour, and a distinct dark band along the anterior flanks. Based on molecular results, the *P.* cf. *tetra* from Ambodiriana showed a 90% molecular similarity in the 16S gene to *P. grandis* from Andohahela, a 89% similarity to *P.* cf. *cowanii* from Betampona, and a 88% similarity to *P.* sp. 2 (VIEITES et al. 2009) from Betampona. Unfortunately, no sequence data for *P.*

*tetra* were available to us. *Platypelis tetra* has so far been thought to be endemic to northeastern Madagascar, where it has been recorded from the Anjanaharibe-Sud Massif and the Masoala Peninsula. If the specimen from Ambodiriana were confirmed to represent *P. tetra*, it would significantly enlarge its known distribution range.

**Mantellidae***Aglyptodactylus* sp. aff. *madagascariensis* "East" (*A.* sp. 2)

The DNA sequence of a specimen from Ambodivoahangy was 100% identical to that of specimens from Maroantsetra, which have been assigned to the CCS *A.* sp. 2 by VIEITES et al. (2009).

*Blommersia* sp. aff. *blommersae* "Nosy Boraha" (*B.* sp. 3), *B.* sp. (new UCS)

The situation of *Blommersia* populations along the central and northern east coast of Madagascar is complex and requires a thorough taxonomic revision that currently is in progress (VENCES et al. 2010b). We had previously identified three CCS, named *B.* sp. aff. *blommersae* "Nosy Boraha", "Maroantsetra", and "Toamasina" (GLAW & VENCES 2007), or *B.* sp. 1, 2, and 3 (VIEITES et al. 2009), respectively. All of these also differ in advertisement calls and details of morphology, and two (*B.* sp. 1 and 3) occur syntopically on Nosy Boraha (GLAW & VENCES 2007). Our data represent new records of *Blommersia* sp. 1, previously only known from Nosy Boraha, from Tampolo, and probably also from Vatomaniry. While the Tampolo specimen sequenced was genetically very similar to those from Nosy Boraha, those from Vatomaniry showed a substantial genetic differentiation and might be considered as a distinct UCS: *Blommersia* sp. [Ca12 HM631877]. The status of this population requires further study.

*Boophis axelmeyeri* VENCES, ANDREONE & VIEITES, 2005

One specimen from Andaparaty was identified by DNA barcoding as representing *B. axelmeyeri*, a species described from the Tsaratanàna and Manongarivo massifs and also known (as a genetically divergent population) from Marojejy, and from a DNA sequence from Masoala (Ilampy). The Andaparaty sequence clusters with the Marojejy and Ilampy sequences, but is divergent from these. The eye colouration of the specimen from Andaparaty is similar to that found in the Marojejy populations (Fig. 4B), with dark brown in the outer iris, as described in GLAW & VENCES (2007). In the IUCN red list of threatened species, this species is listed as Vulnerable because its three certain locations (Marojejy, Manongarivo and Tsaratanàna) are thought to have an expansion of less than 20,000 km<sup>2</sup> (IUCN 2009). This newly discovered deep conspecific lineage thus represents a substantial extension of the known range of more than 100 km to the south for this species.

*Boophis englaenderi* GLAW & VENCES, 1994

Green-coloured species of the *Boophis luteus* group appear to be rather rare at low altitudes along the east coast according to available distribution data (GLAW & VENCES 2007). We collected one specimen at Ambodiriana (Fig. 4A), which showed a 98% molecular similarity in the 16S gene to *Boophis englaenderi* from Marojejy, and a 99%

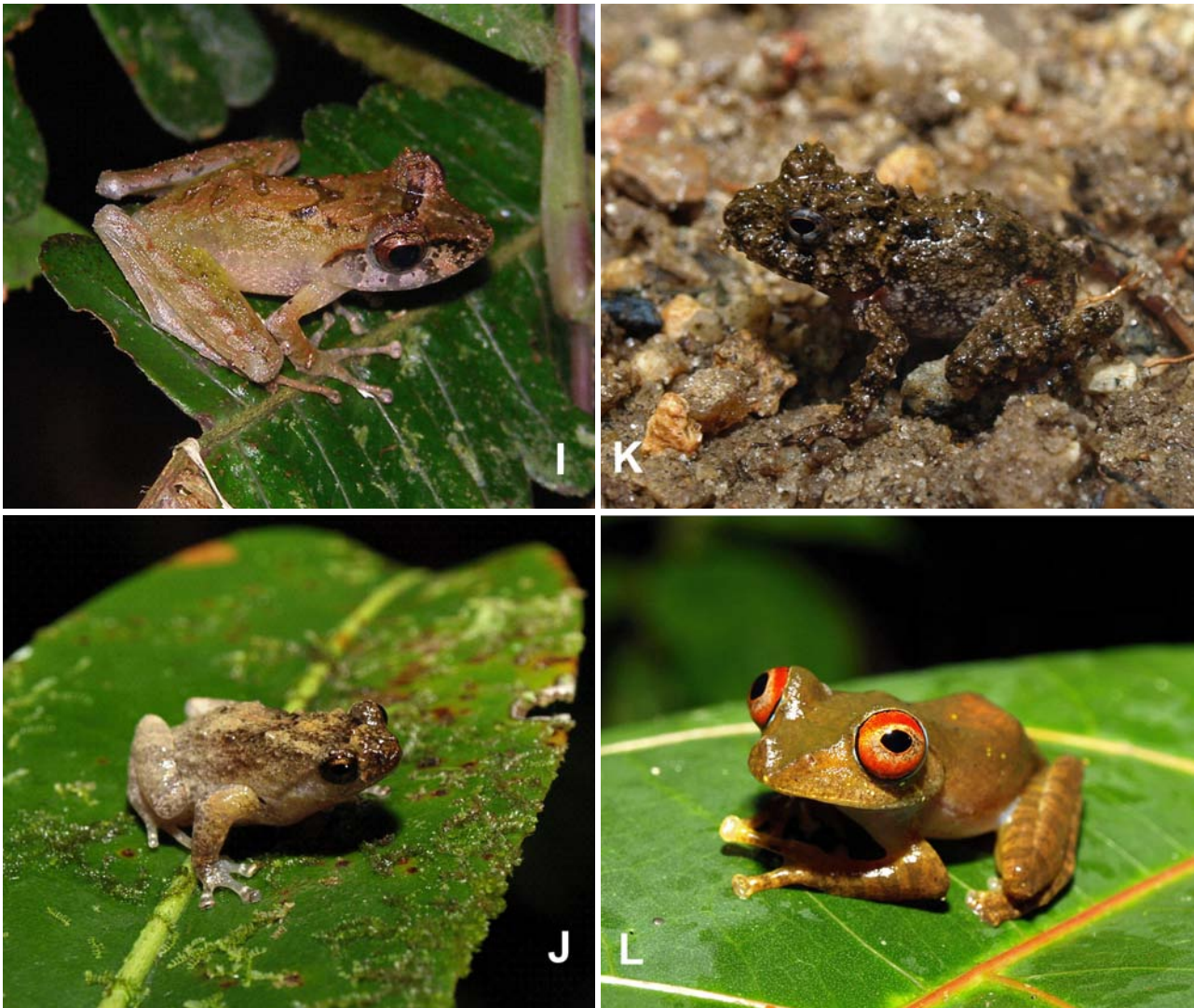


Figure 5. Some of the remarkable amphibian species from eastern forest areas encountered during the present survey: (I) *Gephyromantis* sp. aff. *moseri* (G. sp. 18) from Andaparaty; (J); *Anodonthyla boulengeri* from Vohibola; (K) *Gephyromantis malagasius* from Ambodiriana; (L) *Boophis* sp. aff. *boehmei* from Sahafina.

similarity to samples from Masoala that have also been assigned to this species. By its colouration, the specimen largely agreed with *B. englaenderi* as well, especially with regard to its rather inconspicuous beige iris colour with some reddish tint, but without the clear pattern of red rings or lines of other species (*B. anjanaharibeensis*, *B. elenae*, *B. luteus*), and the lack of light dorsolateral lines (as is typical for *B. andohahela* and *B. septentrionalis*). This record is an important southwards extension of more than 120 km to the known distribution area of this species and adds one more example for a biogeographic connection of low-altitude species between Marojejy in the northeast and the northern central east coast.

*Boophis pyrrhus* GLAW, VENCES, ANDREONE & VALLAN, 2001

A specimen from Marolambo was clearly assignable to this species by its DNA sequences, but showed some molecular divergence from the Andasibe and Ifanadiana populations that were available for comparison.

*Boophis roseipalmatus* GLAW, KÖHLER, DE LA RIVA, VIETES & VENCES, 2010

Several specimens from Antanambe and Ambodiriana were identified in the field as *Boophis roseipalmatus*, a recently described species that has previously been named *Boophis* sp. aff. *madagascariensis* “North” by GLAW & VENCES (2007), or *Boophis* sp. 12 by VIETES et al. (2009), and its molecular data confirmed this identification. In fact, no substitutions were detected in comparisons to sequences assigned to this species from Masoala (Ilampy), which so far was its southernmost record. Our record considerably extends the known distribution area of this species. The specimens from Antanambe and Ambodiriana show the same colouration, being rather uniform light brown dorsally and light pink ventrally. The webbings between fingers and toes are conspicuously pink. In Antanambe, a recently metamorphosed juvenile was found along a small brook in a clearing in primary forest. This juvenile showed a distinctive colouration with a greatly contrasting silver-grey pattern on a dark background (Fig. 4C).

*Boophis* sp. aff. *boehmei* (new UCS)

Specimens from Sahafina, referable by their morphology to *B. boehmei*, were genetically substantially divergent from that species and therefore qualify as a new UCS as well: *Boophis boehmei* [Ca43 HM631885] (Fig. 5L). However, compared to the very strongly divergent sibling species *Boophis* sp. 16 from Ranomafana (see VIEITES et al. 2009), the 16S sequences of the Sahafina specimens (PSG 313, 417, and 418) lacked a characteristic insertion of seven base pairs that is derived for that species, and in preliminary phylogenetic analyses, they clustered with specimens from the geographically closer type locality Andasibe rather than with *B.* sp. 16 from Ranomafana.

*Boophis* sp. aff. *arcanus* (new UCS)

A series of samples of small *Boophis* specimens collected at Marolambo (PSG 1515–1518) was genetically closest to the recently described *B. arcanus* (see GLAW et al. 2010), but had a divergence of 7% in the short 16S fragment compared (231 bp). However, the samples were only slightly more divergent from *B. miniatus*. We flag this population as a new unconfirmed candidate species that requires further study: *Boophis arcanus* [Ca44 HM631879]. Unfortunately, no calls from this UCS are available for direct comparison with *B. miniatus*. In addition, because the specimens observed were males, comparison with *B. arcanus* is hampered by the fact that this species so far is only known from two females.

*Gephyromantis* sp. aff. *boulengeri* (*G.* sp. 24, *G.* sp. 25)

Species of the subgenus *Gephyromantis* (in the genus *Gephyromantis*) are known to exhibit a high degree of microendemism, and those species that are still considered to be widespread (e.g., *G. boulengeri*) are known to contain many deep conspecific lineages. In the course of the present survey we confirmed the presence of *G.* sp. 24 at Sahafina; a UCS similar to *G. boulengeri* but of high genetic divergence, previously known only from the Andasibe region (VIEITES et al. 2009). The Sahafina DNA sequences were very similar to those from the Andasibe area (Torotorofotsy). We furthermore recorded at Sahafina and at Ankanin'ny Nofy (close to Vohibola) specimens identified by DNA barcoding as *G.* sp. 25, a species previously known only from Mahaso forest at the northeastern edge of Lake Alaotra. This species has an advertisement call structure that is strongly divergent from that of *G. boulengeri* and *G.* sp. 24, and it is therefore not unlikely that *G.* sp. 24 and 25 may occur syntopically, as indicated by our data from Sahafina. Unfortunately, we have no call recordings from the new sites to confirm the bioacoustic divergence of *G.* sp. 25. At the Marolambo sites surveyed here, yet another *Gephyromantis* of this complex was recorded. It showed the greatest genetic affinities to populations from the Ranomafana area, which are considered to be a deep conspecific lineage of *G. boulengeri* by VIEITES et al. (2009). Clearly, the taxonomic status of these populations of the *G. boulengeri* complex from the southern central east is also in need of revision. One female from Sahafina contained mature oocytes, indicating that the species reproduces at this time of the year.

*Gephyromantis luteus* (METHUEN & HEWITT, 1913)

Sequences of this widespread eastern species from Ambodiriana, Andaparaty, and Sahafina clustered among se-

quences of *G. luteus* and *G. sculpturatus* from other localities. A taxonomic revision of the *G. luteus/sculpturatus* complex is necessary to re-assess the validity of *G. sculpturatus* as a separate species.

*Gephyromantis malagasius* (METHUEN & HEWITT, 1913)

At Antanambe and Ambodiriana (Fig. 5K), we recorded specimens assigned to this species that were genetically very similar to each other. They clustered with sequences from Ambohitsara in the southern central east despite their significant genetic divergence from those, confirming that *G. malagasius* is rather widespread along the east coast. This species was originally described from Fohohy, a locality not far from our sites. Our records therefore probably represent indeed *G. malagasius* and not one of the several morphologically similar candidate species in the genus.

*Gephyromantis* sp. aff. *moseri* (*G.* sp. 18)

One specimen from Andaparaty (Fig. 5I) clustered with a sequence of the UCS *G.* sp. 18 from Ambolokopatrika, within a cluster of sequences that only comprises the nominal species *G. moseri*. A taxonomic revision of this complex is needed.

*Gephyromantis redimitus* (BOULENGER, 1889)

Molecular data confirmed the identity of one specimen from Andaparaty.

*Gephyromantis silvanus* (VENCES, GLAW & ANDREONE, 1997)

Several specimens of this forest-dwelling frog were found in cavities between boulders close to small brooks in the primary rainforest at Ambodiriana. This species is listed in the IUCN red list of threatened species as Endangered, because its known distribution is limited to the northern part of the bay of Antongil (IUCN 2009). The detection of *G. silvanus* at Ambodiriana (ca. 150 km south of Maroantsetra) represents a significant extension of the known range to the south, and it may be assumed that several populations exist in the area between these localities.

*Gephyromantis webbi* (GRANDISON, 1953)

Our data confirm the existence of a genetically somewhat differentiated population of *G. webbi* at Antanambe. The records for this species are limited to some lowland localities around the Bay of Antongil and the island of Nosy Mangabe in northeastern Madagascar. Therefore, this species is listed as Endangered in the IUCN red list of threatened species (IUCN 2009). The detection of *G. webbi* at Ambodiriana represents a significant extension of the known range for this species to the south.

*Guibemantis bicalcaratus* (BOETTGER, 1913), *Guibemantis* sp. (new UCS)

Besides confirmed records of *Guibemantis liber* from Ambodiriana, Vohibola, Sahafina, Vatomandry, and Tampolo that were sequenced in the framework of a phylogeographic analysis of that species, our data confirm the presence of at least two different species of *Pandanus*-dwelling species of *Guibemantis* in the surveyed localities. A specimen from Vohibola (PSG-242) was genetically very close to speci-

mens from Nosy Boraha, the type locality of *G. bicalcaratus*, and therefore probably correspond to that species. Two specimens from Maroantsetra, on the other hand, were highly divergent from all known *Guibemantis* and therefore represent a new UCS (PSG-29, PSG-31): *Guibemantis bicalcaratus* [Ca21 HM631910].

*Mantidactylus* sp. aff. *betsileanus* (*M. sp. 25*, *M. sp. 34*, *M. sp. 36*)

Our molecular data confirm that we recorded three species, all of which are probably morphologically close to *M. betsileanus*. From Vatoman-dry, Sahafina and Tampolo, we recorded a CCS referred to as *Mantidactylus* sp. 36 by VIEITES et al. (2009), and as *M. sp. aff. betsileanus* “Toamasina” by GLAW & VENCES (2007). From Antanambe and Ambodiriana we recorded *M. sp. 25*, a UCS previously only known from a sequence from another east coast locality (Ampasimazava). Furthermore, from Sahafina and Mahanoro, we recorded the UCS *M. sp. 34*, previously only known from Vohidrazana.

*Mantidactylus* sp. aff. *betsileanus* “slow calls”

This species was found in Marolambo and indicates affinities of the herpetofauna of this locality with moderate-altitude sites. It is common at somewhat higher altitudes and known from around 900–1000 m a.s.l. in the Ranomafana National Park and the Andasibe region.

*Mantidactylus* sp. aff. *charlotteae* (*M. sp. 10*)

Populations similar by external morphology to *M. charlotteae* are genetically highly divergent and have been assigned to different candidate species. Our sequences from Ambodiriana are again strongly divergent but cluster with the UCS *M. sp. 10*. It might be hypothesized that *M. sp. 10* in fact represents the ‘true’ *M. charlotteae* which was described from Foulpointe, a site 100 km south of Ambodiriana, and from which no molecular data are so far available.

*Mantidactylus femoralis* (BOULENGER, 1882)

Our record of *M. femoralis* in Marolambo underscores the affinities of the herpetofauna of this locality with moderate-altitude sites, as in the case of *Mantidactylus* sp. aff. *betsileanus* “slow calls”.

*Mantidactylus majori* BOULENGER, 1896

Sequences of three *Mantidactylus* specimens from Sahafina clustered with high support with those of *M. majori* and therefore would constitute the first reliable record of this species from a locality north of the Mangoro River (Fig. 4D). The molecular differences to specimens from southern localities are substantial, but their comparison is complicated by the presence of a highly repetitive stretch of DNA (probably suggestive of a very high rate of molecular change) in some of the comparative sequences. To assess the status of the Sahafina population, it will be necessary to obtain molecular data from a different gene, and to study the morphology of adults and tadpoles.

*Mantidactylus mocquardi* ANGEL, 1929

Our data confirm the presence of this species at Sahafina. Sequences were 100% identical to those from Andasibe. This species is well defined by its often silvery belly (GLAW

& VENCES 2004) and tadpole morphology (R. D. RANDRIANAINA, unpubl. data).

*Mantidactylus opiparis* (PERACCA, 1893)

Molecular data confirm the occurrence of this species at Sahafina. The DNA sequence from this site is most similar to that from a specimen collected at Andasibe.

*Spinomantis aglavei* (METHUEN & HEWITT, 1913)

Molecular data confirm that the specimen of *Spinomantis* collected at Sahafina is conspecific (although genetically divergent) with specimens in the southern central east (Ranomafana region) that we have previously allocated to *S. aglavei* (e.g., GLAW & VENCES 2007), and that *S. aglavei* is therefore a widespread species at mainly lower altitudes along the east coast.

#### Sampling bias and seasonal effects

The setting of pitfall trapping systems in other rainforest sites in northeastern Madagascar yielded at average three to nine species of Scincidae and typically at least one species of Typhlopidae (e.g., RAXWORTHY et al. 1998, ANDREONE & LUISELLI 2000). In this study, we recorded only three different species of Scincidae and one specimen of Typhlopidae. Because of the limited time available at each study site, no pitfall trapping system was used. Thus, all our specimens were exclusively found by opportunistically searching in suitable habitats and refuges under dead roots and trunks. In the eastern humid forests of Madagascar, pitfall trapping is not particularly important for obtaining information on the presence of anurans, whereas this trapping system is quite productive for reptiles, especially for some skinks and snakes (ANDREONE et al. 2000, 2009). The use of pitfall traps during a herpetological survey in Ambolokopatrika yielded four different species of fossorial reptiles (of Scincidae and Typhlopidae), which accounted for 17% of all reptile species recorded (ANDREONE et al. 2000). Another survey using pitfall trapping systems in Anjanaharibe-Sud yielded ten species of fossorial reptiles (Scincidae and Typhlopidae), which made up 25% of all the reptile species found (RAXWORTHY et al. 1998). Not using pitfalls in this study may explain the relatively low proportion of ground-dwelling or fossorial reptiles recorded (Ambodiriana: 1 species (4%); Sahafina: 2 species (8.7%); Vatoman-dry: 1 species (11%); Mahanoro: 1 species (20%)), since the sandy soils of the littoral forests appear to be particularly favourable habitats for such fossorial species. Furthermore, the fieldwork was probably biased towards arboreal reptiles (e.g., *Uroplatus* spp., *Phelsuma* spp., *Calumma* spp.), because these were the focal genera of the PhD projects of the second and first authors of the present study.

Owing to the short study periods spent at each site and the lack of comparable data on the herpetofauna of most of the localities, it is difficult to make reliable statements on the absolute species diversity of amphibians and reptiles at the visited localities. Species accumulation curves from other surveys in Madagascar’s eastern forests show that the peak of species records is mostly reached after seven to eight days, and there will be no or only a minor increase in species numbers that after this vertex (RAXWOR-

THY et al. 1998, ANDREONE et al. 2000, 2009, BORA et al. 2007, RAMANAMANJATO 2007). On average, we stayed four days (min. 2 to max. 8 days; Fig. 3) at each site. We therefore assume that longer survey periods would have yielded a more realistic picture of herpetofaunal diversity, especially at the species-rich primary forest sites.

For the visited localities, comparable data for other seasons are lacking. Therefore, we largely ignore if and how the diversity and abundances of amphibians and reptiles are seasonally variable. However, seasonality in the herpetofauna of Madagascar's eastern rainforests is thought to be low at low altitudes (RAXWORTHY 1988, ANDREONE et al. 2000), indicating that our observations are unlikely to have been strongly biased by such effects.

#### Comparisons with literature data

In the literature, an additional thirteen species of amphibians and eight species of reptiles have been reported for the littoral forest of Vohibola. These are *Blommersia grandisonae*, *B. cf. grandisonae*, *Boophis idae*\*, *B. mandraka*\*, *Heterixalus punctatus*\*, *Gephyromantis cf. eiselti*\*, *G. luteus*, *Guibemantis tornieri*\*, *Platypelis tuberifera*, *P. grandis*\*, *P. tetra*\*, *Ptychadena mascareniensis* and *Stumpffia* sp. (RANDRIANIRINA et al. 2005) as far as amphibians are concerned, and the reptiles *Dromicodryas bernieri*, *Furcifer lateralis*, *Madascincus cf. melanopleura*, *Phelsuma pusilla*\*, *Pseudoxyrhopus heterurus*, *Thamnosophis stumpffi*, *Trachylepis* sp., and *Zonosaurus aeneus*\* (J. E. RANDRIANIRINA et al. unpubl.). Some of these records (marked with asterisks above) are at least doubtful and might be based on misidentifications, and are therefore here excluded from further discussion. Together with our records, this adds up to a total number of 16 species of amphibians and 29 species of reptiles recorded at Vohibola.

For the Ambodiriana forest, a further seven species of amphibians have been reported: *Boophis* sp. aff. *albilabris*, *Boophis tephraeomystax*, *Mantella nigricans*, *Mantella pulchra*, *Mantidactylus* sp. aff. *biporus*, *Spinomantis aglavei*, *Stumpffia* cf. *grandis*. Photographs of these species were provided by S. BEAUCENT and M. FAYOLLE who have assembled a comprehensive inventory of amphibians and reptiles at Ambodiriana, and these species records are therefore quite reliable. We assume that their *Boophis* sp. aff. *albilabris* refers to the recently described *B. praedictus* (GLAW et al. 2010). Two reptile species have already been reported for Ambodiriana, but were not found by us. These are *Phisalexella arctifasciata* and *Calumma parsonii parsonii*, two elusive arboreal species (RABEARIVONY 2002, RABEARIVONY et al. 2007). In summary, this gives a total number of 20 species of amphibians and 27 species of reptiles that have by now been recorded from the Ambodiriana forest.

For Tampolo, a comprehensive survey of the herpetofauna was carried out by RASELIMANANA et al. (1998) and RASELIMANANA (2005), with 14 species of amphibians and 24 species of reptiles reported from this littoral forest. Most of our findings in Tampolo corroborate those of RASELIMANANA (2005), but for the amphibians, we add *Blommersia* sp. aff. *blommersae* "Nosy Boraha", *Gephyromantis boulengeri*, *Mantidactylus* sp. aff. *betsileanus* (*M.* sp. 36) and *M.* sp. aff. *femoralis*. As far as reptiles are concerned,

we add the snake *Lycodryas gaimardi*, an elusive arboreal species. This increases the total numbers to 18 amphibian and 25 reptile species recorded from Tampolo.

To our knowledge, there are no data published or otherwise available for the remaining localities. In the following, we base our analyses and discussion on our own records only, to ensure comparability among data.

#### Comparisons among primary forest types and diversity patterns

To assess the differences between species communities among localities, we estimated  $\beta$ -diversity as a measure that compares species diversity among habitat types and sites. This involves comparing the number of taxa that are unique to each of the species communities by calculating SØRENSEN'S similarity index (SØRENSEN 1948). The SØRENSEN index ( $G_s$ ) is a very simple measure of beta-diversity, ranging from a value of 0, where there is no species overlap between the communities, to a value of 1 when exactly the same species are found in both communities.

In general, there was considerable variation in the amphibian species composition of the three main habitat types (littoral forests, low-altitude rainforest and secondary forest formations). Comparing the amphibian communities among all habitat types, we generally arrived at low similarity values between the different localities ( $G_{\max} = 0.46$ ;  $G_{\min} = 0.22$ ;  $G_{\text{mean}} = 0.32$ ). The highest degree of similarity in amphibian species was found between Tampolo and Mahanoro ( $G_s = 0.46$ ), whereas the lowest existed between Ambodiriana and Vatomandry ( $G_s = 0.22$ ). The  $G_{\max}$  value for amphibians is relatively high in contrast to the other values found (Tab. 3). This is explained by the fact that these localities share a high number of relatively widespread species and that the absolute species numbers for the localities with secondary habitats like Mahanoro and Vatomandry are quite low. The low extent of similarity in amphibian communities probably indicates a high species turnover of amphibians along the east coast with habitat and/or latitude, and probably can at least partly be explained by the existence of highly microendemic species. Another factor influencing differences in communities might be the fragmentation of forest habitats, considering that fragment size, edge effects, and species diversity are closely correlated (e.g., LEHTINEN et al. 2003, GLOS et al. 2008b).

Among reptile communities, we generally arrived at higher similarity values ( $G_{\text{smax}} = 0.58$ ;  $G_{\text{smin}} = 0.22$ ;  $G_{\text{smean}} = 0.4$ ) as compared to amphibians. The highest degree of similarity between species communities was found between the low-altitude rainforests of Sahafina and Ambodiriana ( $G_s = 0.58$ ) and the lowest between Ambodiriana and the secondary habitats around Mahanoro ( $G_s = 0.22$ ), which represent the most distant localities on a latitudinal scale.

The highest herpetofaunal richness in absolute numbers was found in Ambodiriana and Sahafina. Next, the forests of Tampolo and Vohibola held an intermediate species richness, and values were lowest in the anthropogenic secondary forest formations of Vatomandry and Mahanoro (Fig. 3). This distribution of species richness agrees with habitat classification at these sites: (1) littoral forests (LF;

Table 3. Sørensen's similarity index values ( $G_j$ ) between amphibian (below the diagonal in italics) and reptile communities (above the diagonal in plain font). Abbreviations for localities: Amb – Ambodiriana; Tam – Tampolo; Voh – Vohibola; Sah – Sahafina; Vat – Vatomandry; Mah – Mahanoro.

	Amb	Tam	Voh	Sah	Vat	Mah
Amb		0.55	0.41	0.58	0.29	0.22
Tam	<i>0.30</i>		0.47	0.57	0.33	0.24
Voh	<i>0.26</i>	<i>0.33</i>		0.43	0.25	0.42
Sah	<i>0.26</i>	<i>0.31</i>	<i>0.33</i>		0.37	0.42
Vat	<i>0.22</i>	<i>0.43</i>	<i>0.44</i>	<i>0.25</i>		0.52
Mah	<i>0.23</i>	<i>0.46</i>	<i>0.35</i>	<i>0.26</i>	<i>0.31</i>	

Tampolo and Vohibola); (2) lowland rainforest (LEF; Ambodiriana and Sahafina); (3) cultivated areas (CA; Vatomandry and Mahanoro). Littoral forest remnants still harbour a high species richness especially of plants, with several genera being endemic to this habitat (DE GOUVENAIN & SILANDER 2003, BOLLEN & DONATI 2005). FISHER & GIRMAN (2000) identified littoral forests as one of four major areas for ant endemism in Madagascar. However, previous studies that compared the vertebrate communities of littoral forests with those of nearby dense humid lowland evergreen forests found littoral forests less species-rich, and none of the vertebrate species observed in southeastern littoral forests was endemic to that forest type (GANZHORN et al. 2000, GOODMAN & RAMANAMANJATO 2007). Our data on the amphibian and reptile communities of Vohibola and Tampolo are largely in agreement with these findings. None of the species found either in Vohibola or Tampolo is endemic to this habitat type. However, we cannot exclude that some unconfirmed candidate species or deep conspecific lineages of amphibians might turn out to be littoral forest endemics. For example, our molecular data for *Anodonthyla boulengeri* from Vohibola show that these represent a previously unknown DCL.

In general, we found a higher richness in reptile (27) than amphibian species (14) within the littoral forests, whereas the amphibian species community in littoral forests was conspicuously poorer than those from primary lowland rainforests (14 species LF vs. 38 species LEF). Moreover, at a first glance, species composition seems to be contradicting, because on the one hand representatives of some typical rainforest frog genera of cophyline microhylids (e.g., *Plethodontohyla notosticta*, *Stumpffia* spp., *Platypelis tuberifera* (RASELIMANANA 2005), *Anodonthyla boulengeri*) and mantelline mantellids (e.g., *Gephyromantis boulengeri*, *Gephyromantis malagasius*, *Mantidactylus* cf. *betsileanus*) occur in littoral forests, while other species-rich rainforest genera and subgenera (e.g., *Boophis*, *Spinomantis*, *Vatomantis*) are largely absent in this habitat. Analyses of amphibian species communities in southeastern Madagascar show a similar pattern, which so far has remained unexplored (RAMANAMANJATO 2007). One explanation might be that many of the missing taxa specialize in reproducing in lotic habitats (VENCES et al. 2002, GLAW & VENCES 2007). The flat topology of the coastal lowland results in an absence of fast-flowing streams in the littoral forests of Vohibola and Tampolo. Therefore, the presence

of *Boophis mandraka* or related species of the *B. mandraka* group, all of which appear to have tadpoles adapted to fast-flowing rocky streams, is improbable at Vohibola. On the other hand, *Boophis tephraeomystax* and *Boophis opisthodon* are members of the subgenus *Sahona*, which comprises pond-breeding frogs only. As a consequence, these species were commonly found close to the Canal des Pangalanes in Vohibola, in the leaf axils of *Ravenala madagascariensis* or *Pandanus* sp. (see Fig. 2). In conclusion, all amphibians found at littoral forest sites are either pond-breeders (or breed in very slow-moving waters), reproduce in phytotelmata (*Platypelis tuberifera*, *Plethodontohyla notosticta*, *Anodonthyla boulengeri*, several species of *Guibemantis*), or are nidicolous breeders with nests on the ground or in the leaf litter (*Stumpffia* spp., *Gephyromantis boulengeri*).

Comparing the reptile communities of primary lowland rainforests and littoral forests, no such clear ecological pattern is obvious, although species composition appears to differ in several aspects between the two habitat types. In littoral forests, the reptile species community seems to be a mixture of typical forest-dwelling species (e.g., *Uroplatus sameiti*, *Phelsuma guttata*, *Furcifer willsii*, *Lycodryas gaimardi*) and species predominantly found in more open areas like forest edges, clearings and secondary habitats (e.g., *Zonosaurus madagascariensis*, *Calumma* cf. *nasutum*, *Furcifer pardalis*, *Phelsuma quadriocellata bimaculata*). An explanation of this observation could be that due to the rather low canopy height and less dense growth of the littoral forests, many sun-exposed spots exist within the forest and therefore solar irradiation is higher on average than inside the primary lowland rainforest. Some other considerations are also possible explanations for the absence of some widely distributed reptile species in littoral forests. Especially for large-bodied species, like *Uroplatus fimbriatus* or *Calumma* spp., the absence of tall trees may be a relevant factor, as these are the preferred resting and foraging habitats for these species. Moreover, the higher and denser canopy in lowland rainforests ensures more stable thermal and hygrometric conditions, which might be relevant for smaller species like the chameleons of the *Calumma gastrotaenia* complex that also appear to be absent from littoral forests.

#### Comparisons with other areas of eastern Madagascar and biogeographical considerations

In general, our findings are in accordance with expected biogeographical patterns and confirm previous results from nearby lowland rainforest localities at Marojejy, Anjanaharibe-Sud and Tsaratanàna in the northeast (ANDREONE et al. 2009, ANDREONE et al. 2005, RAXWORTHY et al. 1998) and Zahamena in the northern central east (RABIBISOA et al. 2005). The herpetofaunas of the more northern localities visited during our survey (Andaparaty, Antanambe and Ambodiriana) showed some expected and some surprising affinities to the northeastern region (e.g., *Boophis axelmeyeri*, *B. roseipalmatus*, *B. englaenderi*, *Gephyromantis* sp. aff. *moseri*, *Aglyptodactylus* sp. aff. *madagascariensis* "East", *Calumma* cf. *marojezense*, *Phelsuma pusilla*). Several amphibian and reptile species show a distinct distribution, encompassing lowland localities in the northeast



and ranging southwards along the coast into the northern central east where they reach their distribution limits. This applies both to species restricted to rather undisturbed primary rainforest such as *Paroedura gracilis*, *Phelsuma guttata*, *Lycodryas gaimardi*, *Mantella laevigata*, *Boophis axelmeyeri*, *B. englaenderi*, and more generalist species such as *Furcifer pardalis* and *Heterixalus madagascariensis*. In addition, some lowland species appear to be endemic to the northern central east, i.e., the coastal area roughly between Maroantsetra and the Mangoro River (with their southern range limits usually lying well north of the river) and apparently not reaching northwards far into the northeast, such as *Gephyromantis webbi*, *G. silvanus*, *Zonosaurus brygooi*, and *Blaesodactylus antongilensis*.

For most of the species that depend on primary forests and have such distribution patterns, it is hard to determine their southern distribution limits, because a very high proportion of the primary vegetation in the lowland areas of the northern central east of Madagascar has been cleared. However, several studies emphasize the role of the major rivers at Madagascar's east coast as barriers of dispersal for different animal groups such as reptiles (BOUMANS et al. 2007, PEARSON & RAXWORTHY 2009), lemurs (GOODMANN & GANZHORN 2004, PASTORINI et al. 2003), and beetles (WIRTA 2009). The Mangoro River may act as such a biogeographical barrier for several exclusively lowland-dwelling amphibian and reptile species, with sister species existing on either side of the river (PEARSON & RAXWORTHY 2009, BOUMANS et al. 2007). This is especially obvious for the hyperoliids *Heterixalus madagascariensis* and *H. alboguttatus* and the chameleons *Calumma gallus* and *C. sp. aff. gallus*, which were found either on the northern banks (*H. madagascariensis*, *C. gallus*), or only on the southern banks of the Mangoro (*H. alboguttatus*, *C. sp. aff. gallus*). Interestingly, for several other species, it seems that the Mangoro does not act as a barrier for dispersal and gene flow, given that we confirmed for them a wide range across the river and only a low genetic differentiation among the haplotypes on either river side (e.g., *Mantidactylus majori*, *Spinomantis aglavei*, *Brookesia superciliaris* (RATSOAVINA et al. 2010). It might be relevant, however, that these species are widespread at moderate altitudes as well, which could indicate that dispersal may have taken place closer to the headwaters where the river is narrower and its barrier effect thus less effective (see VENCES et al. 2009).

The herpetofaunas recorded at the Marolambo sites (altitude within the area ranges from about 600 to nearly 800 m a.s.l.) have affinities to that of moderate-altitude sites, as is demonstrated by the occurrence of *Mantidactylus sp. aff. "slow calls"*, *Mantidactylus femoralis*, *Boophis viridis*, *Uroplatus phantasticus* and *Phelsuma quadriocellata quadriocellata*. These species are common at somewhat higher altitudes and elsewhere known from the Ranomafana National Park and Andasibe region, around 900–1000 m a.s.l.

Compared to amphibians, the reptile species of Madagascar's east coast show a less patchy spatial pattern of distribution. Up to now, there are just a few microendemic reptile species known from along the east coast, mainly in the genera *Phelsuma* and *Calumma*. Several *Phelsuma* species from low altitudes along the east coast are only known from a single locality or from a very restricted area, such as *P. serraticauda*, *P. kely*, *P. hoeschi*, *P. berghofi*, *P. flavigula-*

*ris*, *P. masohoala*, *P. parva* and *P. quadriocellata bimaculata*, whereas other syntopic species like *P. lineata lineata* are distributed nearly throughout the whole coastal area in the east. However, some widespread reptile species will probably turn out to be in fact species complexes containing microendemic species.

#### Implications for conservation and further research

The littoral forests of Tampolo and Vohibola and the lowland forests of Sahafina and Ambodiriana are amongst the last remnants of primary vegetation in some of the most disturbed and anthropogenically influenced areas of Madagascar. Due to the isolated position of Sahafina, we suspect that the populations of forest-dwelling species at this site are now isolated from all other populations. The intensive deforestation of this area during the last century (DOLCH 2003) resulted in the isolation of this forest fragment by ca. 30 km from the closest continuous rainforest block (Andasibe-Zahamena corridor). This isolation might have influences on the genetic viability of the Sahafina populations, but in general, we here suggest that such influences will be minor in the short- and mid-term, especially if compared to the disastrous effects of logging and slash-and-burn agriculture. In general, the importance of the sanctuaries at Sahafina, Vohibola, Tampolo and Ambodiriana is evident and the conservation efforts of the involved NGOs are of utmost importance. Our survey indicates that many of the species that are microendemic to the lowlands of the northern central east are somewhat tolerant of forest disturbance (e.g., species of *Blommersia*, *Mantidactylus*, *Phelsuma*, and the *Calumma* of the *C. nasutum* group), and their conservation will therefore be feasible even in relatively small reserves with partly degraded buffer zones. Further studies are necessary to elaborate suitable management practices in more detail.

Surprisingly, so far, no systematic amphibian and reptile inventory data have been published for some of the most prominent and partly most extensively sampled protected areas in eastern Madagascar, such as Analamazaotra-Mantadia or Mananara, although these hold the potential to act as references for future studies. Historical records and previous survey data for several other areas (such as Marojejy, Anjanaharibe-Sud, Ambatovaky, Zahamena) need to be re-evaluated with respect to species identifications in the light of taxonomic progress.

#### Acknowledgements

Fieldwork in 2008 and/or 2009 benefited from the assistance of ANNA-LENA KUBIK, GESINE MÜLLER, EMILE RAJERARISON, FRANÇOIS RANDRIANASOLO and JOJO RAKOTONANDRIANA. We are grateful to the Malagasy authorities, in particular the Ministère de l'Environnement et des Forêts for research and export permits. We thank CHANTAL MISANDEAU from the Association de Défense de la Forêt d'Ambodiriana (ADEFA), OWEN GRIFFITHS and ALDUS ANDRIAMAMONJY from Biodiversity Conservation Madagascar (BCM), and BARBARA MATHEVON from L'Homme et l'environnement (MATE) for their support, the provided facilities, and the research permits for their private reserves. Furthermore, thanks to SÉGOLÈNE BEAUCENT and MARC FAY-

OLLE for providing information on their amphibian and reptile survey in the Ambodiriana forest, to JASMIN E. RANDRIANIRINA and CHLOE DESCHAMPS for making unpublished reports available, and to AURÉLIEN MIRALLES and ZOLTAN T. NAGY for unpublished data on the genetic identity of some specimens. Thanks to EVA SAXINGER, MEIKE KONDERMANN and GABY KEUNECKE for supporting the laboratory work. The work of PHILIP-SEBASTIAN GEHRING was supported by a project of the evolutionary biology funding initiative of the Volkswagen Foundation and (in 2008) by the “Wilhelm-Peters-Fonds” of the Deutsche Gesellschaft für Herpetologie und Terrarienkunde (DGHT). FANOMEZANA RATSOAVINA was supported by a project of the Volkswagen Foundation in the program “Knowledge for Tomorrow – Cooperative Research Projects in Sub-Saharan Africa”.

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- 49°47'40"E; 222 m a.s.l.); *B. madagascariensis*, ZCMV 8940 (20 km north of Vatoman-dry, 19°11'33.5"S, 48°54'46.1"E; 10 m a.s.l.); *B. sp. aff. arcanus*, ZCMV 8975–8978, ZCMV 8981, ZCMV 8984–8987 (Ambodisavoka, 20°05'31.0"S, 48°19'19.9"E; 287 m a.s.l.); *Blommersia* sp. ZCMV 08403 (Andaparaty "Nord", 15°12'12"S, 49°36'44"E; 91 m a.s.l.); *B. sp. 1*, ZCMV 8942–8943 (20 km north of Vatoman-dry, 19°11'33.5"S, 48°54'46.1"E; 10 m a.s.l.), *Gephyromantis* cf. *boulengeri* ZCMV 8905 (Ankanin'ny Nofy, 18°35'33.5"S, 44°14'19.4"E; 19 m a.s.l.); *G. cf. boulengeri* ZCMV 8909 (Vohibola, 18°35'37.0"S, 49°14'15.2"E; 14 m a.s.l.); *G. cf. boulengeri* ZCMV 8919 (Sahafina, 18°48'38.3"S, 48°58'49.2"E; 90 m a.s.l.); *G. sp.* ZCMV 8923 (Sahafina, 18°48'38.3" S, 48°58'49.2"E; 90 m a.s.l.); *G. cf. boulengeri* ZCMV 8925 (Sahafina, 18°48'38.3"S, 48°58'49.2"E; 90 m a.s.l.); *G. cf. boulengeri* ZCMV 8926 (Sahafina, 18°48'38.3"S, 48°58'49.2"E; 90 m a.s.l.); *G. cf. boulengeri* ZCMV 8941 (20 km north of Vatoman-dry, 19°11'33.5"S, 48°54'46.1"E; 20 m a.s.l.); *G. cf. boulengeri* ZCMV 8944 (Mahanoro, 19°39'13.1"S, 48°46'40.7"E; 6 m a.s.l.); *G. cf. boulengeri* ZCMV 8960 & 8961 (Ambodiriana forest, 16°40'28.4"S, 49°42'10.0"E; 65 m a.s.l.); *G. malagasius* ZCMV 8409 (Antanambe, 16°27'05"S, 49°47'40"E; 222 m a.s.l.); *G. sp. aff. tschenki* ZCMV 8966–8969 (Ambodiriana forest, 16°40'28.4"S, 49°42'10.0"E; 65 m a.s.l.); ZCMV *Mantidactylus* sp. ZCMV 8410 (Mananara/Antanambe, 16°27'05"S, 49°47'40"E; 222 m a.s.l.); *M. sp.* ZCMV 8411 (Mananara/Antanambe, 16°27'05"S, 49°47'40"E; 222 m a.s.l.); *M. sp. aff. betsileanus* ZCMV 8924 (Sahafina, 18°48'38.3"S, 48°58'49.2" E; 90 m a.s.l.); *M. majori* ZCMV 8927 and 8928 (Sahafina forest, 18°48'38.3"S, 48°58'49.2"E; 90 m a.s.l.); *M. sp. aff. betsileanus* ZCMV 8929 (Sahafina forest, 18°48'38.3"S, 48°58'49.2"E; 90 m a.s.l.); *M. sp. aff. betsileanus* ZCMV 8945 (Mahanoro, 19°39'13.1"S, 48°46'40.7"E; 6 m a.s.l.); *M. sp. aff. betsileanus* ZCMV 8951 (Tampolo forest, 17°17'19.2"S, 49°24'41.6"E, 7 m a.s.l.); *M. sp. aff. betsileanus* ZCMV 8954 (Tampolo forest, 17°17'19.2"S, 49°24'41.6"E, 7 m a.s.l.); *M. sp. aff. betsileanus* ZCMV 8956 (Tampolo forest, 17°17'19.2"S, 49°24'41.6"E, 7 m a.s.l.); *M. sp. aff. betsileanus* ZCMV 8959 (Ambodiriana forest, 16°40'28.4"S, 49°42'10.0"E; 65 m a.s.l.); *M. sp. aff. femoralis* ZCMV 8955 (Tampolo forest, 17°17'19.2"S, 49°24'41.6"E; 7 m a.s.l.); *Mantella ebenau* ZCMV 8412 (Mananara/Antanambe, 16°27'05"S, 49°47'40"E; 222 m a.s.l.); *M. ebenau* ZCMV 8413 (Mananara/Antanambe, 16°27'05"S, 49°47'40"E; 222 m a.s.l.); *Guibemantis* sp. ZCMV 08405 (Andaparaty "Nord", 15°12'12"S, 49°36'44"E; 91 m a.s.l.); *G. sp.* ZCMV 08406 (Andaparaty "Nord", 15°12'12" S, 49°36'44"E; 91 m a.s.l.); *G. cf. bicalceratus* ZCMV 8908 (Vohibola forest, 18°35'37.0"S, 49°14'15.2"E; 14 m a.s.l.); *G. cf. bicalceratus* ZCMV 8914 (Vohibola forest, 18°35'22.9"S, 49°13'50.6"E; 9 m a.s.l.); *G. cf. bicalceratus* ZCMV 8949 & 8950 (Andoharina, 20°00'48.9"S 48°45'59.1"E; om a.s.l.); *G. cf. bicalceratus* ZCMV 8952 and 8953 (Tampolo forest, 17°17'19.2"S, 49°24'41.6"E, 7 m a.s.l.); *G. cf. bicalceratus* ZCMV 8964 and 8965 (Ambodiriana forest, 16°40'28.4" S, 49°42'10.0"E; 65 m a.s.l.); *G. cf. bicalceratus* ZCMV 8970 (18 km north of Toamasina, 17°58'27.6"S, 49°24'56.0"E; 20 m a.s.l.); *G. liber* ZCMV 8931–8935 (Sahafina forest, 18°48'38.3"S, 48°58'49.2"E; 56 m a.s.l.); *Anodonthyla* cf. *boulengeri* ZCMV 8901 (Ankanin'ny Nofy, 18°36'20.9"S, 49°12'49.8"E; 0 m a.s.l.); *A. cf. boulengeri* ZCMV 8904 (Ankanin'ny Nofy, 18°36'20.9"S, 49°12'49.8"E;

## Appendix

List of voucher specimens from lowland areas of Madagascar, roughly from Maroantsetra to the Mangoro River. For each specimen, we here provide the site name, coordinates and altitude, and field number (Zoological Collection Miguel Vences, ZCMV). Specimens have been deposited in the Zoologische Staatssammlung München (Munich, Germany) and the Université d'Antananarivo, Département de Biologie Animale (UADBA), but final ZSM and UADBA numbers are not yet available for most individuals.

### Amphibians

*Heterixalus alboguttatus*, ZCMV 8979 and 8980 (Ambodisavoka, 20°05'31.0"S, 48°19'19.9"E; 287 m a.s.l.); *Boophis roseipalmatus* ZCMV 8408 (Antanambe, 16°27'05"S,

o m a.s.l.); *A. cf. boulengeri* ZCMV 8911–8913 (Vohibola forest, 18°35'22.9"S, 49°13'50.6"E; 9 m a.s.l.); *A. cf. boulengeri* ZCMV 8920–8922 (Sahafina forest, 18°48'38.3"S, 48°58'49.2"E; 56 m a.s.l.); *A. cf. boulengeri* ZCMV 8947 and 8948 (Bac Sahlehy, 19°59'10.1"S, 48°47'08.3"E; 0 m a.s.l.); *A. cf. boulengeri* ZCMV 8958 (Ambodiriana forest, 16°40'28.4"S, 49°42'10.0"E; 65 m a.s.l.); *A. cf. boulengeri* ZCMV 8963 (Ambodiriana forest, 16°40'28.4"S, 49°42'10.0"E; 65 m a.s.l.); *Stumpffia* sp. ZCMV 8907 and 8910 (Vohibola forest, 18°35'22.9"S, 49°13'50.6"E; 9 m a.s.l.); *Platypelis cf. tetra* ZCMV 8962 (Ambodiriana forest, 16°40'28.4"S, 49°42'10.0"E; 65 m a.s.l.); *P.* sp. ZCMV 8404 (Andaparaty "Nord", 15°12'12"S, 49°36'44' E; 91 m a.s.l.).

#### Reptiles

*Brookesia peyrierasi* ZCMV 08402 (Andaparaty "Nord" 15°12'12"S, 49°36'44"E; 91 m a.s.l.); *Calumma cf. nasutum* ZCMV 8903 (Ankanin'ny Nofy, 18°36'20.9"S, 49°12'49.8"E; 0 m a.s.l.); *C. cf. nasutum* ZCMV 8915–8918 (Vohibola forest, 18°35'22.9"S, 49°13'50.6"E; 9 m a.s.l.); *Lygodactylus miops* ZCMV 8902 (Ankanin'ny Nofy, 18°36'20.9"S, 49°12'49.8"E; 0 m a.s.l.); *Phelsuma parva* ZCMV 8906 (Ankanin'ny Nofy, 18°36'20.9"S, 49°12'49.8"E; 0 m a.s.l.); *P. hoeschi* ZCMV 8938 and 8939 (16 km southwest of Vatomandry, 19°20'34.7"S 48°54'58.8"E; 44m a.s.l.); *P. ravenala* ZCMV 8936 (Vatomandry, 19°20'34.7"S, 48°54'58.8"E; 6 m a.s.l.); *P. lineata lineata* ZCMV 8937 (Vatomandry, 19°20'34.7"S, 48°54'58.8"E; 6 m a.s.l.); *Zonosaurus brygooi* ZCMV 8930 (Sahafina forest, 18°48'38.3"S, 48°58'49.2"E; 56 m a.s.l.); *Ramphotyphlops braminus* ZCMV 08407 (near Maroantsetra, 15°29'10"S, 49°39'55"E; 0 m a.s.l.); *R. braminus* ZCMV 8946 (Andoharina, 20°00'48.9"S, 48°45'59.1"E; 0 m a.s.l.).

#### Supporting information

Additional information is available in the online version of this article at <http://www.salamandra-journal.com>.

**S1.** Amphibian and reptile species found at different sites along Madagascar's east coast.

**Supporting information**

GEHRING, P.-S., F. M. RATSOAVINA & M. VENCES (2010): Filling the gaps – amphibian and reptile records from lowland rainforests in eastern Madagascar. – Salamandra, 46: 215–235.

**S1.** Amphibian and reptile species found at different sites along Madagascar’s east coast. Mahanoro (n) is the locality at the northern banks, Andoharina (s) is the locality at the southern banks of the Mangoro River.

		Andaparaty „north“	Antanambe	Ambodiriana	Tampolo	Vohibola	Sahafina	Vatomandry	Mahanoro (n) Ambodiharina (s)	Marolambo (and surroundings)
<b>AMPHIBIANS</b>										
<b>PTYCHADENIDAE</b>										
<i>Ptychadena</i>	<i>mascareniensis</i>			*	*		*	*	*(n,s)	*
<b>HYPEROLIIDAE</b>										
<i>Heterixalus</i>	<i>alboguttatus</i>								*s	*
<i>Heterixalus</i>	<i>madagascariensis</i>			*	*	*	*	*	*n	
<b>MICROHYLIDAE</b>										
<i>Anodontohyla</i>	<i>boulengeri</i>	*		*						
<i>Anodontohyla</i>	cf. <i>boulengeri</i> 1					*			*(n,s)	
<i>Anodontohyla</i>	cf. <i>boulengeri</i> 2						*			
<i>Platypelis</i>	<i>grandis</i>		*							
<i>Platypelis</i>	<i>tuberifera</i>						*			
<i>Platypelis</i>	cf. <i>tetra</i>			*						
<i>Platypelis</i>	sp.			*						
<i>Plethodontohyla</i>	<i>notosticta</i>			*		*	*			
<i>Stumpffia</i>	sp.					*	*			
<b>MANTELLIDAE</b>										
<i>Aglyptodactylus</i>	aff. <i>madagascariensis</i> “East”	*								
<i>Blommersia</i>	sp.							*		
<i>Blommersia</i>	aff. <i>blommersae</i> “Nosy Boraha”				*					

		Andaparaty „north“	Antanambe	Ambodiriana	Tampolo	Vohibola	Sahafina	Vatomandry	Mahanoro (n) Ambodiharina (s)	Marolambo (and surroundings)
<i>Boophis</i>	sp. aff. <i>arcanus</i>									*
<i>Boophis</i>	<i>axelmeyeri</i>	*								
<i>Boophis</i>	sp. aff. <i>boehmei</i>						*			*
<i>Boophis</i>	<i>englaenderi</i>			*						
<i>Boophis</i>	cf. <i>miniatus</i>									*
<i>Boophis</i>	<i>madagascariensis</i>						*			
<i>Boophis</i>	<i>opisthodon</i>	*				*				
<i>Boophis</i>	<i>pyrrhus</i>						*			*
<i>Boophis</i>	<i>roseipalmatus</i>	*	*	*						
<i>Boophis</i>	<i>tephraeomystax</i>					*		*		*
<i>Boophis</i>	<i>viridis</i>									*
<i>Gephyromantis</i>	<i>boulengeri</i>	*	*	*	*	*	*		*(n,s)	
<i>Gephyromantis</i>	<i>leucomaculatus</i>			*						
<i>Gephyromantis</i>	<i>luteus</i>	*	*	*			*			
<i>Gephyromantis</i>	<i>sculpturatus</i>	*								
<i>Gephyromantis</i>	<i>malagasius</i>		*	*						
<i>Gephyromantis</i>	<i>redimitus</i>	*								
<i>Gephyromantis</i>	<i>silvanus</i>			*						
<i>Gephyromantis</i>	sp.aff. <i>moseri</i> ; G. sp. 18	*								
<i>Gephyromantis</i>	<i>webbi</i>		*	*						
<i>Gephyromantis</i>	sp. aff. <i>boulengeri</i> ; G. sp. 25					*	*			
<i>Gephyromantis</i>	sp. aff. <i>boulengeri</i> ; G. sp. 24						*			
<i>Guibemantis</i>	<i>bicalcaratus</i>					*		*		
<i>Guibemantis</i>	cf. <i>bicalcaratus</i>	*								
<i>Guibemantis</i>	<i>liber</i>			*	*	*	*	*		
<i>Guibemantis</i>	<i>pulcher</i>					*				
<i>Mantella</i>	<i>ebenau</i>		*	*						
<i>Mantidactylus</i>	<i>aerumnalis</i>						*			

		Andaparaty „north“	Antanambe	Ambodiriana	Tampolo	Vohibola	Sahafina	Vatomandry	Mahanoro (n) Ambodiharina (s)	Marolambo (and surroundings)
<i>Mantidactylus</i>	<i>betsileanus</i>		*	*						
<i>Mantidactylus</i>	aff. <i>betsileanus</i> ; M. sp. 36				*		*	*		
<i>Mantidactylus</i>	sp. aff. <i>betsileanus</i> ; M. sp. 25		*	*						
<i>Mantidactylus</i>	sp. aff. <i>betsileanus</i> ; M. sp. 34						*		* (n,s)	
<i>Mantidactylus</i>	sp. aff. <i>biporus</i> „Andaparaty“	*								
<i>Mantidactylus</i>	sp. aff. « slow calls »									
<i>Mantidactylus</i>	<i>biporus</i>		*							
<i>Mantidactylus</i>	<i>charlotteae</i>						*			
<i>Mantidactylus</i>	sp. aff. <i>charlotteae</i> ; M. sp. 10	*	*	*						
<i>Mantidactylus</i>	<i>femoralis</i>						*			*
<i>Mantidactylus</i>	aff. <i>femoralis</i>	*			*					
<i>Mantidactylus</i>	<i>grandidieri</i>	*								
<i>Mantidactylus</i>	aff. <i>lugubris</i>			*			*			
<i>Mantidactylus</i>	<i>majori</i>						*			*
<i>Mantidactylus</i>	<i>mocquardi</i>						*			
<i>Mantidactylus</i>	<i>opiparis</i>						*			
<i>Mantidactylus</i>	<i>sculpturatus</i>						*			
<i>Spinomantis</i>	<i>aglavei</i>						*			
	<b>Total:</b>	<b>15</b>	<b>11</b>	<b>20</b>	<b>7</b>	<b>11</b>	<b>25</b>	<b>7</b>	<b>6</b>	<b>10</b>



		Andaparaty „north“	Antanambe	Ambodiriana	Tampolo	Vohibola	Sahafina	Vatomandry	Mahanoro (n) Ambodiharina (s)	Marolambo (and surroundings)
<b>REPTILES</b>										
<b>TESTUDINIDAE</b>										
<i>Pelusios</i>	<i>subniger</i>			*						
<b>CHAMAELEONIDAE</b>										
<i>Brookesia</i>	<i>peyrierasi</i>	*								
<i>Brookesia</i>	<i>superciliaris</i>			*			*			*
<i>Calumma</i>	<i>cucullatum</i>									*
<i>Calumma</i>	<i>gallus</i>						*		*n	
<i>Calumma</i>	sp. aff. <i>gallus</i>								*s	*
<i>Calumma</i>	<i>glawi</i>									*
<i>Calumma</i>	<i>nasutum</i>			*	*		*			*
<i>Calumma</i>	sp. aff. <i>nasutum</i>							*		
<i>Calumma</i>	sp. aff. <i>marojezense</i>	*								
<i>Furcifer</i>	<i>willsii</i>							*		
<i>Furcifer</i>	<i>pardalis</i>	*	*	*	*	*				
<b>GERRHOSAURIDAE</b>										
<i>Zonosaurus</i>	<i>brygooi</i>			*	*		*			
<i>Zonosaurus</i>	<i>madagascariensis</i>		*	*	*	*	*	*	*(n,s)	*
<b>SCINCIDAE</b>										
<i>Trachylepis</i>	<i>gravenhorstii</i>		*	*		*	*	*	*(n,s)	*
<i>Madascincus</i>	<i>melanopleura</i>						*			
<i>Amphiglossus</i>	sp. aff. <i>phaeurus</i>						*			
<b>GEKKONIDAE</b>										
<i>Blaesodactylus</i>	<i>antongilensis</i>	*		*			*			
<i>Geckolepis</i>	<i>maculata</i>			*	*	*	*			
<i>Geckolepis</i>	<i>polylepis</i>					*				
<i>Gehyra</i>	<i>mutilata</i>			*						*
<i>Hemidactylus</i>	<i>frenatus</i>									
<i>Hemidactylus</i>	<i>mercatorius</i>		*	*	*	*		*	*(n,s)	*
<i>Ebenavia</i>	<i>inunguis</i>			*	*	*	*		*n	*
<i>Paroedura</i>	<i>gracilis</i>	*	*	*			*			
<i>Uroplatus</i>	<i>fimbriatus</i>	*		*						*

		Andaparaty „north“	Antanambe	Ambodiriana	Tampolo	Vohibola	Sahafina	Vatomandry	Mahanoro (n) Ambodiharina (s)	Marolambo (and surroundings)
<i>Uroplatus</i>	<i>lineatus</i>						*			
<i>Uroplatus</i>	<i>phantasticus</i>									*
<i>Uroplatus</i>	<i>sameiti</i>			*	*	*	*			*
<i>Lygodactylus</i>	<i>miops</i>		*	*			*			
<i>Lygodactylus</i>	sp. aff. <i>miops</i>					*				
<i>Phelsuma</i>	<i>guttata</i>			*	*	*	*			
<i>Phelsuma</i>	<i>hoeschi</i>							*		
<i>Phelsuma</i>	<i>laticauda laticauda</i>					*				
<i>Phelsuma</i>	<i>lineata lineata</i>					*	*	*	*(n,s)	*
<i>Phelsuma</i>	<i>madagascariensis</i>		*	*		*	*	*	*(n,s)	
<i>Phelsuma</i>	<i>parva</i>					*	*		*n	*
<i>Phelsuma</i>	<i>pusilla pusilla</i>	*	*	*						
<i>Phelsuma</i>	<i>quadriocellata quadriocellata</i>									*
<i>Phelsuma</i>	<i>quadriocellata bimaculata</i>		*	*	*					
<i>Phelsuma</i>	<i>ravenala</i>					*		*		
<i>Phelsuma</i>	<i>serratauda</i>			*						
BOIDAE										
<i>Acrantophis</i>	<i>madagascariensis</i>					*				
<i>Sanzinia</i>	<i>madagascariensis</i>	*		*						*
COLUBRIDAE										
<i>Madagascarophis</i>	<i>colubrinus</i>				*	*	*	*		*
<i>Lycodryas</i>	<i>gaimardi</i>				*		*			
<i>Leioheterodon</i>	<i>madagascariensis</i>			*		*				*
<i>Langaha</i>	<i>madagascariensis</i>				*	*				
<i>Ithycyphus</i>	<i>perineti</i>					*				
<i>Ithycyphus</i>	<i>goudoti</i>		*			*				
<i>Pseudoxyrhopus</i>	<i>heterurus</i>			*						
<i>Liophidium</i>	<i>rhodogaster</i>		*							
<i>Thamnosophis</i>	<i>lateralis</i>			*	*		*	*		*
<i>Dromicodyras</i>	<i>bernieri</i>				*		*			*
TYPHLOPIDAE										
<i>Ramphotyphlops</i>	<i>braminus</i>								*s	
	<b>Total:</b>	<b>8</b>	<b>11</b>	<b>25</b>	<b>15</b>	<b>23</b>	<b>23</b>	<b>9</b>	<b>10</b>	<b>21</b>